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Response of plant communities to climate change during the late Holocene: palaeoecological insights from peatlands in the Alaskan Arctic

Mariusz Gałka[1], Graeme T. Swindles[2], Marta Szal[3], Randy Fulweber[4], Angelica Feurdean[5,6]

[1]Department of Biogeography and Paleoecology, Adam Mickiewicz University in Poznań, Poland; galka@amu.edu.pl

[2]School of Geography, University of Leeds, UK

[3]Institute of Biology, University of Białystok, Poland

[4]Toolik Field Station, Institute of Arctic Biology, University of Alaska Fairbanks, US

[5]Biodiversity and Climate Research Centre (BiK-F), Frankfurt am Main, Germany

[6]Department of Geology, Babeș-Bolyai University, Cluj-Napoca, Romania

Abstract

A high-resolution plant macrofossil record was examined alongside pollen, micro- and macro-charcoal, and testate amoeba data to elucidate the dynamics of two permafrost peatlands in the northern foothills of the Brooks Range, Alaskan Arctic. The vegetation dynamics of these two peatlands were driven by autogenic processes reflecting the development trajectory of the peatlands towards ombrotrophic status, and allogenic climate change. We observe an increase in shrub pollen and macrofossils (e.g. Ericaceae, Betula nana) during two Late Holocene warm episodes and in recent decades. Pollen data suggest that regional forest cover also responded to temperate increase since ca. AD 1950. An increase of Picea pollen (up to 13%) in the upper part of peat profile is probably associated with long distance pollen transport from populations of Picea mariana and Picea glauca located at the southern foothills of the Brooks Range. Relatively small amount of micro- and macrocharcoal in the two profiles indicates little fire activity around the sampling sites over the last ca. 2000 years, which is in agreement with regional findings. The lack of surface and groundwater influence under prolonged warmer/drier condition can allow Sphagnum to expand in Arctic peatlands. Cold climatic conditions might have been detrimental to Sphagnum populations, that were replaced by Carex spp. and other vascular plants owing to wetter conditions in the peatland.

Key words: global warming; climate change; permafrost; Sphagnum; shrub expansion, fire

1. Introduction

High-latitude ecosystems have experienced more pronounced climate warming than other parts of the globe in recent decades, and are projected to continue to warm rapidly in the future (IPCC, 2013). This rapid warming will lead to plant range shifts, changes in species composition, and variation in peat accumulation rate and carbon sequenstration (Elmendorf et al., 2012; Yu, 2012; Kuhry et al., 2013). Shrub-dominated communities (e.g. Betula, Salix and Alnus) are increasing in cover and height (Myers-Smith et al., 2011; Ropars and Boudreau, 2012), and fires are becoming more frequent in high-latitude ecosystems (Rocha et al., 2012; Young et al., 2016). The expansion of shrubs restricts the growth of other plant species by limiting light availability and exacerbating the frequency and intensity of fire regime. To date, most data on the response of plant communities to recent warming come from observational and experimental studies (e.g. Callaghan et al., 2004; Hollister et al., 2005; Post et al., 2009; Elmendorf et al., 2012; Oberbauer et al., 2013; Edwards and Henry, 2016), with comparatively few studies examining changes on centennial to millennial temporal scales (e.g. Oswald et al., 2003; Gajewski, 2015; Teltewskoi et al., 2016; Treat et al., 2016). In addition, there are major limitations in our understanding of the tolerance of tundra species to fire (Racine et al., 2004; Higuera et al., 2011; Bret-Harte et al., 2013). Therefore, detailed long-term palaeoecological studies of permafrost peatlands are needed to improve understanding of relationships between climate, vegetation, fire, and hydrology, with implications for elucidating the response of high-latitude vegetation to climate warming (Bigelow et al., 2003; Gao and Couwenberg, 2015; Swindles et al., 2015a; Fritz et al., 2016).

Peatlands in the Arctic are important archives of palaeoenvironmental data owing to their sensitivity to climatic and hydrological change (Turetsky et al., 2002; Lamarre et al., 2012). Rising temperatures have driven partial or complete thawing of permafrost peatlands in many arctic regions (Biskaborn et al., 2015). Northern Alaska has experienced rapid climate warming during the twentieth century, degradation of permafrost peatlands and deepening of the active layer (Raynolds et al., 2014). Furthermore, climate models project continued marked temperature increases in the near future in this region (IPCC, 2013). Previous palaeoecological studies conducted in the Arctic including Alaska (Oswald et al., 2003, 2014) and Siberia (Minke et al., 2007; Zibulski et al., 2013; Teltewskoi et al., 2016) indicate that the nature of the soil substrate and microrelief play important role on how tundra environments respond to climate change.

In this study we present the first multiproxy late Holocene (the last 2000 years) palaeoecological dataset (plant macrofossils, pollen, testate amoebae, charcoal) from peat profiles in the Toolik region, Alaskan Arctic (northern foothills of the Brooks Range). We use these data to examine the long-term dynamics of plant communities in arctic peatlands and potential drivers of change. We evaluate the influence of changes in climate and anthropogenic disturbances versus autogenous succession in the development of arctic plant communities. We focus on the late Holocene because this period contains several phases of marked climate change (PAGES 2k Consortium, 2013). During the time covered in this study, warm periods such as the Roman Period and Medieval Climate Anomaly were separated by cold intervals (Migration Period and the Little Ice Age). We hypothesize that during past warm climatic episodes moss and vascular plant-dominated vegetation communities were replaced by shrub-dominated communities. In addition, we hypothesize that a similar shift is observed in recent decades related to rapid climate warming.

2. Study sites

Our study area is located in northern Alaska, close to the northern foothills of the Brooks Range, near the Toolik Field Station run by the University of Alaska Fairbanks (Fig. 1). The Toolik Lake area (68° 37' N, 149° 32' W) was deglaciated about 10,000 cal yr BP (Hamilton, 1986). The Toolik landscape is dotted with small glacial lakes, kames, and moraines. Elevations range from about 670 to 850 m asl. The climate of the region is continental arctic with mean monthly temperatures ranging from -22.5 °C (January) to 11.2 °C (July), and annual precipitation of ca. 250 mm over the period 1989-2007 (Toolik Field Station, EDC, https://toolik.alaska.edu/edc/about/conditions_of_use.php.). The vegetation in wetter habitats at our sampling sites is dominated by Sphagnum spp., Tomentypnum nitens, Paludella squarrosa, Carex spp., Andromeda polifolia, Salix reticulata and Betula nana. Drier habitats are characterised by Betula nana, Dryas octopetala, Salix spp., Empetrum nigrum, Polygonum bistorta, Rubus chamaemorus, Aulacomium turgidum, and Hylocomnium splendens. For further information on the contemporary plant commuinites at Toolik refer to Walker et al. (1994).

3. Material and methods

3.1. Peat sampling and chronology of the profiles

Two short peat monoliths (8x8 cm), TFSI (45 cm long) and TFSII (50 cm), were sampled from sampling locations 290 m apart. The monoliths were taken from the thickest peat layer in a small hummock microform in each location. Our excavation shows that peat formed directly over bedrock in both locations. The peat profiles were wrapped in plastic film and sent by courier to the laboratory in Poznań. In the laboratory the monoliths were unpacked, cleaned and sliced into 1-cm slices using a scalpel.

Four AMS (Accelerator Mass Spectrometry) radiocarbon dates on hand-picked plant macrofossils and one bulk AMS data were used to provide chronology for TFSI. Five AMS dates on macrofossils were carried out for TFSII (Appendix 1). Radiocarbon dating was undertaken at the Poznań Radiocarbon Laboratory. The calibration of the radiocarbon dates and the construction of the age depth models were performed with OxCal 4.1 software

(Bronk-Ramsey, 2009) and the IntCal13 curve (Reimer et al., 2013) applying a P_Sequence function with a k parameter of 1 cm^{-}1 and 1-cm resolution. Distinct changes in the peat composition, which might indicate a change in accumulation rate, were introduced using the “boundary” command (Fig. 2). The modelled ages are expressed as calendar years BC (Before Christ)/AD (Anno Domini).

Palaeoecological data presented in this paper are compared to palaeoclimate compilations from Arctic and North America (PAGES 2k Consortium 2013).

3.2. Plant macrofossil analysis

The analysis of plant macrofossil remains reveals a record of local plant communities and hydrological conditions (Barber et al., 2004; Mauquoy et al., 2008). Plant macrofossils were analysed contiguously at 1-cm intervals, resulting in 95 samples for both profiles. Samples of 20 cm^3 were washed and sieved under a warm-water spray using a 0.20-mm mesh sieve. Initially, the entire sample was examined with a stereomicroscope to obtain volume percentages of individual subfossils of vascular plants and mosses. The subfossil carpological remains and vegetative fragments (leaves, rootlets, epidermis) were identified using identification keys (Smith, 2004; Mauquoy and van Geel, 2007). Refer to Gałka et al. (2017a) for a detailed methodology for plant macrofossil analysis in peatlands.

3.3. Pollen and non-pollen palynomorph analysis

Pollen analysis provides information on vegetation composition and abundance at a regional scale (Berglund et al., 1996). Samples of 1 cm^3 at mainly 2-cm intervals were prepared using the standard procedure of Erdtman’s acetolysis (Berglund and Ralska-Jasiewiczowa, 1986). Analysis was carried out with an Olympus BX43 light microscope with a magnification of 600×; a larger magnification was used to identify problematic microremains. Owing to low pollen concentration, 390 (min=150; max=780) in TFSI and 270 (min=140; max=540) in TFSII terrestrial pollen grains were counted on average per sample. For taxonomical identification, pollen keys (Beug, 2004; Demske et al., 2013) and reference collection at University of Białystok were used. Reliable discrimination between pollen of Betula species was problematic and it was therefore presented as one group without further separation. However, Betula nana is the most common birch species in our study region, and this may indicate that most of fossil birch pollen belongs to B. nana. Non-pollen palynomorphs (NPPs) were counted alongside the pollen. NPPs were identified according to van Geel (1978) and Shumilovskikh et al. (2015). The arboreal pollen (AP) + non-arboreal pollen (NAP) sum was used for percentage calculations. The pollen diagram was stratigraphically ordered and zoned into local pollen assemblage zones (LPAZ) using constrained cluster analysis (CONISS, Grimm, 1987). Nomenclature follows Walker et al. (1994) for vascular plants, Flora of North America Editional Comittee (2007) for bryophytes.

3.4. Micro- and macro-charcoal analysis

We counted micro-charcoal (particles smaller than 150 μm) in our pollen slides and interpret these as an indicator of biomass burning at regional spatial scales. Micro-charcoal particles were counted along with the pollen and were grouped into three size classes: 10-30, 30-100 and 100-150 μm (e.g. Rull, 2009). Micro-charcoal particles were quantified as a percentage of the total terrestial pollen sum (AP+NAP). Macro-charcoal particles (larger than 160 μm) were used to investigate fire activity at a local scale (Whitlock and Larsen, 2001). Macro-charcoal anaylsis on a 2 cm volume of peat was undertaken at 1-cm contiguous intervals at TFSII and at 2 cm interval at TFSI. The methodology is outlined in Feurdean et al. (2017), and includes bleaching, wet-sieving through a 160 μm mesh, and identification and counting the total number of particles (opaque, angular characteristics) using a stereomicroscope. Macro-charcoal values are expressed as concentration (particles/cm^3).

3.5. Testate amoebae

We used subfossil testate amoebae (Protists) to examine hydrological changes through time (cf. Booth, 2008; Swindles et al., 2015a,b). Testate amoebae were extracted from TFSII using a modified version of Booth et al. (2010). Peat samples (2 cm^3) taken in 4-cm resolution were placed in boiling water for 15 minutes and shaken. Extracts were passed through a 300 µm sieve, back-sieved at 15 µm and allowed to settle before sub-samples were used to make slides for microscopy. A total of between 100 and 200 amoebae were counted and identified to species level or 'type' in each sample using high-power transmitted light microscopy at 200 to 400x magnification. For further detailed information on taxonomy and sources used see Swindles et al. (2015b). No transfer function is available for the Toolik region and other models are inappropriate for continuous permafrost peatlands. Therefore, we used the simpler approach of calculating total percentage of wet indicators.

4. Results

4.1. Chronology and lithology

Radiocarbon data for both profiles are presented in Appendix 1 and the age-depth model is shown in Fig. 2. In TFSI the peat has accumulated since ca. AD 650 (the last 700 years) and in TFSII since ca. 150 BC (i.e the past 2150 years). The lowermost units of both profiles (45-21 cm (ca. AD 650-1960) in TFSI and 55-15 cm (ca. 150 BC-AD 195) in TFSII contain herbaceous peat composed mainly of remains of Cyperaceae and Sphagnum species. Peat composed mainly of Sphagnum remains was recorded in the upper part of both profiles.

4.2. Plant macrofossil analysis

Three phases of local vegetation development in TFSI (Fig. 3A) and four phases in TFSII were visually delimited(Fig. 3B). The first phase TFSI-ma-1 (AD 650-870) is characterized by the dominance of Carex sp. macrofossils and the presence of shrub macrofossils: Andromeda polifolia, Betula nana, Empetrum nigrum, and Salix sp. Numerous unknown fungal remains were also recorded. During phase TFSI-ma-2 (AD 870-1960) Carex spp. remained dominant and Sphagnum cf. warnstorfii and Selaginella selaginoides were also noted. In phase TFSI-ma-3 (1960-2015) Sphagnum capillifolium and Sphagnum fuscum become dominant species. A continuous present of dwarf shrubs such as A. polifolia and B. nana were also observed.

In TFSII, A. polifolia and E. nigrum were recorded during the first phase (TFSII-ma-1; 150 BC-AD 250). Phase TFSII-ma-2 (AD 250-1200) is characterised by numerous Carex sp. fruits and the appearance of S. capillifolium. Macrofossils of shrubs including B. nana and Salix sp. were also present. In phase TFSII-ma-3 (AD 1200-1950), a decrease of Carex sp. fruits is observed, whereas Equisetum sp. and S. cf. warnstorfii appear for the first time. In phase TFSII-ma-4 (1950-2015), S. capillifolium and Pleurozium schreberii were dominant. Numerous macrofossils of B. nana and A. polifolia were also observed.

4.3. Pollen, spore and NPP analysis

Our sites are located in an open landscape and it is likely that pollen grains are able to disperse over great distances (Sugita, 1994). The pollen source area is probably in the range of 10 to 100 km^2, reaching the boreal forest south of the Brooks Range. The pollen sum in the upper part of the profiles is based on rather low pollen counts (200 grains), reflecting low pollen concentrations in the samples, which could affect the reliability of our interpretations (especially for minor taxa).

Four pollen zones, representing regional and local vegetation development were numerical delineated at TFSI (Fig. 4). The basal zone TFSI-po-1 (AD 650-1550) is characterised by moderate high pollen percentages of Cyperaceae, Poaceae, Asteraceae and Brassicaceae, while other herbaceous taxa are present sporadically (Fig. 4). Percentages of Betula pollen increase to 32% in the upper part of this zone. Zone TFS1-po-2 (ca. AD1550-1700) is characterised by an increase in Cyperaceae (up to 75.5%) and Alnus (up to 13.5%), and a more frequent occurrence of Ericaceae, Rubus chamaemorus, and Artemisia pollen. In zone TFSI-po-3 (ca. AD 1700-1950) there is a prominent increase of Cyperaceae pollen up to 79%, while Betula and Alnus pollen percentages decline. Spores of Huperzia, Bryales and Sphagnum are abundant. Zone TFS1-4 (ca. AD 1950-2015) was divided into three subzones. Subzone TFSI-4a (ca. 1950-1980) is characterised by a marked increase in tree and shrub pollen percentages – Betula (up to 30%), Picea (up to 16%), Alnus (up to 19%). Artemisia (up to 3.5%) and Cyperaceae pollen percentages (to 29%) decline. NPPs including the remains of Amphitrema, Assulina, Arcella and spores of Xylariaceae and Erysiphales fungi show an abrupt increase. In subzone TFSI-po-4b (ca. 1980-2000) there is a peak of Cyperaceae pollen percentages to 47%. The proportion of Alnus increases but Picea and Betula decreases. Sphagnum spore percentages rise markedly to 78.5%. In subzone TFSI-po-4c (ca. 2000-2015) the proportion of trees and shrubs including Betula, Picea and Ericaceae abruptly increases, while Cyperaceae and Alnus decrease.

Four pollen zones were numerically delineated at in TFSII (Fig. 4). The first zone TFSII-po-1 (ca. 150 BC-AD 600) is characterised by the dominance of Cyperaceae pollen (up to 66%). Poaceae and Asteraceae pollen percentages are consistently below 2%. Betula and Alnus pollen percentages range from 6 to 15.5%, and from 10 to 14.5%, respectively. The abundance of Picea pollen reaches 11% in the lower part of this zone, then declines to 4%. Zone TFSII-po-2 (ca. AD 600-1050) is characterised by higher Betula (up to 26%), Salix (up to 6%), Picea (up to 6.5%) and Alnus (up to 15%) pollen percentage values. The proportion of Ericaceae, Poaceae, Saxifragaceae and Artemisia pollen also increases substantially. In zone TFSII-po-3 (AD 1050-1800) Cyperaceae pollen percentages reach 80% with a simultaneous decline of Betula and Salix. The occurrence of Sphagnum and Equisetum spores increases in this zone. Zone TFSII-po-4 (ca. 1800-2015) was divided into three subzones. Subzone TFSII-po-4a (ca. AD 1800-1970) is characterised by rise of Betula (up to 18%), Picea (up to 12.5%) and Alnus (up to 31.5%) pollen percentages, together with a decrease in Cyperaceae (to 36%). Palynomorphs including the remains of Amphitrema, Assulina, Arcella and spores of Xylariaceae showed an abrupt increase. In subzone TFSII-po-4b (ca. 1970-2005) there is the greatest peak of Cyperaceae pollen (to 84%) and a decrease of tree pollen (Betula, Picea and Alnus). In subzone TFSII-po-4c (ca. AD 2005-2015) the proportion of Betula, Picea, Alnus and Ericaceae pollen abruptly increases, while Cyperaceae pollen percentage decreases.

4.4. Testate amoebae

Samples were barren of testate amoebae from 48 to 50 cm (150 BC-AD 1). Four zones in the testate amoebae profile were identified in TFSII (Fig. 5). The first zone, TFSII-ta-1 (AD 1-1050), is characterised by a small number of specimens (insignificant counts <50 specimens) of Centropyxis aerophila (up to 100%) from a poorly-preserved assemblage. In the second zone, TFSII-ta-2 (ca. AD 1050-1970), there is a decrease in the abundance of Centropyxis aerophila, and appearance of twenty new taxa of testate amoebae including Centropyxis platystoma, Phryganella acropodia, and Trigonopyxis arcula. In the upper part of this zone there is a peak of Hyalosphenia elegans (up to 58%). In TFSII-ta-3 phase (ca. AD 1970-2015) Assulina muscorum, Corythion dubium and Nebela tincta are dominant suggesting a return to relatively dry conditions. Richness and Shannon diversity index values decrease with depth, highlighting the poorer preservation of tests in the lower part of this profile.

4.5. Micro- and macro-charcol

The patterns in micro-charcoal percentages and macro-charcoal concentration show good agreement at both sampling locations (Figs. 6, 7). Generally macro-charcoal counts are low (ranging from 0-5 pieces per sample). However, periods of increased micro- and macro-charcoal values are recorded between AD 650 and 2000 at both sites. Intervals of elevated macro-charcoal concentrations are also noted between AD 150 and 500 at TSF II.

5. Discussion

5.1. Peatland initiation processes

Basal peat dates indicate that the timing for initial peat formation at the two sites differed by ca. 400 years; ; it started at 150 BC in TFSII and ca. AD 650 in TFSI. This difference can potentially be related to local topographical and hydrological variation (Weckström et al., 2010; Loisel et al., 2013**)**. MacDonald et al. (2006) and Beilman et al. (2010) recorded various age of peatland initiation in the circumarctic zone. According to data presented by Reyes and Cooke (2011) the timing of most rapid peat initiation in northern peatlands in Alaska took place between 8 and 10 ka BP. However, a basal peat age of >10,000 years old from a site close to our study sites may indicate that peat accumulation started much earlier in some places in this region (Eisner, 1991; Jones and Yu, 2010). Hence, peat initiation in the Toolik region may have begun earlier than we document here.

In the bottom part of both peat profiles the main peat-forming plants included Cyperaceae (Fig. 2, phase A; Fig. 3, phase A). The presence of Carex fruits and rootlets, as well brown mosses in both sites may indicate that during this initial phase the peatlands were fens that developed through paludification. In the bottommost part of profile TFSI (between ca. AD

650-800) Sphagnum cf. contortum and S. cf. Sphagnum warnstorfii remains were also present. These species occur in minerotrophic habitats and are common in medium to rich fens indicates slightly wetter conditions at this time (McQueen and Andrus, 2007). This wetland type is widespread in the permafrost region of the Northern Hemisphere (Vardy et al., 1998; Kuhry, 2008; Teltewskoi et al., 2016; Treat et al., 2016).

5.2. Response of vegetation to warming climate

Palaeoecological studies, recent field monitoring, experimental studies and modeling approaches show that climate warming can drive changes from more open tundra communities towards increased cover of vascular plants and shrubs including Betula, Salix, Alnus spp. (Oechel et al., 1997; Sturm et al., 2001; Myers-Smith et al., 2011; Ropars and Boudreau, 2012; Gałka et al., 2017b). Moreover, Gajewski (2015) indicated that Arctic ecosystems seem to be more productive during warm periods in the past. The author stressed that the history of the Arctic vegetation in response to past climate variations is complex, but generally when temperatures (reconstructed by pollen) are higher plant biomass and/or cover is greater. Our long-term records close to the Toolik station show periodic expansions of shrubs in the Toolik region, especially within the peatlands themselves, that could potentially be linked to warm climatic stages in the late Holocene. We identified three periods of shrub expansion ca. 150 BC-AD 400, AD 650-1250, and after AD 1850 (Fig. 6, zone A and C; Fig. 7, zones A, C, and E). These periods correspond to warm climatic intervals reconstructed from proxy compilations for Arctic and North America (PAGES 2k Consortium 2013; marked on the Fig. 6 and Fig. 7). During the first warm period (ca. 150 BC and AD 400), we found macrofossils of Andromeda polifolia, Empetrum nigrum, and an increase of Ericaceae pollen. At ca. AD 350 we recorded increased Salix pollen. There were low levels of charcoal throughout the record, however, a slight increase in macro-charcoal concentration is also noted at this time and suggests either a small increase in fire local occurrence or background charcoal from boreal forest fires south of the Brooks Range. The absence of microcharcoal particles would support the inference of local fire activity. Low background charcoal accumulation rates are common for arctic Alaska (Chipman et al., 2015).

Vegetation response to warmer climate is also suggested by an increase in Picea pollen percentage, indicating its range expanded or pollen productivity increased at these times. Low pollen percentages of Picea (up to 11%) at ca. AD 50 is likely associated with long distance pollen transport by air mass movement from population of Picea mariana and Picea glauca located at the southern foothills of the Brooks Range. Picea pollen percentages <20% in Canada are typically assumed to represent long distance transport (King, 1993).

High relative abundance of fungi remains (sclerotia) in peats formed between ca. 150 BC and AD 200 and the presence of macro-scopic charcoal indicate dry hydrological conditions.

The second interval characterized by increased micro- and macro shrub remains (e.g. Ericaceae, Betula nana) in both peat profiles, and the maximum amount of Salix pollen (6% in one sample) in TFSII is dated at from AD 650 to 1250 (Fig. 7, zone C). The rise in pollen percentages of other herbaceous plants (eg. Rubus chamemorus, Artemisia and Saxifraga) may represent their local expansion and/or increased pollen productivity in response to higher temperature at this time. Increased Artemisia pollen could be derived from Artemisia arctica ssp. arctica, a common species in this region (Walker et al., 1994). There are many species of Saxifraga occurring in the study area in the present day (Walker et al., 1994), and therefore it is difficult to relate the pollen of Saxifraga to an individual species. On the other hand, Panchen & Gorelick (2015) found no relationship between flowering and fruting time and warming climate for Saxifraga oppositifolia in Arctic Canada (Tanquary Fiord). Furthermore, the highest amount of Carex sp. fruits are found between AD 700 and 1100 and may suggest the positive role of climate warming on fruiting and increase of ability to generative reproduction of this genus. We also recorded a temporary increase of micro- and macro-charcoal values during this period (Fig. 7). Greater fire activity at this time in the Toolik region agrees with some paleofire records from Upper Capsule Lake, located in the Brooks Range Foothills ecoregion (Chipman et al., 2015). However, past patterns of tundra fires in Alaska appear to be spatially variable with little syncroneicity among sites (Chipman et al. 2015).

An increase of Alnus, Betula and Picea pollen percentages since ca. AD 1850 in TFSII coincides with climate warming after the Little Ice Age (LIA) in the Arctic (Overpeck et al., 1997), and subsequent expansion of Ericaceae, Andromeda polifolia, and Betula nana shrubs between AD 1900 and 1950 is coherent with the marked temperature rise recorded in Alaska (Overpeck et al., 1997). Dry conditions at these times are suggested by increased peat decomposition, numerous fungi remains and the colonization of Sphagnum species typical of dry habitats eg. Sphagnum fuscum or Sphagnum capillifolium (Fig. 7, zone E). Based on the micro- and macro-charcoal data local and regional fire events occurred in the first part of this period. A documented fire close to Anaktuvuk River occurred in 2007, but the absence of micro-, and macro-charcoal in the most upper part of both profiles suggest that our charcoal record may underestimate past fire activity. Similar to our finding, charcoal from the 2007 fire event has been recorded in some sites from this region, whereas other sites show no charcoal related to this event (Chipman et al., 2014).

A temporally-short lived increase of water table level ca. AD 1950 is indicated by abundant presence of the testate amoeba Hyalosphenia elegans, a species that usually occurs in wet habitats (Swindles et al., 2015b). An increase of water level at this time at sampling site is also supported by the re-apperance of Equisetum sp. (macrofossils) and Cyperaceae (pollen) that are most interpreted as wet indicators (Kuhry, 2008). Dry hydrological conditions during the most recent decades is clearly illustrated by the presence of mosses

Aulacomnium turgidum and Pleurozium schreberi (Fig. 7, zone E), species which usually occur in dry habitats (Smith 2004), alongside the presence of dry-indicator testate amoebae including Assulina muscorum, Corythion dubium and Nebela tincta (Swindles et al., 2015b).

5.3. Response of vegetation to cold climatic changes

Distinctive changes in plant communities are manifested by the reduction of shrubs (Ericaceae, Salix) and/or a decline in pollen production between AD 1250-1850. (Fig. 6, zone B; Fig. 7, zone D). This vegetation change concides with colder climatic conditions during the LIA (PAGES 2k Consortium, 2013). Interestingly, Gajewski (2015) indicated that there is even evidence for the disappearance of Arctic plant taxa in response to cool periods of the late Holocene. Although palaeoclimatic reconstructions from northern Alaska indicate unstable temperature conditions with short-term warm spells during the Little Ice Age (Anchukaitis et al., 2013; Boldt et al., 2015), we did not identify any temporary expansion of shrubs related to such short-temporal warm events. Only small peaks of Salix, Ericaceae and Rubus chamaemorus pollen percentages were observed between AD 1550 and 1650 (Fig. 6, zone B). An increase in micro- and macro-charcoal between ca. AD 1000 and 1600 suggest that fires were more common at this time and likely associated with accumulation of dry biomass during dry or dry/warm climate conditions. Tinner et al. (2015) stressed that in Alaska high fire activity in boreal region could be interpreted as a response to dry climate, but also noted that fire occurred during the cool climate of the LIA (Tinner et al., 2008). The decrease of Betula, Alnus, and Picea pollen we observe in the upper part of both profiles may be linked to a decrease in pollen productivity as a response to a recent colder period noted in Arctic North America between AD 1960 and 1985 (Hudson and Henry, 2009; https://earthobservatory.nasa.gov).

5.4. Periodic Sphagnum community development. Impact of climate change or autogenic succession?

Plant communities dominated by Sphagnum species started developing during warm climatic stages at ca. AD 700, 1200, and 1900 (TFS I - Fig. 6) and ca. 350, 1050 and 1950 (TFSII) and then disappeared during cold phases ca. AD 1250 (TFSI) and at ca. AD 500 and 1700 (TFSII - Fig. 6 and Fig. 7). This may suggest that climatic and environmental conditions during cold/wet climatic stages were not favorable for Sphagnum colonization and sustenance Cold climatic conditions (e.g. low temperatures, long-term snow cover and shorter growing season) might have been detrimental to Sphagnum, as during cold periods, Sphagnum spp. (Sphagnum capillifolium and S. warnstorfii) were replaced by Carex spp. and other vascular plants owing to wetter conditions in the peatland when it was not completely frozen. The appearance of Sphagnum during warm periods may thus partly result from deepening of peatland water tables. Loisel and Yu (2013b) proposed that recent warming has led to Sphagnum establishment in wet boreal peatlands in Alaska, because the peatlands become drier and nutrient poorer. Indeed, certain Sphagnum species are resistant to deeper water tables e.g. Sphagnum fuscum, S. capillifolium (Andrus, 1986; Hölzer, 2010).

The lack of surface and groundwater influence under prolonged warmer/drier conditioncan allow Sphagnum to expand in rich fens and cause a shift to a poor fen or bog within decades (Granath et al., 2010; Tahvanainen, 2011). Sphagnum species are common during rich fen-poor fen transitions and play an important role in peat accumulation and its acidification (Overbeck, 1975; Kuhry et al., 1992, 1993). The paleohydrological changes that have triggered periodic development of Sphagnum populations at both sites probably result from the processes described above, and did not from periodic permafrost degradation, because the thin peat layer accumulated directly over bedrock. A periodic appearance of various Sphagnum species triggered by permafrost degradation was observed in subarctic

Canada (Zoltai, 1993; Kuhry, 2008). However, the high capacity of Sphagnum species to cope with environmental variability and a high level of acclimatization through mechanisms of resistance was also documented (Rydin and Barber, 2001; Gunnarsson et al., 2002; Zona et al., 2011). Furthermore, the lack of macro-charcoal particles in peat layers with Sphagnum suggests that fire did not drive the disappearance of Sphagnum. Changes in Sphagnum populations may partly result from autogenic drivers of peatland development. Plant autogenic succession is also an important factor to be considered when examining peatland development (Swindles et al., 2012; Loisel and Yu, 2013a; Gałka et al., 2017a, b). The lack of other detailed plant macrofossil data from peats in this region do not allow a deeper understanding of local plant succession. However, detailed palaeobotanical studies in different habitat from a polygon mire from Arctic Russia suggested that local plant succession can link to both climatic changes and local microrelief (Zibulski et al., 2013; Teltewskoi et al., 2016).

Our work represents the first detailed multiproxy study (using plant macrofossils, pollen and testate amoebae) to understand the response of peatland plant communities in northern Alaska to climate change, and provides some insights into how these ecosystems might respond under future climate warming. However, further work is needed in this region to improve our understanding of the dynamics of these unique arctic ecosystems.

6. Conclusions

1. We observed an increase in the abundance of shrub macrofossils and pollen (e.g. Ericaceae, Betula nana, and Salix) in two peatlands during late Holocene warm climate periods. The increase in shrub abundance is even more pronounced in recent decades along with an increase in Picea pollen percentages (up to 13%), likely originating from populations of Picea mariana and Picea glauca growing in the southern foothills of the Brooks Range.

2. We suggest that local plant succession in peatlands was a response to changes in climate. However, autogeneous plant succession during peatland development towards ombrotrophic status was also an important driver.

3. Relatively small amount of micro- and macro-charcoal in both peat profiles indicate low fire activity over the last ca. 2000 years, which is in agreement with regional fire activity trends in Artic Alaska.

4. The lack of surface and groundwater influence under prolonged warmer/drier condition can allow Sphagnum to expand in Arctic peatlands. Cold climatic conditions might have been detrimental to Sphagnum populations, that were replaced by Carex spp. and other vascular plants owing to wetter conditions on the peatland.

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References

Anchukaitis, K.J., D'Arrigo, R.D., Andreu-Hayles, L., Frank, D., Verstege, A., Curtis, A., Buckley, B.M., Jacoby, G.C., Cook, E.R. 2013. Tree-ring-reconstructed summer temperatures from northwestern North America during the last nine centuries. J. Cli. 26, 3001-3012.

Andrus, R.E. 1986. Some aspects of Sphagnum ecology. Can. J. Bot. 64, 416-426.

Barber, K.E., Chambers, F.M., Maddy, D., 2004. Late Holocene climatic history of northern Germany and Denmark: peat macrofossil investigations at Dosenmoor, Schleswig-Holstein, and Svanemose, Jutland. Boreas 33, 132-144.

Beilman, D.W., MacDonald, G.M., Yu, Z., 2010. The northern peatland carbon pool and the Holocene carbon cycle. PAGES news 18, 22-25.

Berglund, B.E., Barnekow, L., Hammarlund, D., Sandgren, P., Snowball, I.F., 1996. Holocene forest dynamics and climate changes in the Abisko area, northern Sweden – The Sonesson model of vegetation history reconsidered and confirmed. Ecol. Bull. 45, 15-30.

Berglund, B.E., Ralska-Jasiewiczowa, M., 1986. Pollen analyses and pollen diagrams. In Handbook of Holocene palaeoecology and palaeohydrology, Berglund BE (ed.). pp. 455-484. John Wiley, Chichester.

Beug, H.J. 2004. Leitfaden der Pollenbestimmung für Mitteleuropa und angrenzende Gebiete. Pfeil, München.

Bigelow, N.H., Brubaker, L.B., Edwards, M.E., Harrison, S.P., Prentice, I.C., Anderson, P.M., Andreev, A.A., Bartlein, P.J., Christensen, T.R., Cramer, W., Kaplan, J.O., Lozhkin, A. V., Matveyeva, N.V., Murray, D.F., McGuire, A.D., Razzhivin, V.Y., Ritchie, J.C., Smith, B., Walker, D.A., Gayewski, K., Wolf, V., Holmqvist, B.H., Igarashi, Y., Kremenetski, K., Paus, A., Pisaric, M.F.J., Volkova V.S., 2003, Climate change and Arctic ecosystems: 1. Vegetation changes north of 55°N between the last glacial maximum, mid-Holocene, and present. J. Geophys. Res. D: Atmospheres 108, 8170.

Biskaborn, B.K., Lanckman, J.-P., Lantuit, H., Elger, K., Streletskiy, D.A., Cable, W.L., Romanovsky, V.E., 2015. The Global Terrestrial Network for Permafrost Database: metadata statistics and prospective analysis on future permafrost temperature and active layer depth monitoring site distribution. Earth Syst. Sci. Data Discuss. 8, 279-315.

Boldt, B.R., Kaufman, D.S., McKay, N.P., Briner, J.P., 2015. Holocene summer temperature reconstruction from sedimentary chlorophyll content, with treatment of age uncertainties, Kurupa Lake, Arctic Alaska. Holocene 25, 641-650.

Booth, R.K., 2008. Testate amoebae as proxies for mean annual water-table depth in Sphagnum-dominated peatlands of North America. J. Quat. Sci. 23, 43-57.

Booth, R.K., Lamentowicz, M., Charman, D.J., 2010. Preparation and analysis of testate amoebae in peatland paleoenvironmental studies. Mires and Peat 7, 1-7.

Bronk Ramsey, C., 2009. Bayesian analysis of radiocarbon dates. Radiocarbon 51, 337-360.

Callaghan, T.V., Bjorn, L.O., Chernov, Y., Chapin, T., Christensen, T.R., Huntley, B., Ims, R.A., Johansson, M., Jolly, D., Jonasson, S., Matveyeva, N., Panikov, N., Oechel, W., Shaver, G., Henttonen, H., 2004. Effects on the function of arctic ecosystems in the short- and long-term perspectives. Ambio 33, 448-458.

Chipman, M.L., Hudspith, V., Higuera, P.E., Duffy , P.A., Kelly, R., Oswald, W.W., Hu, F.S., 2015. Spatiotemporal patterns of tundra fires: late-Quaternary charcoal records from Alaska. Biogeosciences 12, 4017-4027.

Demske, D., Tarasov, P.E., Nakagawa, T., 2013. Atlas of pollen, spores and further non-pollen palynomorphs recorded in the glacial-interglacial late Quaternary sediments of Lake Suigetsu, central Japan. Quatern. Int. 290-291, 164-238.

Edwards, M., Henry, G.H.R., 2016. The effects of long-term experimental warming on the structure of three High Arctic plant communities. J. Veg. Sci. 27, 904-913.

Eisner, W.R., 1991. Palynological Analysis of a Peat Core from Imnavait Creek, the North

Slope, Alaska. Arctic 44, 279-282.

Elmendorf, S.C., Henry, G.H.R., Hollister, R.D., Bjork, R.G., Bjorkman, A.D., Callaghan, T.V., Collier, L.S., Cooper, E.J., Cornelissen, J.H.C., Day, T.A., Fosaa, A.M., Gould, W.A., Gretarsdottir, J., Harte, J., Hermanutz, L., Hik, D.S., Hofgaard, A., Jarrad, F., Jonsdottir, I.S., Keuper, F., Klanderud, K., Klein, J.A., Koh, S., Kudo, G., Lang, S.I., Loewen, V., May, J.L., Mercado, J., Michelsen, A., Molau, U., Myers-Smith, I.H., Oberbauer, S.F., Pieper, S., Post, E., Rixen, C., Robinson, C.H., Schmidt, N.M., Shaver, G.R., Stenstrom, A., Tolvanen, A., Totland, O., Troxler, T., Wahren, C.-H., Webber, P.J., Welker, J.M., Wookey, P.A., 2012. Global assessment of experimental climate warming on tundra vegetation: heterogeneity over time and space. Ecol. Lett. 15, 164-175.

Environmental Data Center Team. Year of data retrieval. Meteorological monitoring program at Toolik, Alaska. Toolik Field Station, Institute of Arctic Biology, University of Alaska Fairbanks, Fairbanks, AK 99775. http://toolik.alaska.edu/edc/abiotic_monitoring/data_query.php.

Feurdean, A., Florescu, G., Vanniere, B., Tanţău, I., O'Hara, R.B., Pfeiffer, M., Hutchinson, S.M., Gałka, M., Moskal-del Hoyo, M., Hickler, T., 2017. Fire has been an important driver of forest dynamics in the Carpathian Mountains during the Holocene. Forest Ecol. Manag. 389, 15-26.

Flora of North America North of Mexico. 2007. Vol. 27. New York and Oxford. Oxford University Press.

Fritz, M., Wolter, J., Rudaya, N., Palagushkina, O., Nazarova, L., Obu, J., Rethemeyer, J., Lantuit, H., Wetterich, S., 2016. Holocene ice-wedge polygon development in northern Yukon permafrost peatlands (Canada). Quat. Sci. Rev. 147, 279-297.

Gajewski, K., 2015. Impact of Holocene climate variability on Arctic vegetation. Global and Planet. Change 133, 272-287.

Gałka, M., Tobolski, K., Lamentowicz, Ł., Ersek, V., Jassey, V.E.J., van der Knaap, W.O.. Lamentowicz, M., 2017a. Unveiling exceptional Baltic bog ecohydrology, autogenic succession and climate change during the last 2000 years in CE Europe using replicate cores, multi-proxy data and functional traits of testate amoebae. Quat. Sci. Rev. 156, 90-106.

Gałka, M., Szal, M., Watson, E.J., Gallego-Sala, A., Amesbury, M.J., Charman, D.J., Roland, T., Turner, T.E., Swindles, G.T. 2017b. Vegetation succession, carbon accumulation and hydrological change in sub-Arctic peatlands (Abisko, northern Sweden). Permafrost Periglac.. DOI: 10.1002/ppp.1945.

Gao, Y., Couwenberg, J., 2015. Carbon accumulation in a permafrost poligon peatland:steady long-term rates in spite of shifts between dry and wet conditions. Global Change Biol. 21, 803-815

Granath, G., Strengbom, J., Rydin, H., 2010. Rapid ecosystem shifts in peatlands: linking plant physiology and succession. Ecology 91, 3047-3056.

Grimm, E.C., 1987. CONISS: a FORTRAN 77 program for stratigraphically constrained cluster analysis by themethod of incremental sum of squares. Comput. Geosci. 13, 13-35.

Gunnarsson, U., Malmer, N., Rydin, H., 2002. Dynamics or constancy in Sphagnum dominated mire ecosystems? A 40 year study. Ecography 25, 685-704.

Hamilton, T.D., 1986. Late Cenozoic glaciation of the Central Brooks Range. In: Hamilton, T.D., Reed, K.M., Thorson, R.M. (eds.) Glaciation in Alaska: the geologic record, pp. 9-49. Alaska Geological Society, Fairbanks, AK.

Higuera, P.E., Chipman, M.L., Barnes, J. L., Urban, M. A., Hu, F.S., 2011. Variability of tundra fire regimes in Arctic Alaska: millennial scale patterns and ecological implications. Ecol. App. 21, 3211-3226.

Hollister, R.D.,Webber, P.J., Tweedie, C.E., 2005. The response of Alaskan arctic tundra to experimental warming: differences between short- and long-termresponses. Global Change Biol. 11, 525-536.

Hölzer, A. 2010. Die Torfmoose Südwestdeutschlands und der Nachbargebiete. Weissdorn Verlag Jena, Jena.

Hudson J.M.G., Henry, G.H.R., 2009. Increased plant biomass in a High Arctic heath community from 1981 to 2008. Ecology 90, 2657-2663.

IPCC. 2013. Summary for Policymakers. In: Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Stocker TF, Qin D, Plattner DK, Tignor M, Allen SK, Boschung J, Nauels A, Xia Y, Bex V, Midgley PM (eds.). Cambridge University Press; Cambridge.

Jones, M.C., Yu, Z.C., 2010. Rapid deglacial and early Holocene expansion of peatlands in Alaska. Proc. Natl. Acad. Sci. U. S. A., 107, 7347-7352.

King, G.A., 1993. Vegetation and pollen relationships in eastern Canada. Canadian Journal of Botany, 71, 193-210.

Kuhry, P., 2008. Palsa and peat plateau development in the Hudson Bay Lowlands, Canada: Timing, pathways and causes. Boreas 37, 316-327.

Kuhry, P., Grosse, G., Harden, J.W., Hugelius, G., Koven, C.D., Ping, C.-L., Schirrmeister, L., Tarnocai, C., 2013. Characterisation of the permafrost carbon pool. Permafrost Periglac. 24, 146-155.

Kuhry, P., Halsey, L.A., Bayley, S.E., Vitt, D.H., 1992. Peatland development in relation to

Holocene climatic change in Manitoba and Saskatchewan (Canada). Can. J. Earth Sci. 29, 1070-1090.

Kuhry, P., Nicholson, B.J., Gignac, L.D., Vitt, D.H., Bayley, S.E., 1993. Development of Sphagnum dominated peatlands in boreal Continental Canada. Can. J. Bot. 71, 10-22.

Lamarre, A., Garneau, M., Asnong, H., 2012. Holocene paleohydrological reconstruction and carbon accumulation of a permafrost peatland using testate amoeba and macrofossil analyses, Kuujjuarapik, subarctic Quebec, Canada. Rev. Palaeobot. Palynol. 186, 131-141.

Loisel J, Yu Z., 2013a. Surface vegetation patterning controls carbon accumulation in peatlands. Geophys. Res. Lett. 40, 1-6.

Loisel, J., Yu, Z., 2013b. Recent Acceleration of Carbon Accumulation in a Boreal Peatland, South Central Alaska. J. Geophys. Res. 118, 41-53.

Loisel, J., Yu, Z., Parsekian, A., Nolan, J., Slater, L., 2013. Quantifying landscape morphology influence on peatland lateral expansion using ground penetrating radar (GPR) and peat core analysis. J. Geophys. Res.: Biogeosciences 118, 373-384.

Loranty M.M., Goetz S.J., 2012. Shrub expansion and climate feedbacks in Arctic tundra. Environmen. Res. Lett. 7: 011005.

MacDonald, G.M., Beilman, D.W., Kremenetski, K.V., Sheng, Y., Smith, L.C., Velichko, A.A., 2006. Rapid development of the circumarctic peatland complex and atmospheric CH4 and CO2 variations. Science 314, 285-288.

Mauquoy D, van Geel B., 2007. Mire and peat macros. In: Encyclopedia of Quaternary Science. Elias S.A. (ed.). pp. 2315-2336. Elsevier, Amsterdam.

Mauquoy, D., Yeloff, D., van Geel, B., Charman, D., Blundell, A., 2008. Two decadally resolved records from north-west European peat bogs show rapid climate changes associated with solar variability during the mid-late Holocene. J. Quat. Sci. 23, 745-763.

McQueen, C.B., Andrus, R.E. 2007. Sphagnaceae. In: Flora of North America Editorial Committee (eds.). Flora of North America North of Mexico. 27, pp. 45-101, Oxford University Press, New York and Oxford.

Minke, M., Donner, N., Karpov, N.S., De Klerk, P.R., Joosten, H., 2007. Distribution, diversity, development and dynamics of poligon mires: examples from Northeast Yakutia (Siberia). Peatlands Int. 1, 36-40.

Myers-Smith, I.H, Forbes, B.C., Wilmking, M., Hallinger, M., Lantz, T., Blok, D., Tape, K. D., Macias-Fauria, M., Sass-Klaassen, U., Lévesque, E., Boudreau, S., Ropars, P., Hermanutz, L., Trant, A., Collier, L.S., Weijers, S., Rozema, J., Rayback, S.A., Schmidt, N.M., Schaepman-Strub, G., Wipf, S., Rixen, C., Ménard, C.B., Venn, S., Goetz, S., Andreu-Hayles, L., Elmendorf, S., Ravolainen, V., Welker, J., Grogan, P., Epstein, H.E., Hik, D.S., 2011. Shrub expansion in tundra ecosystems: dynamics, impacts and research priorities. Environ. Res. Lett. 6: 045509.

Oberbauer, S.F., Elmendorf, S.C. Troxler, T., Hollister, R.D., Rocha, A.V., Bret-Harte, M.S., Fosaa, A.M., Hoye, T.T., Henry, G.H.R., Høye, T.T., Jarrad, F.C., Jónsdóttir, I.S., Klanderud, K., Klein, J.A., Molau, U., Rixen, C., Schmidt, N.M., Shaver, G.R., Slider, R.T., Totland, Ø., Wahren, C.-H., Welker, J.M., 2013. Phenological responses of tundra plants to background climate warming tested using the International Tundra Experiment. Philos. T. R. Soc. B. 368, 2012481.

Oechel, W.C., Callaghan, T.V., Gilmanov, T.G., Holten, J.I., Maxwell, B., Molau, U., Sveinbjörnsson, B. (eds)., 1997. Global change and Arctic terrestrial ecosystems. Springer-Verlag, New York, NY.

Oswald, W.W., Brubaker, L.B., Hu, F.S., Kling, G.W., 2014. Late-Quaternary Environmental and Ecological History of the Arctic Foothills, Northern Alaska. In: Alaska's Changing Arctic: Ecological Consequences for Tundra, Streams, and Lakes, pp. 81-89. Oxford University Press.

Oswald, W.W., Linda, B., Brubaker, L.B, Hu, F.S., Kling, G.W., 2003. Holocene pollen records from the central Arctic Foothills, northern Alaska: testing the role of substrate in the response of tundra to climate change. J. Ecol. 91, 1034-1048.

Overbeck, F., 1975. Botanisch-geologische Moorkunde, unter besonderer Berücksichtigung der Moore Nordwestdeutschlands als Quellen zur Vegetations-, Klima- und Siedlungsgeschichte. Karl Wachholtz Verlag, Neumünster.

Overpeck, J., Hughen, K, Hardy, D., Bradley, R , Case, R., Douglas, M., Finney, B., Gajewski, K., Jacoby, G., Jennings, A., Lamoureux, S., Lasca, A., MacDonald, G. Moore, J., Retelle, M., Smith, S., Wolfe, A., Zielinski, G., 1997. Arctic environmental change of the last four centuries. Science 278, 1251-1256.

PAGES 2k Consortium, 2013. Continental-scale temperature variability during the last two millennia. Nat. Geosci. 6, 339-346.

Panchen, Z.A., Gorelick, R., 2015. Flowering and fruiting responses to climate change of two Arctic plant species, purple saxifrage (Saxifraga oppositifolia) and mountain avens (Dryas integrifolia). Arctic Sci. 1, 45-58.

Ropars, P., Boudreau, S., 2012. Shrub expansion at the forest-tundra ecotone: spatial 559 heterogeneity linked to local topography. Environ. Res. Lett. 7, 015501.

Post, E., Forchammer, M.C., Bret-Harte, M. S.**,** Callaghan, T.V., Christensen, T.R., Elberling, B., Fox, A.D., Gilg, O., Hik, D.S., Høye, T.T., Ims, R.A., Jeppesen, E., Klein, D.R., Madsen, J., McGuire, A.D., Rysgaard, S., Schindler, D.E., Stirling, I., Tamstorf, M.P., Tyler, N.J., van der Wal, R., Welker, J., Wookey, P.A., Schmidt, N.M., Aastrup, P., 2009. Ecological dynamics across the Arctic associated with recent climate change. Science 325, 1355-1358.

Racine, C., Jandt, R., Meyers, C., Dennis, J., 2004. Tundra fire and vegetation change along a hillslope on the Seward Peninsula, Alaska, U.S.A. Arc. Antar. Alp. Res. 36, 1-10.

Raynolds, M.K., Walker, D.A., Ambrosius, K.J., Brown, J., Everett, K.R., Kanevskiy, M., Kofinas, G.P., Romanovsky, V.E., Shur, Y., Webber, P.J., 2014. Cumulative geoecological effects of 62 years of infrastructure and climate change in ice-rich permafrost landscapes, Prudhoe Bay Oilfield, Alaska. Global Change Biol. 20, 1211-1224.

Reimer, P.J., Bard, E., Bayliss, A., Beck, J.W., Blackwell, P.G., Ramsey, C.B., Buck, C.E., Cheng, H., Edwards, R.L., Friedrich, M., Grootes, P.M., Guilderson, T.P., Haflidason, H., Hajdas, I., Hatté, C., Heaton, T.J., Hoffmann, D.L., Hogg, A.G., Hughen, K.A., Kaiser, K.F., Kromer, B., Manning, S.W., Niu, M., Reimer, R.W., Richards, D.A., Scott, E.M., Southern, J.R., Staff, R.A., Turney, C.S.M., van der Plicht, J., 2013. Intcal13 and Marine13 radiocarbon age calibration curves 0-50,000 years cal BP. Radiocarbon 55: 1869-1887.

Reyes, A.V., Cooke, C.A., 2011. Northern peatland initiation lagged abrupt increases in deglacial atmospheric CH_4. P. Natl. Acad. Sci. USA 108, 4748-4753.

Rocha, A.V., Loranty, M.M., Higuera, P.E., Mack, M.C., Hu, F.S., Jones, B.M., Breen, A.L., Rastetter, E.B., Goetz, S.J., Shaver, G.R., 2012. The footprint of Alaskan tundra fires during the past half-century: implications for surface properties and radiative forcing. Environ. Res. Lett. 7: 044039.

Ropars, P., Boudreau, S., 2012. Shrub expansion at the forest-tundra ecotone: spatial heterogeneity linked to local topography. Environ. Res. Lett. 7, 10.1088/1748-9326/7/1/015501.

Rydin, H., Barber, K.E., 2001. Long-term and fine-scale coexistence of closely related species. Folia Geobot. 36, 53-61.

Rull, V., 2009. New paleoecological evidence for the potential role of fire in the Gran Sabana, Venezuelan Guayana, and implications for early human occupation. Veg. Hist. Archaeobot. 18, 219-224.

Shumilovskikh, L.S., Schlütz, F., Achterberg, I., Kvitkina, A., Bauerochsem, A., Leuschner, H.H., 2015. Pollen as nutrient source in Holocene ombrotrophic bogs. Rev. Palaeobot. Palynol. 221, 171-178.

Sturm, M., Racine, C., Tape, K. 2001. Increasing shrub abundance in the Arctic. Nature 411, 546-547.

Smith, A.J.E., 2004. The Moss Flora of Britain and Ireland. Cambridge University Press, Cambridge.

Swindles, G.T., Morris, P.J., Baird, A.J., Blaauw, M., Plunkett, G., 2012. Ecohydrological feedbacks confound peat-based climate reconstructions. Geophys. Res. Lett. 39, L11401.

Swindles, G.T., Morris, P.J., Mullan, D., Watson, E.J., Turner, T.E., Roland, T., 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., 2015a. The long-term fate of permafrost peatlands under rapid climate warming. Sci. Rep. 5, 17951.

Swindles, G.T., Amesbury, M., Turner, T.E., Carrivick, J.L., Woulds, C., Raby, C., Mullan, D., Roland, T.P., Galloway, J., Parry, L., Kokfelt, U., Garneau, M., Charman, D.J., Holden, J., 2015b. Evaluating the use of testate amoebae for palaeohydrological reconstruction in permafrost peatlands. Palaeogeogr. Palaeoclimatol. Palaeoecol. 424, 111-122.

Tahvanainen, T., 2011. Abrupt ombrotrophication of a boreal aapa mire triggered by hydrological disturbance in the catchment. J. Ecol. 99, 404-415.

Teltewskoi, A., Beermann, F., Beil, I., Bobrov, A., de Klerk, P., Lorenz, S., Lüder, A., Michaelis, D., Joosten, H., 2016. 4000 years of changing wetness in a permafrost polygon peatland (Kytalyk, NE Siberia): a comparative high-resolution multi-proxy study. Permafrost Periglac. 27, 76-95.

Tinner, W., Beer, R., Bigler, C., Clegg, B.F., Jones, R.T., Kaltenrieder, P., Van Raden, U.J., Gilli, A., Hu, F.S., 2015. Late-Holocene climate variability and ecosystem responses in Alaska inferred from high-resolution multiproxy sediment analyses at Grizzly Lake. Quat. Sci. Rev. 126, 41-56.

Tinner, W., Bigler, C., Gedye, S., Gregory-Eaves, I., Jones, R.T., Kaltenrieder, P., Krähenbühl, U., Hu, F.S., 2008. A 700-year paleoecological record of boreal ecosystem responses to climatic variation from Alaska. Ecology 89, 729-43.

Treat, C.C., Jones, M.C., Camill, P., Gallego-Sala, A., Garneau, M., Harden, J.W., Hugelius, G., Klein, E.S., Kokfelt, U., Kuhry, P., Loisel, J., Mathijssen, P.J.H., O'Donnell, J.A., Oksanen, P.O., Ronkainen, T.M., Sannel, A.B.K., Talbot, J., Tarnocai, C., Väliranta, M., 2016. Effects of permafrost aggradation on peat properties as determined from a pan-Arctic synthesis of plant macrofossils. J. Geophys. Res. Biogeosciences 121, 78-94.

Turetsky, M.R., Wieder, R.K., Vitt, D.H., 2002. Boreal peatland C fluxes under varying permafrost regimes. Soil Biol. Biochem. 34, 907-912.

Van Geel, B. 1978. A palaeoecological study of Holocene peat bog sections in Germany and the Netherlands. Rev. Palaeobot. Palynol. 25, 1-120.

Vardy, S.R., Warner, B.G., Aravena, R., 1998. Holocene climate and the development of a subarctic peatland near Inuvik, Northwest Territories, Canada. Cli. Change 40, 285-313.

Vierling, L.A., Eitel, J.U.H., Boelman, N.T., Griffin, K.L., Greaves, H., Magney, T.S., Prager, C., Ajayi, M., Gibson, R., 2013. Bare earth LiDAR dataset for Toolik Field Station, AK, and nearby field sites along Dalton Highway. doi: 10.7923/G4057CV5.

Walker, M.D., Walker, D.A., Auerbach, N.A., 1994. Plant communities of a tussock tundra landscape in the Brooks Range Foothills, Alaska. J. Veg. Sci. 5, 843-866.

Whitlock, C., Larsen, C., 2001. Charcoal as a fire proxy. In: Tracking Environmental Change Using Lake Sediments, pp. 75-97. Springer, Netherlands.

Weckström, J., Seppä, H., Korhola, A., 2010. Climatic influence on peatland formation and lateral expansion in sub-arctic Fennoscandia. Boreas 39, 761-769.

Young, A.M., Higuera, P.H., Duffy, P.A., Hu, F.S., 2016. Climatic thresholds shape northern high-latitude fire regimes and imply vulnerability to future climate change. Ecography 39, 01-12.

Yu, Z.C., 2012. Northern peatland carbon stocks and dynamics: a review. Biogeosciences 9, 4071-4085.

Zibulski, R., Herzschuh, U., Pestryakova, L.A., Wolter, J., Müller, S., Schilling, N., Wetterich, S., Schirrmeister, L., Tian, F., 2013. River flooding as a driver of polygon dynamics: modern vegetation data and a millennial peat record from the Anabar River lowlands (Arctic Siberia). Biogeosciences 10, 5703-5728.

Zoltai, S.C., 1993. Cyclic development of permafrost in the peatlands of Northwestern Alberta, Canada. Arc. Antar. Alp. Res. 25, 240-246.

Zona, D., Oechel, W.C., Richards, J.H., Hastings, S., Kopetz, I., Ikawa, H., Oberbauer, S., 2011. Light-stress avoidance mechanisms in a Sphagnum-dominated wet coastal arctic tundra ecosystem in Alaska. Ecology 92, 633-644.

Figure caption

Figure 1. Map showing locations of the two study sites in the Toolik region.

A) Arctic setting;

B) Regional setting; Fire occurred in 2007.

C) Geobotanical view of sampling sites (based on Vierling et al., 2013);

Figure 2. Age-depth models for the peat profiles: A - TFSI, B - TFSII.

Figure 3. Plant macrofossil diagram presenting vegetation development in TFSI and TFSII. Taxa with ‘%’ are estimated volume percentages, the others are counts (note scale differences on the x-axes).

Figure 4. Percentage pollen diagram vegetation changes in TFSI and TFSII.

Figure 5. Percentage testate amoebae diagram presenting changes in testate amoebae communities and reconstructed hydrological changes in TFSII.

Figure 6. Comparison of selected taxa from plant macrofossils and pollen with micro- and macro-charcoal data from TFSI. Climatic data are shown (PAGES 2k Consortium, 2013).

Figure 7. Comparison of selected taxa from plant macrofossils and pollen with micro- and macro-charcoal data in TFSII. Climatic data are shown (PAGES 2k Consortium, 2013).

Appendix caption

1. Radiocarbon dates from TFSI and TFSII.