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RESPONSES OF ARCTIC PERMAFROST PEATLANDS TO CLIMATE CHANGES OVER THE PAST MILLENNIA

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ACADEMIC DISSERTATION

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ABSTRACT

Northern circumpolar permafrost peatlands store ~300 Pg of organic carbon (C), and play a critical role in regulating global biogeochemical cycles. Amplified warming in high-latitude regions is threatening this large C stock, because permafrost thawing will expose previously frozen C to decomposition. Permafrost thaw-induced hydrological changes together with warming will influence plant photosynthesis and decomposition processes and thus C accumulation patterns. However, it is still unresolved how C accumulation, warming and associated hydrological changes are interlinked.

In this study, I used 14 peat records from four sites in northeast European Russia and Finnish Lapland to reconstruct permafrost peatland vegetation, hydrology and C dynamics. The studied records were dated by radiocarbon (^{14}C) and lead (^{210}Pb) methods. In order to reconstruct hydrology, i.e. water-table depth (WTD), I first developed a new modern testate amoeba-WTD training set. The training set represented different habitats and comprised 145 surface peat samples collected from the four study sites. The training set data were then applied to six peat records to reconstruct last millennium hydrological changes. Plant macrofossil analysis was also conducted for these six cores to study changes in the vegetation, habitat conditions and permafrost dynamics, and to evaluate testate amoeba-based WTD reconstructions. In order to calculate and model C accumulation patterns, bulk density and C content (occasionally loss on ignition) analyses were carried out for 14 cores. C modelling enabled the C capacity analyses of peat that was accumulated during recent centuries *vs.* older peat layers. Several environmental variables, such as nitrogen (N) content, C/N ratio, WTD, plant functional types and summer temperature were used to evaluate allogenic C accumulation forcing in the past.

The data show that testate amoebae are powerful indicators of hydrological conditions in permafrost peatlands. Testate amoeba and plant macrofossil reconstructions suggest that permafrost peatlands are sensitive to climate changes. Warm climate phases (Medieval Climate Anomaly: MCA, and warming since 1850 AD) caused permafrost thawing and temporarily wet

conditions, but peat surfaces later desiccated due to accelerated evapotranspiration. In turn, during the cool climate phase of the Little Ice Age (LIA) peat surfaces mainly remained dry due to peat surface uplift causing desiccation of the peat surface. However, the proxies indicate occasional wetter than MCA habitat conditions possibly due to decreased evapotranspiration. This again highlights the importance of evapotranspiration in regulating eco-hydrological feedback mechanisms in permafrost peatlands.

The studied peatlands have been persistent C sinks during mid- to late-Holocene with an average accumulation rate of 10.80 - 32.40 g C m^{-2} yr^{-1} during this period. Apparent C accumulation rate (ACAR) analyses suggest inconsistent response to warming. The data from Russia indicate that the Holocene Thermal Maximum stimulated faster ACARs, while the MCA did not. The likely reason is that permafrost aggradated only during the late Holocene. Moreover, sometimes relatively high ACARs were dated to the LIA, suggesting that ACARs were controlled more by other factors than by cold climate per se.

In conclusion, the current data suggest there is no single environmental factor that alone drives C accumulation. This is manifested by the pattern where in some of the studied permafrost peatlands, warming since 1850 AD has increased C accumulation rates while elsewhere there is a slight decrease in C accumulation over the same period. These divergent trends suggest that there are alternative response directions to warming in the future and that also an overall decrease in the C sequestration ability may occur for permafrost peatlands.

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LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following publications, referred to in the text by their Roman numerals:

I H Zhang, MJ Amesbury, T Ronkainen, DJ Charman, AV Gallego-Sala, M Väliranta. 2017. Testate amoebae as palaeohydrological indicators in the permafrost peatlands of north-east European Russia and Finnish Lapland. *Journal of Quaternary Science* 32(7): 976-988.

II H Zhang, SR Piilo, MJ Amesbury, DJ Charman, AV Gallego-Sala, M Väliranta. 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.

III H Zhang, AV Gallego-Sala, MJ Amesbury, DJ Charman, SR Piilo, M Väliranta. 2018. Inconsistent response of Arctic permafrost peatland carbon accumulation to warm climate phases. *Global Biogeochemical Cycles* (*pending revision*).

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AUTHOR'S CONTRIBUTIONS TO THE PUBLICATIONS

For all the publications, H Zhang prepared and analysed testate amoeba samples under the supervision of MJ Amesbury and M Väliranta.

I The study was planned by M Väliranta and DJ Charman. T Ronkainen and M Väliranta collected the training set samples. H Zhang analysed living plants from the surface samples and peat plant macrofossils from fossil samples under the supervision of M Väliranta. H Zhang carried out the data analysis and performed the transfer function with guidance from MJ Amesbury. H Zhang was responsible for writing the manuscript with contributions from all co-authors.

II All co-authors participated the study plan setting. H Zhang and SR Piilo analysed peat plant macrofossil samples under the supervision of M Väliranta. H Zhang and SR Piilo analysed ^{210}Pb dating samples. H Zhang analysed the chronological data and performed the hydrological reconstruction. H Zhang prepared the manuscript with contributions from all co-authors.

III All co-authors participated the study plan setting. H Zhang and SR Piilo analysed peat plant macrofossil samples under the supervision of M Väliranta. H Zhang and SR Piilo analysed ^{210}Pb dating samples and prepared peat samples for peat property analyses. H Zhang analysed the data in collaboration with AV Gallego-Sala. H Zhang wrote the manuscript with contributions from all co-authors.

ABBREVIATIONS

ACAR	apparent carbon accumulation rate (g C m^{-2} yr^{-1})
BD	bulk density (g cm^{-3})
C	carbon
cal. BP	calibrated years before present (present = 1950 AD)
CAR	carbon accumulation rate
CFM	carbon flux reconstruction model
CH_4	methane
C/N	carbon-to-nitrogen mass ratio
CO_2	carbon dioxide
DOC	dissolved organic carbon
EDM	exponential decay model
GDD0	annual growing degree-days above 0°C
HTM	Holocene Thermal Maximum
LIA	Little Ice Age
LOI	loss on ignition (%)
MCA	Medieval Climate Anomaly
N_2O	nitrous oxide
NPP	net primary productivity
PAR0	photosynthetically active radiation above 0°C during the growing season
PDM	peat decomposition model
P/Eq	annual precipitation/annually integrated equilibrium evapotranspiration
RMSEP	root mean square error of prediction
SD	standard deviation
UOM	unidentifiable organic matter
WTD	water-table depth (cm)

1 INTRODUCTION

Peat is mainly composed of incompletely decomposed plant remains that have accumulated over time (Joosten & Clarke, 2002). At least 30% (dry mass) of the peat matrix consists of organic material (Loisel *et al.*, 2017). Most definitions require a minimum peat thickness of 40 cm for an ecosystem to be considered as peatland (National Wetlands Working Group, 1997, Joosten & Clarke, 2002). Peatlands can be found distributed in both northern and southern hemispheres in the tropics and in temperate, boreal and Arctic regions, although 80% of the world's peatlands are found in the boreal region (Joosten & Clarke, 2002). Despite their relatively small global areal extent (3% of Earth's land surface area), peatlands are disproportionately important to ecosystem–climate feedbacks because they are efficient carbon (C) sequestering ecosystems (Joosten & Clarke, 2002, Yu *et al.*, 2010).

1.1 FORMATION AND FEATURES OF PERMAFROST PEATLANDS

Permafrost is defined as ground (soil or rock and included ice and organic material) that has been at or below 0° C for two or more years (Osterkamp, 2001). Northern permafrost soils comprise approximately 16% of the global soil area, and *c.* 19% of the circumpolar permafrost soil area is covered by peatlands (Tarnocai *et al.*, 2009).

The initiation of peatland permafrost occurred during cold climate phases (Treat & Jones, 2018), e.g., historical late Holocene Neoglacial climate cooling (Porter & Denton, 1967, Matthews & Dresser, 2008) and/or the Little Ice Age (LIA; *c.* 550–100 cal. BP) (e.g., Esper *et al.*, 2002, Cook, *et al.*, 2004) in northern Europe (Oksanen, 2006), western Siberia (Kremenetski *et al.*, 2003) and western Alaska (Hunt *et al.*, 2013). Although there are no specific plant species that directly indicate permafrost initiation or presence in peatlands, a rapid vegetation shift from a wet to dry assemblage can be used to infer permafrost inception (Oksanen *et al.*, 2001, Oksanen, 2006, Sannel & Kuhry, 2008). Geochemical properties, such as carbon/nitrogen (C/N) ratio or nitrogen content, can also be used to imply the occurrence of permafrost

(Sannel & Kuhry, 2009, Treat *et al.*, 2016).

When permafrost develops in peatlands and forms palsas and peat plateaus, it influences the local microtopography, hydrology, vegetation and related C dynamics (Christensen *et al.*, 2004, Seppälä, 2011). Under the presence of permafrost, the peat surface is uplifted because of the expansion of ground ice. The raised peat mounds can be a few metres higher (*c.* 1–7 m) than the surrounding landscape (Seppälä, 2006). This raising process causes desiccation of the peat surface, and is usually followed by colonisation of woody/shrubby vegetation or dry habitat mosses (Oksanen, 2005). In some cases, cryoturbation (Repo *et al.*, 2009) and/or changes in hydrology and vegetation associated with permafrost aggradation increase susceptibility to erosion (Väliranta *et al.*, 2018 unpublished) and promote formations of bare peat surfaces (Fig. 1) (Kaverin *et al.*, 2016, Ogneva *et al.*, 2016). These processes can result in very slow peat accumulation rates or cessation of accumulation altogether, thus leading to a hiatus in the peat accumulation record (Seppälä, 2006, Routh *et al.*, 2014, Sannel *et al.*, 2017).



Fig. 1. Permafrost peatland and bare peat features in northeast European Russia. © M. Väliranta.

Thermal insulation by *Sphagnum* moss and thick snow cover contributes to the persistence and protection of permafrost, and thus there may be a disequilibrium between peat temperatures and the air mean annual or summer temperatures (Camill & Clark, 1998, Camill, 1999). In areas with an effective summer temperature above 0° C, thawing occurs during summer and forms a *c.* 30-50 cm melt surface layer (active layer), which then refreezes during winter. The thickness of the active layer varies according to various

factors, such as the surface temperature, the physical and thermal properties of the surface cover and the substrate, vegetation and snow cover (Brown *et al.*, 2000, Frauenfeld *et al.*, 2004, Zhang *et al.*, 2005). The active layer is very important, because most ecological and biogeochemical processes take place there and as a result of climate warming the thickness of this layer is increasing (Kane *et al.*, 1991, https://www2.gwu.edu/~calm/).

1.2 ROLE OF ARCTIC PERMAFROST PEATLANDS IN GLOBAL BIOGEOCHEMICAL CYCLING

The Arctic plays an important role in the global dynamics of both carbon dioxide (CO_2) and methane (CH_4) (McGuire *et al.*, 2009). Arctic permafrost peatlands have for a long time acted as C stores due to their consistently low air temperature and the presence of permafrost, both of which inhibit the mineralisation of soil carbon (Kwon *et al.*, 2016), even though they have emitted high amounts of CH_4 since their formation (Korhola *et al.*, 2010). While the net primary production (NPP) and standing biomass of the Arctic are lower than adjacent climate zones (Saugier *et al.*, 2001), low decomposition rates have resulted in the accumulation of ~300 Pg of organic carbon in northern circumpolar permafrost peatlands (Tarnocai *et al.*, 2009, Hugelius *et al.*, 2014), which is approximately 14% of the global soil carbon store (IPCC, 2000, Tarnocai *et al.*, 2009) and equivalent to >1/3 of the carbon stock in the atmosphere (Houghton, 2007).

Peatlands fix CO_2 through plant photosynthesis during the growing season. Dead plant biomass starts to decompose and the litter undergoes complex transformation processes by soil fauna and microbes in the oxic acrotelm and anoxic catotelm (Clymo *et al.*, 1998). Peatlands release carbon to the atmosphere mainly as CO_2 and CH_4 through decomposition, respiration and anaerobic processes. Carbon is also transferred to aquatic ecosystems as dissolved organic carbon (DOC) typically via water flow, between the thawed and frozen part of the soil profile (Woo, 2012, Raudina *et al.*, 2018). Oxic decomposition returns *c.* 90% of the fixed organic carbon back to the atmosphere as CO_2 (Clymo, 1983), and the remaining fraction of carbon becomes buried into the catotelm, increasing peat thickness because of the

very slow decay rate.

Fluxes of CO_2 and CH_4 between peatlands and the atmosphere (Fig. 2) are closely linked to vegetation, in particular through differences between plant species and their productivity and litter decomposability (Leppälä *et al.*, 2011, Laine *et al.*, 2012). These processes are, in turn, strongly controlled by moisture and temperature. Furthermore, vegetation partly controls CH_4 transportation pathways from the peat layers to the atmosphere and may provide microhabitats for the microbial communities responsible for CH_4 oxidation (Bellisario *et al.*, 1999, Larmola *et al.*, 2010). Dry permafrost peat plateau surfaces are normally net sources of CO_2, while CH_4 emissions from the plateau areas are negligible (Voigt *et al.*, 2017a, Wilson *et al.*, 2017). Low temperatures in the deep soil layers also effectively restrict CH_4 production and emissions (Yu *et al.*, 2017). The high primary productivity of sedges in thaw depressions forms a CO_2 sink, while the waterlogged conditions limit oxygen diffusion and facilitate anaerobic CH_4 production (Wilson *et al.*, 2017). Additionally, well-developed aerenchyma of sedges can facilitate CH_4 fluxes (Chanton *et al.*, 1992). Peatland surface moisture conditions and associated plant functional types mainly regulate C cycling but changes in climate conditions may also have an importantly direct or indirect role in C fixation and release processes. In addition, bare surfaces on permafrost peatlands have been observed to emit large amounts of another important greenhouse gas nitrous oxide (N_2O), because of the lack of competition for nitrogen between plants and microbes (Repo *et al.*, 2009).

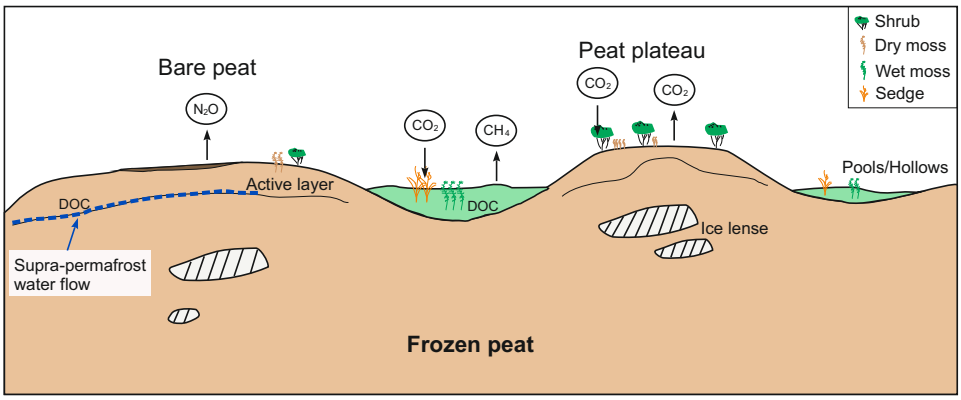

Fig. 2. Schematic illustration of permafrost peatland landform features and key fluxes of greenhouse gases (N_2O: nitrous oxide; CO_2: carbon dioxide; CH_4: methane) and dissolved organic

carbon (DOC).

1.3 PERMAFROST PEATLAND RESPONSE TO CLIMATE CHANGE

The ability of peatland ecosystems to sequester CO_2 from the atmosphere and create a long-term C store means that they play a critical role in modulating global biogeochemical cycles and therefore the climate (Gorham, 1991, Frolking & Roulet, 2007). Given the large quantity of stored C in high-latitude peatlands, the response of these ecosystems to the changing climate is a major issue of global concern (ACIA, 2004).

Peatland dynamics are sensitive to environmental changes (e.g., Strack *et al.*, 2006, Riutta *et al.*, 2007, Turetsky *et al.*, 2008, 2014), and considerable uncertainties are associated with these enormous C stores under a changing climate (Frolking *et al.*, 2011, Swindles *et al.*, 2015a). Changes in moisture and temperature are particularly important because they are the main environmental drivers of peatland C exchange (Shaver *et al.*, 2006, Oberbauer *et al.*, 2007) exerting a control over photosynthesis (Field *et al.*, 1995), over decomposition (Ise *et al.*, 2008, Dorrepaal *et al.*, 2009), and even over geographical peatland distribution (Yu *et al.*, 2009). In Arctic conditions, very local-scale warming (as related to, for instance, topographical features), as well as external disturbances (e.g., fire) and changes in vegetation that may provide shade and/or insulation, can cause permafrost thawing and a collapse of the plateau (Jones *et al.*, 2013). Compared with younger formations, more mature permafrost features inside continuous or discontinuous permafrost zones may be more resistant to temperature or other environmental changes (Zuidhoff & Kolstrup, 2000). This has to be taken into account when evaluating impacts of warming, for instance the warming that has occurred during recent decades.

In high-latitude regions, the annual temperature has risen by *c.* 0.6 °C per decade over the last 30 years, which is twice as fast as the global average, and warming is projected to continue (Stocker *et al.*, 2013). Warming is expected to increase permafrost thawing (Oberman, 2008, Romanovsky *et al.*, 2010) with a recent estimation of permafrost area loss of *c.* 4.0 million km² per 1 °C

increase in global temperature (Chadburn *et al.*, 2017). Monitoring studies on permafrost ground temperature have documented a rising trend during the last 20–30 years (e.g., Brown & Romanovsky, 2008, Johansson *et al.*, 2011, Sannel *et al.*, 2016) and circumpolar active layer measurements (https://www2.gwu.edu/~calm/) suggest permafrost thaw at the southern margins of the permafrost area. Even though these observations are not homogeneous in space or time (Romanovsky *et al.*, 2017), a widespread permafrost thaw can be expected as a consequence of global warming (Chaudhary *et al.*, 2017). Consequently, permafrost thawing will expose substantial quantities of organic C to decomposition and thus lead to a possible release of CO_2 and CH_4 to the atmosphere, which would be a positive climate feedback effect, i.e. it would result in further warming (Hodgkins *et al.*, 2014, Schuur *et al.*, 2015, Jones *et al.*, 2017). Besides warmer temperatures increasing peatland decomposition rates, they can also stimulate NPP. Some palaeo-peatland studies suggest higher C accumulation during the warm Holocene Thermal Maximum (HTM; *c.* 8000-4000 cal. BP; with warm summers and strong climate seasonality) (Renssen *et al.*, 2009, 2012, Väliranta *et al.*, 2015) and the Medieval Climate Anomaly (MCA; *c.* 1000 and 750 cal. BP; with warmer summers and also warmer winters) (e.g., Esper *et al.*, 2002, Cook *et al.*, 2004) relating to accelerated C sequestration (MacDonald *et al.*, 2006, Yu *et al.*, 2009, Jones & Yu, 2010, Charman *et al.*, 2013). However, whether the net effect of increased C sequestration coupled with C release from thawing permafrost will lead to a positive or negative feedback to global warming has remained uncertain (Schuur *et al.*, 2009).

It can be expected that living peat plants and surface peat layers will readily respond to increasing temperatures, but also the large deep reservoir of C is under pressure (Schuur *et al.*, 2009). Along with permafrost thawing, the active layer is likely to deepen, extending oxic and/or anoxic decomposition processes to the previously frozen layers. As associated with thermokarst collapse, plant biomass may increase due to changes in plant composition from lichens and shrubs to an ecosystem dominated by sedges and *Sphagnum*. In areas experiencing thawing, sedges have a higher rate of biomass production, but also faster decomposition. Additionally, warming has

been detected to increase peatland CH_4 emissions (Voigt *et al.*, 2017a), and especially abruptly formed thermokarst lakes and wetlands have been observed to be hotspots of CH_4 emissions (Turetsky *et al.*, 2002, Christensen *et al.*, 2004, Walter *et al.*, 2006). While Väliranta *et al.* (2018 unpublished) suggest that the area of bare surface formations on permafrost peatlands is likely to diminish, substantial permafrost thaw-induced increase of N_2O release has recently been reported (Voigt *et al.*, 2017b).

The magnitude of greenhouse gas release from permafrost soils differs depending upon a number of factors, including, most importantly, changes in the soil water content (Elberling *et al.*, 2013, Natali *et al.*, 2015, Blanc-Betes *et al.*, 2016), the length of the growing season, winter temperatures (Natali *et al.*, 2012), soil temperature (Hicks Pries *et al.*, 2013), active layer depth (O'Donnell *et al.*, 2011), anaerobic conditions, microbial activity, and the quantity and composition of the available organic matter (Treat *et al.*, 2014). Uncertainties in the budget of these greenhouse gases limit the accuracy of climate projections (Collins *et al.*, 2013).

1.4 PEATLANDS AS ARCHIVES OF ENVIRONMENTAL CHANGE AND CARBON DYNAMICS

Peat accumulates over time and peat layers form archives that reflect local environmental conditions at the time of deposition. Palaeoecological reconstructions provide tools to predict interlinked peatland dynamics under a changing climate (Väliranta *et al.*, 2007, Booth 2010, Charman *et al.*, 2013, 2015, Swindles *et al.*, 2015a). During the past few millennia, there have been notable climate phases such as the warm HTM and MCA, and cold phases such as the LIA. These climate anomalies provide an opportunity to examine peatland–climate response mechanisms and thus help us to study the current and future feedbacks of peatlands to recent warming since pre-industrial times (Hartmann *et al.*, 2013) and to projected warming (Collins *et al.*, 2013).

Plant macrofossils and testate amoebae are the most commonly used proxies to reconstruct past dynamics in peatlands (Booth and Jackson, 2003, Charman *et al.*, 2006, 2015, Väliranta *et al.*, 2007, 2012, Booth 2010, Jones *et al.*, 2013, Swindles et al., 2015a, Mathijssen, 2016). Plant macrofossil analysis

is based on the species-level identification of plant remains that represent *in situ* deposition. Reconstructed plant assemblages have proven to be a good proxy to quantitatively reconstruct changes in the water-table level (Väliranta *et al.*, 2007, 2012) and can also be used to infer changes in nutrient status (Tuittila *et al.*, 2012) and temperature (Kultti *et al.*, 2004). Testate amoebae are a group of single-celled microbial organisms that form a shell (or test), which is often well-preserved in peats (Tolonen *et al.*, 1992; Charman *et al.*, 2000). They are essential food web components that comprise a major proportion of the microbial mass of the peat and play an important role in nutrient and thus also carbon cycling (Mitchell *et al.*, 2008, Jassey *et al.*, 2015). In palaeoecological studies of peatlands, they are commonly used as hydrological indicators (Amesbury *et al.*, 2013, 2016).

In terms of reconstructing hydrological conditions in permafrost peatlands, however, it has been suggested that plant remains can be highly decomposed and that this may hinder plant-based reconstruction (Ronkainen *et al.* 2015). While testate amoebae have considerable potential as more widely applicable and precise indicators of changing hydrology (Bobrov *et al.*, 2013, Swindles *et al.*, 2015b), data on testate amoeba communities and their ecological constraints in permafrost peatland environments are still scarce (Amesbury *et al.*, 2016), and only limited data are available to calibrate reconstruction models. Other approaches such as plant biomarkers (Ronkainen *et al.*, 2015) and possibly stable isotopes (Markel *et al.*, 2010, Willis *et al.*, 2015) are also useful in studying past permafrost peatland dynamics, especially as complementary proxies.

Peatland C dynamics can also be reconstructed by measuring bulk density, C content and the age of peat segments throughout peat cores (Tolonen & Turunen, 1996). The interaction of environmental factors with changing climate will determine the role and relative strength of the peatland C source or sink. However, the complexity of peatland dynamics often restricts the identification of the main driving factors. Such understanding of interlinked relationships would nevertheless be essentially important for future C balance estimations and evaluation of climate feedbacks (Charman *et al.*, 2015). Additionally, temporal variations related to peat decomposition rates *vs.* peat

quality and age challenge the identification of climate forcing on C accumulation and the comparison of C dynamics between different study sites and time periods (Charman *et al.*, 2013, Garneau *et al.*, 2014). Therefore, model exercises separating autogenic and allogenic forcing on peat processes (Tuittila *et al.* 2007, 2012, Charman *et al.*, 2013) and simulations of potential decomposition processes (Loisel & Yu, 2013) will reduce these uncertainties and, for instance, provide us with a way to evaluate whether recent warming has clearly stimulated C fixation when compared to past millennia.

Research on permafrost peatland dynamics has developed over time. Earlier research was generally about the formation (e.g., Brown, 1968, Seppälä, 1982), distribution and classification (e.g., Zoltai & Tarnocai 1975, Vitt *et al.*, 1994) of permafrost peatlands. Since 2000, many studies on the Holocene development of permafrost peatlands appeared using proxy and peat property data, for example in European Russian Arctic (Oksanen *et al.*, 2001, Routh *et al.*, 2014), subarctic Sweden (Kokfelt *et al.*, 2010, Sannel *et al.*, 2017), Finnish Lapland (Oksanen, 2006), Siberia (Teltewskoi *et al.*, 2016,) and Canada (Bhiry *et al.*, 2007, Kuhry 2008, Bauer *et al.*, 2011, Tremblay *et al.*, 2014). Some of them applied carbon accumulation rate calculations (e.g., Vardy *et al.*, 2000, Lamarre *et al.*, 2012, Klein *et al.*, 2013, Gałka *et al.*, 2017a, Sannel *et al.*, 2017) and palaeohydrological reconstructions (e.g., Lamarre *et al.*, 2012, Swindles *et al.*, 2015a, Gałka *et al.*, 2017a) and to some extent enabled the estimation of interlinks between C accumulation and hydrological changes in permafrost environments. However, results have often based on single records, which has been suggested to be less informative in peatland studies (e.g., Mathijssen, 2016). Post *c.* 1900 peat accumulation has also been seldom considered, due to issues with incomplete decomposition (see however Klein *et al.*, 2013). It is also common that either long-term and coarse resolution (e.g., Sannel *et al.*, 2017) or short-term and fine resolution was applied (e.g., Swindles *et al.*, 2015a).

2 RESEARCH AIMS AND HYPOTHESES

In this study I investigated the response of permafrost peatlands to past climate changes. These data help in understanding current processes and future climate feedbacks. I applied testate amoeba and plant macrofossil analyses on replicate peat cores collected from Arctic peatlands in Russia and Finland to reconstruct past peatland dynamics, especially hydrology and vegetation successions and C dynamics. Biological data was supplemented by peat property analyses and chronological data. My hypotheses were:

1. Permafrost thawing triggered by warm climate conditions (e.g., MCA and warming since 1850 AD), is reflected in the proxy records as a change towards wetter plant communities and more hydrophilic testate amoeba assemblages.

2. Permafrost aggradation under colder climate conditions (e.g., LIA) results in dry conditions because of the up-heave of the peat surface.

3. Changes in carbon accumulation rates are driven by climate.

Furthermore, I evaluated if and how the peatland hydrology, vegetation and carbon response-dynamics differ between the MCA warming and the on-going recent warming.

I first established a new modern testate amoeba training set to enable WTD reconstructions for Arctic peatlands using fossil testate amoeba data. The model was first applied only to one Arctic peat record as a test (**I**). Next, when the approach appeared credible, the transfer function was applied to six peat records to reconstruct hydrological conditions over the last millennium in four permafrost peatlands (**II**). For these sections I also analysed plant macrofossils to reconstruct vegetation history and to validate, and to compare with, the testate amoeba-based WTD reconstructions (**II**). Finally, I used 14 peat records to reconstruct past C dynamics. To do this I applied peat decay modelling to derive non-autogenic C dynamics and to investigate the links between non-autogenic C dynamics and environmental variables. The modelling approach was also used to facilitate spatio-temporal comparison between the records (**III**).

3 STUDY SITES

In total, four permafrost peatlands were selected for this study (Table 1 and Fig. 3). Two of them (Indico and Seida) are located in the discontinuous permafrost zone in Russia, whereas the other two (Kevo and Kilpisjärvi) are in Finnish Lapland and represent the sporadic permafrost zone (**I**, **II** and **III**).

Table 1. Detailed study site information. Mean annual temperature (MAT) and mean annual precipitation (MAP) data for Indico are from the Naryan-Mar meteorological station (1961-1990), for Seida from the Vorkuta meteorological station (1977-2006); for Kevo from the Utsjoki Kevo meteorological station and for Kilpisjärvi from the Enontekiö Kilpisjärvi Kyläkeskus meteorological station (Pirinen *et al*., 2012), both for the period 1981-2010. Annual growing degree-days above 0°C (GDD0, temperature sum), cumulative annual photosynthetically active radiation during the growing season (PAR0) and annual precipitation/annually integrated equilibrium evapotranspiration moisture index (P/Eq) were developed using the CRU 0.5° gridded climatology for 1961-1990 (CRU CL1.0) using PeatStash (Gallego-Sala & Prentice, 2013).

Site	Latitude (N)	Longitude (E)	MAT (°C)	MAP (mm)	GDD0	PAR0	P/Eq
Indico	67°16′01″	49°52′59.9″	-4.0	501	1074.27	3649.54	1.57
Seida	67°07′0.12″	62°57′	-5.6	501	971.65	3165.96	1.63
Kevo	69°49′26.1″	27°10′20.7″	-1.3	433	1151.86	3683.14	1.61
Kilpisjärvi	68°53′4.5″	21°3′11.94″	-1.9	487	985.85	3505.50	1.79

3.1 Northeast European Russia

Indico and Seida are located in the Arctic northeast European Russian tundra. The peat plateaus in these two peatlands are elevated several metres from the surrounding mineral soil and the vegetation is dominated by shrub-lichen-moss communities, such as *Betula nana*, *Rhododendron tomentosum*, *Empetrum nigrum*, *Sphagnum fuscum*, *Polytrichum strictum*, *S. lindbergii* and sedges such as *Eriophorum* spp. As opposed to Seida, at Indico extensive areas are covered by lichens and mosses, while shrubs are less abundant. Large bare peat surfaces occur at both sites (field observations 2012 by M. Väliranta). Some cracking features were detected on bare/lichen -covered surface, and can be considered as natural permafrost peatland development and life-cycle features (Seppälä, 2006).

3.2 Finnish Lapland

At the two sites in Finnish Lapland, Kevo and Kilpisjärvi, the peatlands are characterised by separate permafrost mounds a few metres high and surrounding wet flarks. The mound vegetation is dominated by dwarf shrubs such as *Betula nana*, *Empetrum nigrum*, *Rubus chamaemorus* and bryophytes *Polytrichum strictum* and *Dicranum* spp. Different *Sphagnum* species such as *S. fuscum*, *S. balticum*, *S. majus* and *S. riparium* occur along a hydrological gradient from dry to wet. *Eriophorum* spp. are also present. Cracking features can be found on the edges of permafrost mounts. There are also patches of bare peat, but they are smaller than those in Russia.

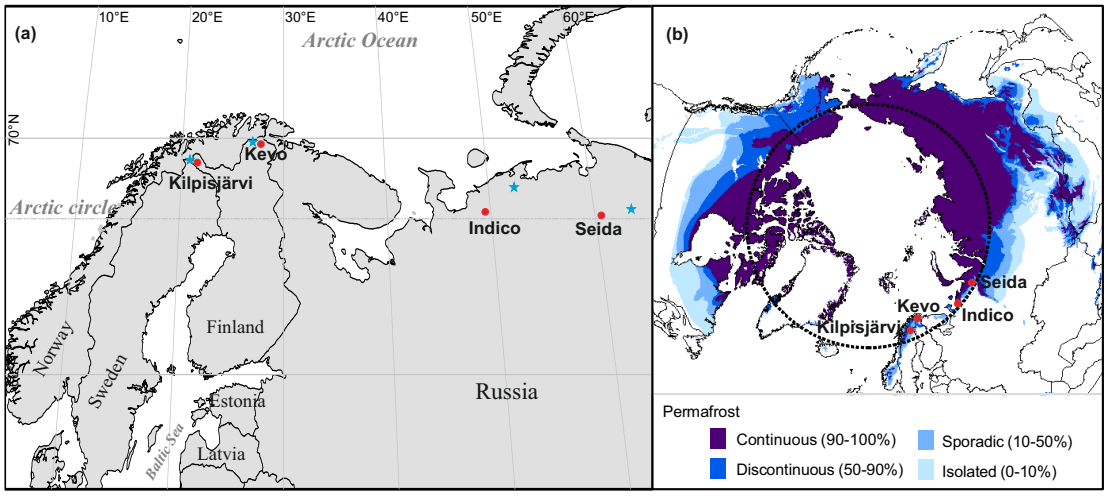

Fig. 3. (a) Locations of the study sites (red dots). Climate data for each site are derived from the nearest meteorological station (blue stars), see details in Table 1. (b) Circum-Arctic permafrost zonation map, data are from Brown *et al.* (1998).

4 METHODS

4.1 SAMPLE COLLECTION

4.1.1 Modern testate amoeba training set

A total of 145 surface samples (*ca.* 10*10*10 cm^3) were collected (Table 2) from the four peatlands (**I**) following the ACCROTELM project protocol (http://www2.glos.ac.uk/accrotelm/fieldtst.html). At each site, several hydrological transects were established. The amount of sample plots along each transect varied from four to seven. Sampling plots were selected to cover the micro-topographical gradient from hummock to hollow/pool as well as to cover different vegetation types. At each sampling point, WTD and pH were measured, and the general plant composition was also surveyed.

4.1.2 Peat cores

In total, 14 peat cores (Table 2) were collected during August 2012 and 2015. Only the non-frozen peat layer above the permafrost (active layer) was collected using a Russian peat corer (Ø 5 cm). All the cores were collected from the medium dry habitats of either a raised peat plateau (Russia) or a permafrost mount (Finland). The active layer of the most sampling sites did not reach the peat bottom, as an exception the core Ind5 extended to the mineral ground. Therefore, the reported basal age represents the age of the active layer bottom most peat layer. Measured active layer thicknesses for the studied peatlands were between 20 and 50 cm. Individual cores were wrapped in plastic and transported to the laboratory in sealed PVC tubes and stored in a freezer. The cores were later defrosted and sub-sampled in 1-cm or 2-cm thick slices for further analyses.

4.2 CHRONOLOGY

As the peat appeared to be very decomposed, instead of picking out plant remains I chose to submit bulk peat samples for radiocarbon dating. In total, 44 bulk peat samples were sent to the Finnish Museum of Natural History (LUOMUS, Helsinki, Finland) or the Poznan Radiocarbon Laboratory (Poznan, Poland) for accelerator mass spectrometry ^{14}C dating (Table 2). I

acknowledge the potential sources of error related to bulk peat samples but a recent study on circum-Arctic peatlands suggests that there is no significant difference between ages derived from bulk materials and plant macrofossils (Holmquist *et al.*, 2016). For five peat cores, the chronology of the top part was determined with ^{210}Pb dating (Table 2). The samples were processed at the University of Exeter, UK. A dry *c.* 0.2-0.5 g subsample from each 1-cm interval was analysed for ^{210}Pb activity after spiking with a ^{209}Po yield tracer; see Kelly *et al.* (2017) and Estop-Aragonés *et al.* (2018) for detailed procedure. The surface (0-1 cm) ages of other cores were based on ^{14}C dating, or assumed to be the collecting year (Table 2). For the latter case, the first ^{14}C dated depth was always at *c.* 10 cm.

When performing the age-depth modellings, at first I always tried both "Clam" (Blaauw, 2010) and "Bacon" (Blaauw and Christen, 2011) methods but in the end found out that differences between modelled age and the dated age were often smaller when using "Clam" instead of "Bacon". Considering the wide application of "Clam" in peatland studies and also the comparability of the two methods in the case of higher dating density (more than one date per millennium) (Blaauw et al., 2018), I decided to consistently use "Clam". Age-depth models (**III**: Fig. S1) were established using the package "Clam" in R version 3.2.4 (R Core Team, 2014). ^{14}C ages were calibrated using the INTCAL13 calibration curve (Reimer *et al.*, 2013). ^{210}Pb ages were obtained by applying the Constant Rate of Supply model (Appleby & Oldfield, 1978). Both ^{210}Pb and ^{14}C dates were included in the final age-depth models (**II** and **III**). For most of the cores, a smooth spline method (smoothing 0.3) was selected to develop the age-depth model. There were also cores that yielded age reversals when the default smoothing parameter 0.3 was employed and relatively large deviations of the calibrated ^{14}C dates to the age-depth model curve when changing the parameter, so a linear interpolation method was used instead for those cores.

4.3 BIO-INDICATOR ANALYSIS

In total, eleven peat cores were analysed for testate amoebae and/or plant macrofossils (Table 2). Testate amoeba and plant macrofossil analyses were

carried out at 1- or 2- cm resolution. When there was not enough material to carry out both analyses from the same sample, adjacent sample level from the same core was analysed. There were also cases when only one proxy was analysed for the whole core due to limited material.

4.3.1 Testate amoeba

Processing of testate amoeba samples followed a modified version of the standard method (Booth *et al.*, 2010). Samples (*ca.* 2 cm^3) were boiled in distilled water for 15 minutes and stirred occasionally. Modern samples were sieved with a 300-µm mesh and back-sieved with a 15-µm mesh (**I**). A 180-µm mesh was used for fossil samples instead of the standard 300-µm mesh, as fossil samples contained a large quantity of decomposed plant detritus (**I**, **II** and **III**). Materials retained on the 15-µm sieve were centrifuged at 3000 rpm for 5 minutes. At least 150 (modern samples) or 50-100 (fossil samples) individual shells for each sample were counted (Payne & Mitchell, 2009) and identified to species or 'type' level under a light microscope at 200–400x magnification. Taxonomy follows (Charman *et al.*, 2000), supplemented with online sources (e.g., user.xmission.com/~psneeley/Personal/FwrPLA.htm; www.arcella.nl).

Occasionally the lower part of the peat section was highly decomposed and decomposed plant material hindered testate amoeba identification. These samples were treated with 5% KOH to disaggregate and remove fine organics before sieving (Charman *et al.*, 2010, Barnett *et al.*, 2013). However, if the test count did not reach 50 specimens after reasonable effort, these samples were omitted from the WTD reconstructions.

4.3.2 Plant macrofossil

Plant species compositions for modern sample points were described in the field and the more detailed species identification was done in the laboratory under a stereomicroscope at 10-40× magnification and a high-power light microscope at 100-200× magnification. Plant composition data were then classified into plant functional types following Tuittila *et al.* (2012) and references therein (**I**). For plant macrofossil analysis (**I**, **II** and **III**),

volumetric samples (*c.* 2-5 cm^3) were gently rinsed under running water using a 140-μm sieve. No chemical treatment was necessary. Remains retained on the sieve were identified. Following Väliranta *et al.* (2007), proportions of different plant types and unidentifiable organic matter (UOM) were estimated with aid of scale paper under the petri dish using a stereomicroscope. Further identification to species level was carried out using a high-power light microscope.

4.4 TRANSFER FUNCTION FOR RECONSTRUCTION OF WATER-TABLE DEPTH

A testate amoeba-based WTD transfer function (**I**) was developed firstly by applying ordination analyses to investigate the species-environment relationship using Canoco 5 (ter Braak & Šmilauer, 2012), secondly by developing four transfer functions: weighted averaging, tolerance-downweighted weighted averaging; weighted average partial least squares and maximum likelihood using the "Rioja" package (Juggins, 2015) in R version 3.2.4 (R Core Team, 2014), and thirdly by testing and validating the performance using various statistical methods (Telford & Birks, 2009, 2011, Telford, 2015) and independent modern samples. Moreover, the newly established model was compared with other models from European temperate and boreal peatland data (Charman *et al.*, 2007) and the Swedish Arctic peatland data (Swindles *et al.*, 2015b) and also with plant macrofossil data.

The best-performing transfer function was applied to fossil testate amoeba data to carry out the WTD reconstruction (**II** and **III**). Z scores of the reconstructed WTD values were calculated to show the hydrological shifts, as the reconstructions may poorly represent the actual magnitude of the water table changes (Swindles *et al.*, 2015c).

4.5 CARBON ACCUMULATION RATE CALCULATONS AND MODELLING

4.5.1 Peat property analysis

Contiguous samples of known volume were extracted from the cores at 1 or 2 cm resolution and oven-dried (50°C overnight and then 110° C for 6 hours).

Samples were then weighed to enable calculation of peat bulk density (BD; **III**). BD (g/cm^3) was calculated by dividing the dry peat weight (g) by the wet peat volume (cm^3). Percentage carbon and nitrogen content by mass (**III**) were measured on homogeneous ground sub-samples using LECO TreSpec Elemental Determinator at the University of Helsinki, Finland. Carbon-to-nitrogen mass ratios (C/N) were calculated from C and N content measurements. For some cores, loss on ignition (LOI) at 550°C (**III**) was measured instead of percentage carbon. In these cases it was assumed that ignited organic material contained 50% of organic carbon (Loisel *et al.*, 2014).

4.5.2 Apparent carbon accumulation rate (ACAR)

Peat vertical growth rates for each core were calculated based on the most probable age estimates derived from the age-depth models (**II** and **III**). ACAR (g C m^{-2} yr^{-1}) was calculated by multiplying the bulk density of depth-specific increment by its C content and by the accumulation rate (Tolonen & Turunen, 1996; **III**).

4.5.3 Peat decay and modelling of past C dynamics

Measured ACARs are usually higher for more recent peat layers due to incomplete decomposition processes. This makes direct ACAR comparisons between recent and past peat sections challenging. To solve this, based upon changes in bulk density and C/N variations (Yu *et al.*, 2001, Robinson, 2006) and the instantaneous rate of change of the age-depth model (Loisel & Yu, 2013), I identified a division boundary separating less decomposed young upper peat from the more decomposed older peat (henceforth Dec_{part} and Dec_{full}). In most cases, this boundary corresponds approximately to layers dated to *c.* 100-200 cal. BP. However, occasionally, for example in Kil1 BS, this boundary corresponds to a shift from deep *Sphagnum* peat to overlying ligneous peat dated to *c.* 1470 cal. BP. In such cases, the peat that has accumulated after AD 1850 was classified as a separate Dec_{part} section to enable the estimation of impact of recent warming on C accumulation. In other words, the partially decomposed peat section was divided into two sections, but both sections were modelled separately from the Dec_{full} section.

Then three models were applied: (1) the exponential decay model (EDM) (Clymo, 1984):

$$\mathrm{M} = \frac{p}{\alpha} * (1 - e^{-\alpha * t})$$

where p is the peat addition rate, α is the peat decay coefficient, t is time and M is the observed cumulative peat organic matter pool; (2) the C flux reconstruction model (CFM) (Yu, 2011):

$$\mathrm{NCU}_t = \frac{\mathrm{NCP}_t}{e^{-\alpha * t}}$$

where the net peat C pool (NCP) is used to calculate C uptake (NCU), α is calculated using EDM, t is time; and (3) a simplified peat decomposition model (PDM) (Frolking *et al.*, 2001):

$$\mathrm{M}_t = \frac{p}{1 + \alpha t}$$

where p and α are derived from EDM, M_t is the remaining peat at time t. The EDM was used to derive p and α directly from the peat core data. EDM was applied separately for $\mathrm{Dec}_{\mathrm{full}}$ and $\mathrm{Dec}_{\mathrm{part}}$ peats and assumed that they have constant peat decay rates within these sections. These values were then used to drive the CFM (for $\mathrm{Dec}_{\mathrm{full}}$ peat C fluxes) and PDM (for $\mathrm{Dec}_{\mathrm{part}}$ peat C fluxes), which are independent from one another (Loisel & Yu, 2013). For $\mathrm{Dec}_{\mathrm{full}}$ peats, CFM was used to back-calculate the amount of C that was initially deposited (C uptake). For $\mathrm{Dec}_{\mathrm{part}}$ peats, PDM was used to simulate potential peat decomposition over a certain period of time (100 and 300 years) and to calculate the remaining amount of peat (which is equivalent to the C uptake if multiplied by the assumed 50% C content in peat organic matter) that will be eventually buried into deeper layers (i.e. the initial C deposits of $\mathrm{Dec}_{\mathrm{full}}$ peats) (Loisel & Yu, 2013).

4.5.4 Relationships between non-autogenic C accumulation and environmental variables

To separate the impact of autogenic processes *vs.* allogenic forcing on ACARs, the EDM model was applied (Clymo, 1984). The EDM-derived p and α were used to simulate the carbon accumulation rate (CAR) under constant

conditions (without external environmental disturbances). The differences (△CAR) between modelled CARs and actual ACARs are therefore due to non-autogenic processes, thus driven by environmental factors. Z scores of △CAR were then calculated over the total length of cores from each site to enable better within-site comparison.

Correlation analyses of the relationship between △CAR z scores and core-specific environmental variables (WTD, plant function type, N% and C/N) and regional summer temperature (T_{sum}) (Wilson *et al.*, 2016) were carried out in R version 3.2.4 (R Core Team, 2014) using the corr.test function in the "psych" package to test the relative importance of each variable in determining C accumulation for each core, each site, each region (Russia and Finland) and for all cores combined. Only a sub dataset for the last millennium was used here. Then a multiple linear regression analysis (stepwise) was applied to data from each site, each region and all sites combined dataset to evaluate the influences of variables on the non-autogenic C accumulation. Three interaction terms (T_{sum}*WTD, T_{sum}*N% and T_{sum}*UOM) were used as additional variables in the multiple linear regression analysis.

Table 2. Detailed description of modern training set sample sets, peat cores, applied methodology and analyses.

Site	Surface samples (n)	WTD	pH	TA	PI	Peat cores	Depth (cm)	Surface age control	^{14}C dates (n)	Basal age (cal.BP)	BD	LOI	C%	N%	TA	PM
Indico	47	√	√	√	√	Ind1	39	Col year	4	3420 ± 64	√	√				
						Ind2 BS	38	^{14}C	4	7040 ± 48	√		√	√	√	√
						Ind3 BS	48	^{14}C	3	6260 ± 24	√		√	√	√	√
						Ind4	35	^{210}Pb	2	2050 ± 65	√		√	√	√	√
						Ind5	45	^{210}Pb	3	7230 ± 64	√		√	√	√	√
						Ind6	44	Col year	3	1885 ± 65	√	√			√	√
Seida	52	√	√	√	√	Sei1	39	Col year	4	6575 ± 88	√	√			√	
						Sei2	24	^{210}Pb	3	3295 ± 82	√		√	√	√	√
						Sei3 BS	30	^{14}C	2	6485 ± 85	√		√	√		
						Sei4	29	Col year	2	580 ± 29	√	√				
Kevo	27	√	√	√	√	Kev1 BS	31	^{14}C	4	1485 ± 72	√		√	√	√	√
						Kev2	33	^{210}Pb	2	1975 ± 78	√		√	√		√
Kilpisjärvi	19	√	√	√	√	Kil1 BS	40	^{14}C	5	3900 ± 73	√		√	√		√
						Kil2	32	^{210}Pb	3	1645 ± 78	√		√	√	√	√

Note the peat core codes were renumbered for publication **II**. BS represents bare peat surface, other cores are from vegetated peat surfaces. Col year: collecting year, WTD: water-table depth, TA: testate amoeba, PI: plant identification, BD: bulk density, LOI: loss on ignition, C%: carbon content, N%: nitrogen content, PM: plant macrofossil. PM-based WTD reconstructions were applied for cores Kev2 and Kil1 BS using an extended training set of Väliranta *et al*. (2012), for other cores WTD reconstructions were based on TA data. Colour coding indicates the publication where the material is published: red (**I**), blue (**II**) and green (**III**).

5 RESULTS AND DISCUSSION

5.1 TESTATE AMOEBAE AS PALAEOHYDROLOGICAL INDICATORS IN PERMAFROST PEATLANDS

A total of 59 testate amoeba taxa from 20 genera were recorded from the 145 analysed surface peat samples (**I**: Table 2). The Shannon diversity index, 1.75 ± 0.47, indicates relatively diverse environments overall (Magurran, 1988). Low values (<1.5) occurred in both very wet (WTD around 0 cm) and very dry (WTD at -45 cm) habitats, while high values (>2.5) also appeared in both wet and dry habitats, suggesting no correlations between diversity and WTD. The most dominant taxa of the whole modern training set were *Assulina muscorum*, *Archerella flavum*, *Hyalosphenia papilio*, *Nebela tincta* type and *Trigonopyxis minuta* type (**I**: Fig. 2). Many taxa showed a cosmopolitan distribution (**I**: Fig. 3a), and their distributions displayed a good relationship with the hydrological gradient (**I**: Fig. 3b). Among the studied environmental variables, WTD and hollow *Sphagna* were found to have the strongest influence on testate amoeba assemblages (**I**: Fig. 4). Correlation analysis of these two variables suggests that they significantly correlated also with each other ($r = 0.545$, $p = 0.001$).

Generally, the WTD preferences of the majority of the investigated testate amoeba taxa (**I**) resembled those observed in other studies on temperate, boreal and subarctic peatland testate amoebae (Charman *et al.*, 2007, Amesbury *et al.*, 2013, Swindles *et al.*, 2015b). However, there is still a demand for a broader ecological understanding of testate amoebae on permafrost peatland environments because of some disparate features. For example, in permafrost environments *Pseudodifflugia fulva* type has a clearly higher WTD optimum (17 cm) than that derived from European bogs (7 cm) (Charman *et al.*, 2007) (**I**: Fig. 6). Furthermore, some taxa, such as *Amphitrema wrightianum*, were totally absent from our samples, suggesting that they may not tolerate the more extreme winter climate and associated permafrost conditions at these sites. Overall, in my dataset, the taxon-specific WTD ranges are comparatively narrow (I: Fig. 6) (Charman *et al.*, 2007, Amesbury *et al.*, 2013, Lamarre *et al.*, 2013). This might be associated with

the presence of permafrost and the consequent extreme temperatures, which may reduce moisture tolerance (Pianka, 2011).

The newly developed best-performing transfer function was based on tolerance-downweighted weighted averaging with inverse deshrinking (R^2 = 0.77, RMSEP = 5.62 cm with leave-one-out cross validation; **I**: Table 4). In order to test the model's reliability, it was compared with two other reconstruction models, one from European temperate and boreal peatlands (Charman *et al.*, 2007) and the other from subarctic Sweden (Swindles *et al.*, 2015b). The comparison showed that the modelling outcome when using the new subarctic training set was more coherent with the previous subarctic training set model and the results differed more when compared to the temperate and boreal peatlands model. This indicates that specifically designed Arctic training sets may provide more reliable reconstructions for peatlands in these regions (**I**: Fig. 9 and Table 5). The robustness of the established reconstruction model was also validated against plant macrofossil data from the same core (**I**: Fig. 9). Both testate amoeba and plant macrofossil data suggested two major wetness shifts. However, testate amoeba-based WTD reconstructions indicate more fluctuations than WTD reconstructed from plant macrofossils (**I**: Fig. 9). The discrepancies between the two proxies suggest that testate amoebae are more sensitive to wetness changes than plant communities (Väliranta *et al.*, 2012, Gałka *et al.*, 2017b).

In summary, testate amoebae are a powerful proxy for palaeohydrological reconstruction in permafrost peatlands, but there requires specific training sets. Moreover, using testate amoeba and plant macrofossil analyses in parallel can provide more robust and reliable reconstructions.

5.2 HYDROLOGICAL AND VEGETATION RESPONSES TO CLIMATE CHANGE DURING THE LAST MILLENNIUM

The high amount of well-decomposed plant material in samples coming from deeper peat sections impeded visibility of microscope slides, and thus the identification of testate amoebae was difficult, sometimes impossible. Therefore, testate amoeba-based hydrological reconstruction using the newly developed transfer function (**I**) was only applied for the top part of the peat

sections covering the last millennium (**II**). Accordingly, also plant macrofossil data are discussed only for this period (**II**).

Extensive regional-scale permafrost aggradation in northeast European Russia occurred from *c.* 2200 cal. BP onwards (Hugelius *et al.*, 2012, Routh *et al.*, 2014). Hence, any MCA-induced permafrost dynamics and hydrological changes should be recorded in the studied cores from Russia, even though the regional MCA signal may be relatively weak and it is relatively uncertain if recent warmth has exceeded the temperatures of the MCA (Briffa *et al.*, 2013). Consistent with the first hypothesis, the data suggest that the MCA warming resulted in permafrost thawing and the consequent establishment of moist fen-type communities or alternatively *S. fuscum*-dominated communities (Fig. 4; **II**: Fig. 3a and c). The former case corresponds to previous European Russian studies (Routh *et al.*, 2014). However, the moist communities were subsequently replaced by shrubs, and this is supported by testate amoeba reconstructed dry conditions. These habitat conditions prevailed over the latter part of the MCA. Dry development may reflect either melt water drainage (Wilson *et al.*, 2017) and/or increased evaporation (Swindles *et al.*, 2015a). A dry MCA has been reported from a nearby region (Kremenetski *et al.*, 2004) and some other areas for example in Arctic Canada (Linderholm *et al.*, 2018), continental north-central Europe (Cook *et al.*, 2015) and southern Finland (Helama *et al.*, 2009). In Fennoscandia, MCA temperatures were potentially *c.* 0.5° C lower than at present (Luoto, 2017), and relative humid conditions were suggested by Ljungqvist *et al.* (2016). The results from Kevo and Kilpisjärvi suggest that those sites remained permafrost-free until the LIA, corresponding what has been reported earlier (Oksanen, 2006). Throughout the MCA, a relatively dry habitat sustained at Kevo, while at Kilpisjärvi, a wet fen prevailed (**II**: Fig. 3e and f).

In northeast European Russia, in line with the second hypothesis, plant data suggest relatively stable dry hummocky habitats during the LIA. Interestingly, while testate amoeba data mainly indicate drying conditions at this time, the data also suggest occasional wet phases at around 450–400 and 175 cal. BP (**II**: Figs 3 and 4). These wet phases may reflect wet climate events recorded elsewhere in northwest and central Europe during the LIA (Charman

et al., 2006, Väliranta *et al.*, 2007, Gałka *et al.*, 2014). However, in general, the LIA was a dry period in NE European Russia, or cooling-stimulated permafrost aggradation effects on peat surface moisture overrode the influences of a wet climate. Unlike at Russian sites, the beginning of the LIA at Kevo and Kilpisjärvi appears to have been wet, and this corresponds to the humid climate recorded in Finland (Väliranta *et al.*, 2007, Linderholm *et al.*, 2018). Afterwards, cool temperature-induced permafrost aggradation played a more important role in regulating peatland hydrological conditions over wet climate. Consistent with the second hypothesis, conditions subsequently shifted and remained dry for the rest of the LIA, from *c.* 550–100 cal. BP. Drying was most evident in testate amoeba records but Kilpisjärvi plant macrofossil data also support this shift by showing a vegetation change from *Sphagnum* domination to a dwarf shrub community (**II**: Fig. 3f), whilst at Kevo no clear vegetation changes occurred (**II**: Fig. 3e).

Analysed data consistently suggest habitat changes towards drier communities over recent decades (Fig. 4; **II**: Figs 3 and 4), which contradicts the first hypothesis that warming results in wetting. Drying is reflected as a change from wet *Sphagna* to dry *Sphagna* (**II**: Fig. 3a and b), from *Sphagnum* spp. to Ericales shrubs (**II**: Fig. 3c) or by the appearance of lichens and dry non-*Sphaganum* bryophyte taxa (**II**: Fig. 3e). A similar trend towards drier conditions was also found previously in northern Sweden (Gałka *et al.*, 2017a). Chronologically, this habitat change corresponds to extensive permafrost degradation reported for the last *c.* 50 years (Kokfelt et al., 2009, Sannel & Kuhry, 2011, Swindles *et al.*, 2015a, Jones *et al.*, 2016, Borge *et al.*, 2017). Generally, the current mean annual temperature in northeast European Russian regions still remains below 0 °C. Recently, however, individual years have exceeded or approached 0°C, e.g., 2007 and 2004, when the annual temperature was 0.4 and -0.7 °C, respectively. Moreover, in Finnish Lapland, the mean annual temperature has frequently been above 0°C in recent years and warming is projected to continue (Collins *et al.*, 2013). This may have two-fold consequences for permafrost peatlands: accelerated wetting due to the thawing of permafrost but followed by desiccation afterwards due to drai-

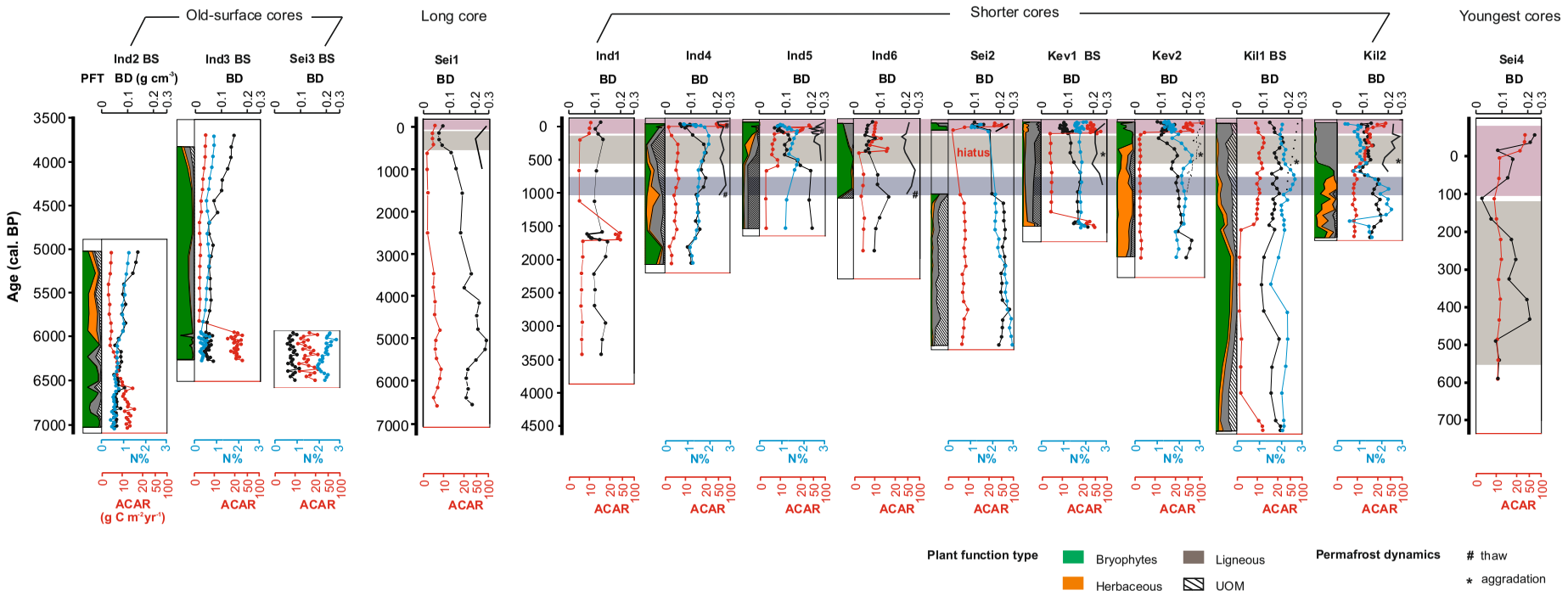

Fig.4. Summary of the results. Plant macrofossil data are classified as plant function types (PFT) and unidentifiable organic matter (UOM). Bulk density (BD; black line with symbol), nitrogen content (N%; blue line with symbol) and apparent carbon accumulation rates (ACAR; red line with symbol) are plotted against ages. Note the scales of Y-axes (ages) vary due to large variation in age-depth. Black lines (without symbols) indicate hydrological shifts reconstructed using testate amoeba data, and black dash lines indicate results from plant macrofossil data (left: wet; right: dry; no scales are shown). Inferred permafrost aggradation and thaw are indicated. Climate phases are indicated using purple (Medieval Climate Anomaly), grey (Little Ice Age) and red (post LIA warming) shadings.

-nage and/or an increase in evapotranspiration. Speculatively, the final stage following permafrost degradation and collapsing mounds resembles current northern oligotrophic aapa mires with string and flark microtopography, or if the nutrient input from the surroundings increases a minerotrophic fen establishes (cf. Swindles *et al.*, 2015a).

5.3 PERMAFROST PEATLAND CARBON DYNAMICS

5.3.1 PEAT ACCUMULATION RATES AND PEAT PROPERTIES

Vertical peat growth rates have not been consistent during the last few millennia at the study sites (**III**: Table 1 and S1). The thickness of the peat cores ranged from 24 to 48 cm, determined by the depth of underlying frozen peat, and the basal ages of the collected peat columns ranged from 580 ± 29 to 7040 ± 48 cal. BP. Three cores collected from bare peat surfaces (Ind2 BS, Ind3 BS and Sei3 BS) yielded old surface ages of 4950, 3660 and 5970 cal. BP, respectively (**III**: Table S1). The mean peat accumulation rate calculated over each core ranged from 0.08 to 0.67 mm yr^{-1} (**III**: Table 1).

Peat properties varied with depth and also between different cores and sites (Fig. 4; **III**: Table S1). When all cores are combined, the mean BD (± standard deviation (SD)) was 0.13 ± 0.06 g cm^{-3}, which resembles the value of 0.111 ± 0.067 g cm^{-3} previously reported for peats from western Russia and Fennoscandia (Loisel *et al.*, 2014). N content analyses yielded an average value of 1.49 ± 0.70%, similar to the value of 1.48 ± 0.72% reported in a permafrost peat compilation by Treat *et al.* (2016). The average LOI value was 79.67% (± 13.86%), which is lower than the value of 92.4 ± 6.4 reported by Treat *et al.* (2016) and 94.6 ± 10.3 for western Russia (Loisel *et al.*, 2014). The mean C content of 50.23 ± 4.37% is slightly higher than the previously reported mean from these regions, i.e. 49.2 ± 3.2% for western Russia and 44.4 ± 5.7% for Fennoscandia (Loisel *et al.*, 2014), but still within their standard deviation range. The average C/N ratio was 51.94, with a large SD of ± 50.71, which indicate more variations than reported by Loisel *et al.* (2014) and Treat *et al.* (2016). Also core-to-core peat property values varied (Table S1). For instance, Ind3 BS the average BD was 0.07 ± 0.03 while Sei2 value was 0.20 ± 0.05 g cm^{-3}. Within-core LOI values showed large variations only

for core Sei1, with an SD of ± 18.9%, while the other cores, e.g. Ind6 and Sei4, had more congruent LOI values. Additionally, Sei4 had the highest mean LOI value of 93.71 ± 5.70%. The measured C content of organic matter averaged over the core ranged from 44.92 ± 4.18 (Ind5) to 52.67 ± 0.79% (Kev1 BS), while the N content ranged from 0.41 ± 0.18% (Ind3 BS) to 2.27 ± 0.22% (Sei3 BS). The C/N ratio varied notably between the cores; the range spanned from 23.17 ± 2.27 (Sei3 BS) to 148.61 ± 65.44 (Ind3 BS).

5.3.2 REGIONAL AND LOCAL-SCALE INCONSISTENCIES IN ACARs

Generally, the ACAR values of ~12 g C m^{-2} yr^{-1} detected in this study are notably low when compared to 22.9 g C m^{-2} yr^{-1} for northern non-permafrost peatlands (Loisel *et al.*, 2014), probably due to the lower Arctic NPP and standing biomass (Saugier *et al.*, 2001). The mean long-term ACAR values at the Russian sites were 13.66 g C m^{-2} yr^{-1} for Indico and 12.90 g C m^{-2} yr^{-1} for Seida (**III**: Table 2). At the Finnish Lapland sites, ACAR values for the Kilpisjärvi cores had a low value of 10.80 g C m^{-2} yr^{-1}, while a much higher value (32.40 g C m^{-2} yr^{-1}) for ACARs was recorded at Kevo (**III**: Table 2). The slightly higher GDD0 and PAR0 at Kevo than at other sites (Table 1) might partially explain the recorded higher ACARs, because both indices are suggested to drive NPP (Field *et al.*, 1995). All our cores except the two from Kevo (33.88 and 30.91 g C m^{-2} yr^{-1}) had distinctly lower ACARs than reported for northern peatlands (22.9 g C m^{-2} yr^{-1}) in Loisel *et al.* (2014), but the difference was insignificant (p = 0.437) when compared to the values reported for permafrost peats (14.0 g C m^{-2} yr^{-1}) by Treat *et al.*, (2016). The detected differences when compared to previous studies may be explained by our data set where only three records (Ind2 BS, Ind3 BS and Sei3 BS) extend to mid Holocene, with basal ages of >6000 cal. BP. Consequently, only these records may capture parts of the HTM, when peat accumulation was presumably higher than during the late Holocene (Yu *et al.*, 2010, Loisel *et al.*, 2014). In summary, our records represent a shorter period of time than those published earlier from similar regions (Botch *et al.*, 1995, Oksanen *et al.*, 2003, Turunen, 2003, Oksanen, 2006) and accordingly this may be reflected as lower mean ACAR values.

Relatively large within site ACAR variations were detected at most of the sites (**III**: Figs 3–5 and Table 2). For example, at Indico, the mean ACAR calculated over a single core ranged from 8.14 to 20.99 g C m^{-2} yr^{-1} and at Seida from 4.32 to 16.89 g C m^{-2} yr^{-1}. The inconsistent C accumulation patterns through the past millennia are clearly indicated by large standard errors (**III**: Fig. 5). It appeared that external environmental forcing factors sometimes had opposing influences on C accumulation processes from one study point to another. And even when the external drivers had the same forcing (either increase or decrease in C accumulation), the magnitudes varied (**III**: Fig. S2).

5.3.3 CARBON ACCUMULATION RESPONSE TO CLIMATE CHANGE

C accumulation patterns in permafrost peatlands appear to be driven by complex interactions and processes aside from hydrology and vegetation composition alone. Yet, the detected ACAR patterns are largely in line with the third hypothesis, and the climate forcing is to some extent registered in the C accumulation records (**III**). However, it has to be concluded that in this study there was no clear linear correlation between C accumulation rates and the examined environmental variables (**III**: Table 3). Moreover, C accumulation responses to warm climate phases varied, and even conflicting responses were evident. In permafrost peatlands, the interactions between permafrost dynamics and other environmental variables may play more important roles in regulating C accumulation than in more southern locations without permafrost.

The distinctly higher ACARs at around 6000–7000 cal. BP in Russia (Fig. 5; **III**: Figs 4 and 5) was in line with the Holocene-scale pattern for northern peatlands (Yu *et al.*, 2010, Loisel *et al.*, 2014). Contrary to the HTM, the warm MCA did not trigger rapid C accumulation (Fig. 5; **III**: Figs 4 and 5). One important difference between these two warm phases is that, at least in northeast European Russia, the MCA was preceded by permafrost-occupied conditions, while there was no permafrost before HTM (Hugelius *et al.*, 2012, Routh *et al.*, 2014). The duration of the MCA was also shorter and the spatial features, geographic distribution and strength of the anomaly were more

variable (Mann, 2002, 2009). Therefore, the MCA signal may be less clearly detectable at our sites (**II**).

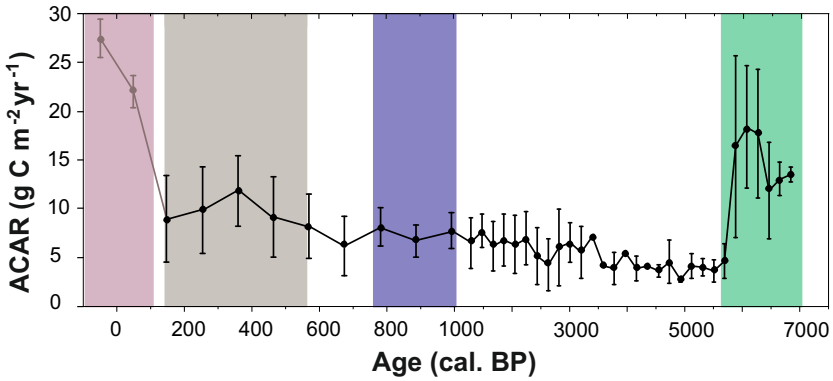

Fig. 5. Apparent carbon accumulation rates (ACARs) for all peat cores, a combined dataset with error bars representing standard errors of the means. Up to 1000 cal. BP, the calculations are expressed in 100-yr bins; while for the later periods, calculations are in 200-yr bins. ACAR values for the post-LIA warming period (26 ± 3.7 and 44.7 ± 5.5 g C m^{-2} yr^{-1}) are not according to the scales of Y-axis. Focus climate phases are indicated in green (Holocene Thermal Maximum), purple (Medieval Climate Anomaly), grey (Little Ice Age) and red (post-LIA warming) shadings.

Interestingly, ACARs during the LIA are higher than during the MCA (Fig. 5; **III**: Figs 4 and 5). Similarly, Gao & Couwenberg (2015) also reported of carbon accumulation peaks which occurred during the LIA. This is in contrast to the pattern recorded for more southern peatlands (Charman *et al.*, 2013), where the data suggest that ACAR was slower during the cold period. This could mean that in Arctic regions, during cold periods, C accumulation may be controlled more by decreased decomposition process rather than by cold temperature-related low productivity (Klein *et al.*, 2013).

Recent warming has also had inconsistent impacts on C accumulation at the study sites (**III**: Fig.6). At most of the sites, C sink capacity has increased. This may be driven by longer and warmer growing seasons experienced during the recent decades. Detected changes correspond to findings of Charman *et al.*, (2013). In addition, changes in vegetation composition and a decrease in N% seem to explain part of the enhanced C sink capacity (**III**: Fig. 4). On the other hand, decreased C sink capacity was also detected for some other sites. It is possible that in these cases the positive effect of higher temperatures and increased solar radiation (https://earthobservatory.nasa.gov/images/84930/the-arctic-is-absorbing-more-sunlight) could not counter-

balance the negative effect caused by, for instance, moisture deficiency (**II**).

This study indicates that there are alternative responses of permafrost peatlands to climate change (Fig. 6; **III**; Swindles *et al.*, 2015a). Warming may either cause wetting through thawing or surface drying through an increase in evapotranspiration or drainage processes (**II**). In both cases corresponding changes in vegetation can be expected (e.g., Mäkiranta *et al.*, 2018). In warm conditions, carbon accumulation may increase due to higher NPP, while it may also decrease because of moisture limitation. Therefore, the final C uptake ability is also linked to, for instance, local microtopographical conditions (**III**). Intense permafrost thawing eventually causes peatland collapse and saturation with thaw water. This case has the potential for large carbon sequestration through increased NPP and decreased CO_2 emissions, but also promotes CH_4 emissions (Swindles *et al.*, 2015a). Consequently, in the future the net effect can either be an increase or reduction in ACAR, or we may even see the transformation of peatlands from a sink to a net C source (Zhang *et al.*, 2013, Wang *et al.*, 2015, Chaudhary *et al.*, 2017).

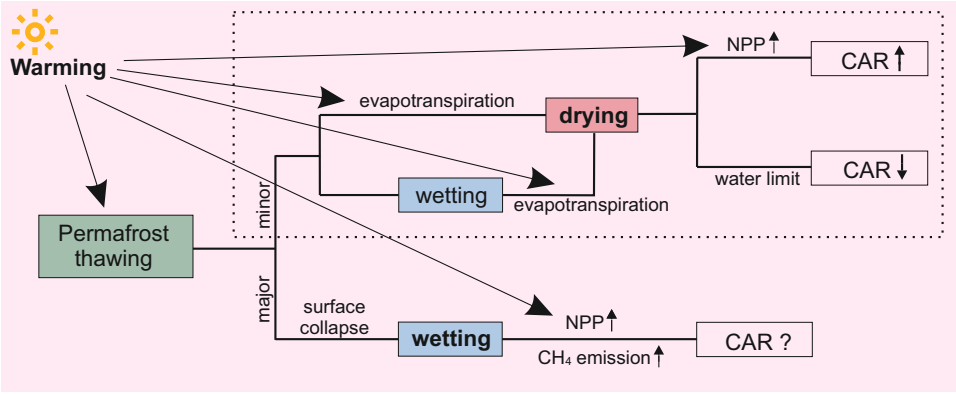

Fig. 6. Alternative permafrost peatland response-scenarios to climate warming regarding hydrology and carbon accumulation rates (CARs). The pathways enclosed by the dashed line are derived from this particular study. The arrows starting from the "Warming" symbol indicate positive forcing by warming climate. The upward arrows of NPP, CH_4 emission and CAR indicate increasing trend and the arrow of CAR pointing downwards indicates decreasing trend. NPP: net primary productivity.

6 CONCLUSIONS

My hypotheses were that 1) warm climate caused permafrost thawing, leading to wet conditions; 2) cold climate conditions triggered permafrost aggradation that led to dry conditions; and that 3) carbon accumulation variations are linked to climate changes. The study showed that permafrost peatlands have a complex nature and sensitivity to various environmental forcing that is not straightforward. Reconstructed hydrological, vegetation and carbon dynamics patterns often revealed variable core-to-core features, while regionally consistent patterns also emerged. To summarise, the main results were:

- The Medieval Climate Anomaly and post-LIA warming resulted in conspicuous short wet events, which probably indicate permafrost thawing.

- Warming-induced wet phases were followed by a change towards drier conditions. This suggests that evapotranspiration is an important factor in regulating surface peatland moisture conditions during warm periods in the Arctic.

- During the Little Ice Age, mainly hummocky habitat conditions prevailed, indicating cool and dry climate, which triggered permafrost aggradation. However, some short wet interruptions were also detected, implying occasionally wet climate.

- Large spatio-temporal variations in carbon accumulation rates occurred, both at very local and regional scales. This study did not reveal any single main driving factor behind the detected patterns. Small-scale permafrost dynamics-related factors are potentially important.

- Warming appeared to have an inconsistent effect on carbon accumulation rates. During the Holocene Thermal Maximum, carbon accumulation increased, while for the Medieval Climate Anomaly the same response

was not detected. Post-LIA warming has had a variable influence, driving both increases and decreases in carbon accumulation rates. The Holocene Thermal Maximum impact may be related to preceding non-permafrost environmental conditions. It seems that cold climate (Little Ice Age) did not induce strong forcing on carbon accumulation patterns.

- Currently permafrost peatlands' feedback to climate warming is negative i.e. they are cooling landscape elements. However, a probable future scenario is a transformation of high latitude peatlands to a net C source therefore becoming a positive feedback to the climate.

7 FUTURE PERSPECTIVES

This study indicates that in permafrost peatlands, testate amoebae are sensitive to WTD changes and they are effective indicators for (semi-)quantitative palaeohydrological reconstructions. Moreover, plant macrofossils are also informative in interpreting habitat wetness. However, plant communities may be more persistent and resilient to hydrological changes. Plants may better help to evaluate presence of permafrost and microtopographical evolutions as testate amoeba communities do not appear to reflect presence or absence of permafrost. Therefore, in studies that focus on these issues a single-proxy approach might hamper achieving a comprehensive picture of past peatland dynamics. Then again, if only one proxy is applied, then increasing of number of study sites could provide supportive replications. Hence, depending on the research question, the future study plans should include this consideration; fewer sites and several proxies or more sites but fewer proxies.

This study highlights the within peatland differences in response to environmental variables. Replicated records from the same peatland definitely provide a more robust and comprehensive picture of past peatland dynamics. It is thus recommended that multiple peat cores per site are investigated in palaeoecological studies.

When aiming towards profound research outcomes, analysis at as high a resolution as possible is always beneficial. Because peat accumulation is typically very slow in permafrost environments, the 1 or 2-cm resolution (sometimes equal to several hundreds of years per cm) may not enable capturing the fast environmental changes. Accordingly, even higher resolution analysis – supplemented by multiple coring points – may be required to achieve a complete picture of the past processes. Again, in practice the tradeoffs regarding temporal resolution and the number of sites analysed also need to be taken into account.

When the ACAR approach is applied in investigating the C accumulation patterns through time large uncertainties emerged as related to clearly different decomposition conditions. It may appear that ACARs for the most

recent period will eventually be higher when compared to the past periods, which is partly caused by the less decomposition of recent peats. When investigating the role of environmental variables in driving C accumulation, caution is needed to distinguish autogenic process from environmental forcing. In addition, sometimes permafrost dynamics seems to largely override the influence of other environmental variables regarding peat/carbon dynamics. Thus it would be beneficial to first preliminarily reconstruct the permafrost history and then examine the driver of carbon accumulation patterns. Moreover, as autogenic peat decay models do not perform trajectories related to the changes caused by permafrost dynamics, future efforts on the links between permafrost dynamics and decay changes are needed.

This study suggests that in permafrost peatlands, evapotranspiration associated to warm climate is an important factor regulating hydrological conditions. It is likely that future warming will result in extensive permafrost degradation and subsequent increased surface wetness and fen-type development. The current data show that permafrost peatland ecosystems may also respond in more complex ways, including drying. Future changes in precipitation and evapotranspiration are more uncertain than temperature development, but these may be particularly critical in determining hydrological and vegetation processes in permafrost peatlands. Our results point towards an inconsistent C accumulation response to drying and warming, highlighting how complex permafrost peatlands C dynamics are. Therefore, it is required that various alternative response-patterns are considered when peatland dynamics are modelled for future projections.

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Hui Zhang

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22 May 2018, Helsinki

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