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1 Warming climate forcing impact from a sub-arctic peatland as a result of late Holocene permafrost
2 aggradation and initiation of bare peat surfaces

3

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1 Highlights:

- 2 • permafrost aggradation triggered by late Holocene cooling led to warming climate forcing
- 3 • bare peat surfaces were more extensive in the past and led to stronger N₂O forcing, towards
- 4 modern times the bare surface area has diminished
- 5 • sub-arctic peatlands have strong impact on atmospheric greenhouse gas dynamics but
- 6 predictions for future development pathways remain uncertain

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1 Abstract

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3 Effects of permafrost aggradation on greenhouse gas (GHG) dynamics and climate forcing have not
4 been previously quantified. Here, we reconstruct changes in GHG balances over the late Holocene
5 for a sub-arctic peatland by applying palaeoecological data combined with measured GHG flux data,
6 focusing on the impact of permafrost aggradation in particular. Our data suggest that permafrost
7 initiation around 3000 years ago resulted in GHG emissions, thereby slightly weakening the general
8 long-term peatland cooling impact. As a novel discovery, based on our chronological data of bare
9 peat surfaces, we found that current sporadic bare peat surfaces in subarctic regions are probably
10 remnants of more extensive bare peat areas formed by permafrost initiation. Paradoxically, our data
11 suggest that permafrost initiation triggered by the late Holocene cooling climate generated a positive
12 radiative forcing and a short-term climate warming feedback, mitigating the general insolation-driven
13 late Holocene summer cooling trend. Our work with historical data demonstrates the importance of
14 permafrost peatland dynamics for atmospheric GHG concentrations, both in the past and future. It
15 suggests that, while thawing permafrost is likely to initially trigger a change towards wetter conditions
16 and consequent increase in CH₄ forcing, eventually the accelerated C uptake capacity under warmer
17 climate may overcome the thaw effect when a new hydrological balance becomes established.

18

19 Introduction

20

21 The carbon (C) stock stored in currently frozen peatlands is large, nearly 200 Pg (Hugelius et al.,
22 2020), and is vulnerable to permafrost thaw (Borge et al., 2017). However, there are complex, poorly
23 understood interactions between peat accumulation, hydrology and vegetation changes (Hugelius et
24 al., 2014; Olefeldt et al., 2016; Schuur et al., 2015; Zhang et al., 2018b). Ecosystem-atmosphere flux
25 measurements of the key GHGs, i.e. carbon dioxide (CO₂), methane (CH₄) and nitrous oxide (N₂O),

1 from sub-arctic areas have shown considerable differences between different habitat microforms,
2 such as the dry uplifted permafrost mounds, vegetated or bare, and the subsided non-permafrost fen
3 habitats (Bäckstrand et al., 2010; Voigt et al., 2017). Permafrost initiation involves peatland surface
4 upheaval that results in drying of the peat surface, which is often prone to abrasion and erosion
5 processes (Seppälä, 2011). In general, all vegetated surfaces, wet or dry, act as net sinks of C
6 (Gorham, 1991) in contrast to bare peat surfaces which do not sequester C due to absence of plants
7 but are substantial net sources of CO₂ because of high rate of organic matter decomposition of the
8 dry oxic surface peat and small sources of CH₄ to the atmosphere (Marushchak et al., 2013, 2016;
9 Voigt et al., 2017). These bare peat surfaces on uplifted permafrost peatlands are typical landscape
10 features in permafrost environments in Canada (Zoltai and Tarnocai, 1975), Scandinavia (Seppälä,
11 2003), European Russia (Kaverin et al., 2016) and Siberia (Kaverin et al., 2016; Seppälä 2003;
12 Ogneva, 2016; Zoltai 1995). The non-permafrost fens have a dual effect on climate: they are generally
13 stronger CO₂ sinks than ombrotrophic peatland surfaces due to higher productivity and slow
14 decomposition in wet, anoxic conditions, but at the same time their CH₄ emissions are high
15 (Marushchak et al., 2016; Nykänen et al., 2003; Turetsky et al., 2014). Typically, the net climatic
16 forcing of the fens is positive (warming) at century scales because the CH₄ emissions offset the CO₂
17 uptake (Hugelius et al., 2020; Johnston et al., 2014). Consequently, the predicted changes in
18 environmental conditions leading to changes in distributions of landscape components will largely
19 determine the magnitude and direction of sub-arctic carbon-feedbacks to climate change (Deng et al.,
20 2014; Johnston et al., 2014; Swindles et al., 2015; Zhang et al., 2018a).

21 Compared to C, studies on nitrogen (N) processes and, particularly, emissions of N₂O are rare
22 in the sub-arctic, although currently N₂O is contributing ca. 6% to the global warming due to well-
23 mixed GHGs (IPCC, 2013), and N₂O emissions from permafrost-affected soils could contribute as
24 much as 7.1% to the global N₂O budget (Voigt et al., 2020). Due to the low availability of reactive N
25 in cold soils with low N mineralization rates (Nadelhoffer et al., 1991), N₂O-related climate feedbacks

1 have so far been considered unimportant for the sub-arctic, but Voigt et al. (2020) showed that climate
2 change related disturbances increase N₂O emissions in permafrost regions. Contrary to expectations,
3 bare peat surfaces on permafrost peatlands, where reactive N availability for microbial processes is
4 enhanced by well-drained conditions and absence of plant N uptake have been identified as N₂O
5 emission hotspots (Marushchak et al., 2011; Repo et al., 2009). At the same time, the adjacent
6 vegetated peat surfaces do not emit N₂O (Marushchak et al., 2011; Repo et al., 2009). As a first back-
7 of-the-envelope calculation, the global source strength of N₂O from the current bare peat surfaces in
8 the sub-arctic was estimated to be ca. 0.1 Tg N₂O yr⁻¹ (Repo et al., 2009) which falls within the range
9 estimated for current industrial processes (IPCC, 2013).

10 Valuable information is stored in thick sub-arctic peat deposits, which can help to unravel how
11 the GHG flux dynamics of these peatlands in the past responded to changing climate, thus providing
12 us means to predict the future. To our knowledge, none of the previous studies has quantified the
13 long-term post-glacial radiative forcing (RF) of sub-arctic peatlands, in particular, while future RF
14 trajectories following permafrost thaw were recently estimated and modelled (Hugelius et al., 2020).
15 Previous Holocene RF reconstructions are available for non-permafrost peatlands, and accordingly
16 they do not take into account permafrost dynamics or initiation of bare peat surfaces; also the N₂O
17 emission component is missing (Frolking and Roulet, 2007; Mathijssen et al., 2017; Piilo et al., 2020).
18 Thus, to fill this gap, we carried out detailed case studies for permafrost peat cores collected from six
19 locations, three from NE European Russia (Seida, Rogovaya, Indico), two from northernmost Finland
20 (Kevo, Kilpisjärvi) and two peatlands in northern Sweden (Tavvavuoma) (Fig. 1). For Tavvavuoma,
21 previously published chronological data exist for the habitats covered by vegetation (Sannel et al.,
22 2017). To complement these, we dated two additional surface samples from Tavvavuoma and
23 Rogovaya, but now collected on the bare peat surfaces. Chronological data from Russia and Finland
24 were supplemented with subfossil plant data. These studies, with Seida as the key site, provided us
25 detailed background information of past and present permafrost peatland dynamics. All study sites

1 are characterised by a mixture of shrub–lichen–moss tundra vegetation including taxa such as *Betula*
2 *nana*, *Empetrum nigrum*, *Rubus chamaemorus* and, on lawns, *Eriophorum* spp., *Sphagnum fuscum*,
3 *Polytrichum strictum* and *Dicranum elongatum* are the dominant bryophytes on hummocks, while on
4 wetter depressions *Sphagnum lindbergii* is common. Bare peat surfaces are lacking all living flora
5 (Fig. 1). To model the past RF pattern for the Seida site over the last 3000 years, we used locally
6 obtained palaeoecological data in combination with on-site measured GHG fluxes. In addition, we
7 used high-resolution spatial satellite images from the Seida site to capture possible changes in the
8 bare peat surface distribution and area over the last decade.

9

10 Methods

11

12 Sediment coring

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14 Seida peat cores were collected in August 2012, two from bare peat surfaces (Seida BS I and Seida
15 BS II) and two from adjacent vegetated surfaces (Seida VS I and Seida VS II). Moreover, previous
16 peat stratigraphy data with peat property analyses and chronological data were available from the
17 same peatland (Biasi et al., 2014; Ronkainen et al., 2015). A Russian peat corer was used to collect
18 the unfrozen uppermost 35–50 cm peat layer, overlying the permafrost. The frozen peat layers were
19 collected with a motorized corer. The peat was underlain by silty/sandy mineral ground. The peat
20 cores were sampled into 2-cm slices at the field station and stored in sealed plastic bags.

21 In Indico three active-layer peat cores were collected in August 2015, two from bare peat
22 surfaces (Indico BS I and Indico BS II) and one from a vegetated surface (Indico VS I). A Russian
23 peat corer was used for coring and only the unfrozen peat layer overlying the permanently frozen peat
24 (ca. 50 cm) was collected. While the cores Indico BS I and BS II overlaid frozen peat, the core Indico

1 VS I overlaid mineral ground. The cores were transported intact to the laboratory in Helsinki and cut
2 into 2-cm slices, which were stored in a freezer.

3 In Finnish Lapland the bare peat surface cores were collected in August 2015, one from Kevo
4 (Kevo BS) and one from Kilpisjärvi (Kilpisjärvi BS) using a specially made box corer (cf. Jeglum et
5 al., 1992). For each site, only the unfrozen peat layer, ca. 50 cm, was collected. The peat cores were
6 wrapped inside plastic gutters and transported to Helsinki. In the laboratory the peat cores were sliced
7 into 2-cm samples and stored in a freezer in sealed plastic bags.

8 In Swedish Lapland and Rogovaya the bare peat surface samples were collected in August
9 2017 and 2018, respectively with a box corer. The peat cores were wrapped inside plastic gutters and
10 transported to Helsinki, where they were cut in 1-cm slices and kept frozen.

11

12 Radiocarbon ^{14}C and lead ^{210}Pb dating

13

14 In total, 19 bulk peat samples were dated from the four Seida peat cores. In addition, birch bark found
15 on the surface of BS I was dated. The samples were sent to the Poznan Radiocarbon Laboratory,
16 Poland for ^{14}C accelerator mass spectrometry (AMS) dating. Additional chronological data were
17 available from a 45-cm long and radiocarbon dated peat core from Seida (Seida BS III), collected
18 previously in 2007 from a bare peat surface (Biasi et al., 2014).

19 In total, 10 bulk peat samples were dated for the three Indico peat cores. All samples were
20 dated by the ^{14}C AMS method in the Finnish Museum of Natural History (LUOMUS) or in the Poznan
21 Radiocarbon Laboratory, Poland.

22 Four samples were dated for each Finnish Lapland peat cores Kevo BS and Kilpisjärvi BS.
23 For both cores the topmost 1 cm of the bare peat surface was dated, two samples in the middle and
24 one from the lower-most part of the peat core. Bulk peat samples were sent for AMS radiocarbon
25 dating to Poznan, Poland.

1 Two surface peat samples (0–2 cm) from Tavvavuoma, Sweden, and two from Rogovaya,
2 Russia, were sent for AMS radiocarbon dating to Poznan Radiocarbon Laboratory, Poland.

3 Radiocarbon BP ages were calibrated in the program Calib 7.0. using the IntCal 13 calibration
4 curve (Stuiver and Reimer, 1993). Calibrated ages were rounded to the nearest 5 years using the 2σ
5 age range (probability 95%). ^{210}Pb analyses for Seida VS II and Indico VS I cores were carried out at
6 Exeter University and the ^{210}Pb chronology was established using the CRS model (Appleby and
7 Oldfield, 1978).

8

9 Plant macrofossil analysis

10

11 Plant macrofossils were analysed for Seida BS I and Seida VS I, for Indico BS I and Indico VS I, and
12 for Kevo BS and Kilpisjärvi BS. The plant macrofossil subsample size was 5 cm^3 . The subsamples
13 were rinsed under running water and the material retained on a $140\text{-}\mu\text{m}$ sieve was examined under a
14 stereomicroscope. The species were identified using a high power light microscope. The proportions
15 of the different plant remains were visually estimated according to the protocol described by Väiliranta
16 et al. (2007).

17

18 Greenhouse gas flux data

19

20 Present-day habitat-specific GHG fluxes at the Seida study site were used to represent the peatland
21 GHG fluxes before and after permafrost initiation (Table 1). We used the annual GHG flux estimates
22 for permafrost bogs (vegetated and bare surfaces) and non-permafrost fens measured at the site in
23 October 2007 – October 2008. The CO_2 (Marushchak et al., 2013), CH_4 (Marushchak et al., 2016)
24 and N_2O (Marushchak et al., 2011) fluxes were monitored by chamber techniques and a snow-

1 gradient method as a part of a regional GHG balance assessment. To our knowledge, this is the only
2 available dataset from sub-arctic peatlands with year-round flux estimates for all three GHGs.

3
4 Reconstruction of the habitat changes and radiative forcing calculations

5
6 For Seida, we reconstructed the habitat changes within the current permafrost peatland area of 23.22
7 km², determined within the total study region of 98.6 km². We formulated a scenario where an uplifted
8 peat bog started to develop at 3000 cal yr BP as a result of permafrost aggradation replacing an equal
9 area of the fen surface, reaching the maximum extent at 2000 cal yr BP (Fig 2A). Half of the newly
10 formed uplifted peatland surfaces were assumed to be initially bare (Seppälä 2011) but re-vegetated
11 gradually, halving the bare surface area by 1000 cal yr BP. A linear decrease in the bare peat surface
12 area was assumed from 1000 cal yr BP to the current extent of 0.27 km², coupled with an equal
13 increase in the vegetated uplifted peatland area to the current 22.95 km².

14 RF was calculated for the difference in the emission/uptake rates of CO₂, CH₄ and N₂O that
15 occurred within the present permafrost peatland area as a result of the habitat-type changes described
16 above. The temporal variation of mean fluxes within this area (Fig. 2B, C, D) was estimated by
17 multiplying the areal development of habitats (Fig. 2A) by the present-day habitat-specific flux
18 densities measured within the study area (Table 1). The GHG flux dynamics directly related to
19 climate, such as those linked to variations in temperature, precipitation and ground water level, were
20 not explicitly accounted for. However, they were included in the analysis indirectly through the
21 habitat-type changes considered.

22 RF was calculated annually for CO₂, CH₄ and N₂O with a sustained impulse–response model
23 (Lohila et al., 2010; Piilo et al. 2020). This RF model includes a parameterization of the atmospheric
24 lifetime and radiative efficiency for each gas. The model input data consist of the fluxes of CO₂, CH₄
25 and N₂O within the study area (Fig. 2B, C, D) and the atmospheric background concentrations of

1 these gases (Köhler et al., 2017), both estimated annually during the study period. RF was calculated
2 as a marginal effect with respect to the varying background concentration assuming instantaneous
3 atmospheric mixing and globally uniform concentration distribution (Lohila et al., 2010). The annual
4 atmospheric GHG pulses were modelled to decay according to characteristic perturbation time scales
5 corresponding to global biogeochemical cycles. For CO₂, this was implemented as a weighted sum
6 of four exponential functions (Joos et al., 2013), whereas for CH₄ and N₂O a first-order decay was
7 assumed (IPCC, 2013). In each year, the effect of all preceding pulses was integrated to obtain the
8 time series of atmospheric concentration changes. The instantaneous RF resulting from these
9 concentration changes was calculated with the parameterization of Etminan et al. (2016), which takes
10 into account the spectral interactions between CO₂, CH₄ and N₂O. For more details of the RF model
11 employed here, see Lohila et al. (2010) and Piilo et al. (2020).

12

13 Satellite image analysis

14

15 To determine the dynamics of bare peatland surface in the recent past, we compared a QuickBird
16 image acquired on 6 July 2007 and a WorldView-3 image from 9 August 2015. Both images were
17 resampled to the 2.4-m pixel size, and the same bands (blue, green, red, near-infrared) were used for
18 both images. The images were first segmented using full lambda schedule segmentation and then
19 classified using one-class and binary approaches. The satellite image classifications and their
20 accuracy depend on the classification procedure applied (Mack et al., 2014; Stenzel et al., 2017). To
21 reduce a potential bias due to method selection, the bare peat areas were classified using four different
22 classification methods: random forest, rotation forest, one-class support vector machine and
23 biased/binary support vector machine classifiers. Each of these was applied in two settings: fully
24 supervised and with the help of positive and un-labeled samples. In the training of the classifiers, field
25 data from the summers 2007 and 2016 were used. Different methods produced to some extent

1 differing results, but as there is no simple criterion to select the best method, we reported the
2 consensus of five methods, while the consensus of three and seven methods were used as the upper
3 and lower range of the uncertainty estimate, respectively (Räsänen et al., 2019).

4

5 Results

6

7 Reconstructed permafrost peatland dynamics and initiation of bare peat formations

8

9 The Seida chronologies showed that peat accumulation started during the early Holocene, 8500-8000
10 cal yr BP (Figs. 3, 4). Very old peat was found at the top of the bare peat surfaces: the dated bark on
11 the surface of Seida BS I (BS = bare surface) (Fig 1.) yielded an age of ca. 5965 cal yr BP, while the
12 Seida BS I horizon at 20 cm was dated to 6680 cal yr BP (Fig. 3, 4). These results suggest that the
13 peat that accumulated after ca. 6000 cal yr BP has been eroded away, and thus the age of the currently
14 bare peat surface merely provides an estimate of the maximum age. The historical plant composition,
15 especially finds of *Filipendula ulmaria* and *Menyanthes trifoliata*, suggest a fen-type environment
16 (Fig 3). The peatland was forested until ca. 7000 cal yr BP (Fig 3). At the study point Seida VS I (VS
17 = vegetated surface) the peat started to accumulate ca. 8000 years ago (Fig. 3, 4). Interestingly, the
18 chronology suggests that between ca. 6000 and 3000 cal yr BP the peat accumulation either stopped
19 or slowed down considerably or, more likely, a substantial layer of the once-accumulated peat was
20 eroded away, as at Seida BS I. Non-permafrost fen conditions prevailed before the hiatus (Fig. 3).
21 Later on, the surface at Seida VS I was revegetated by typical permafrost peatland taxa, such as
22 lichens, dry *Sphagna* and *Polytrichum*; peat accumulation resumed. The radiocarbon dates from the
23 other peat cores, Seida BS II, III and VS II, largely confirmed the observed accumulation history of
24 Seida BS I and VS I: the bare peat surfaces had old ages, while the vegetated peat cores had young
25 top ages and periods of slow accumulation or gaps in the chronology after ca. 5000 cal yr BP (Figs.

1 3, 4). The general vegetation development indicates a succession from a minerotrophic fen with
2 spruce (*Picea abies*) and birch (*Betula pubescens* sl. type) towards a dry dwarf shrub-dominated bog
3 environment (Fig. 3).

4 Similarly to Seida, the bare peat surfaces in Indico were several thousands of years old, the ages
5 being ca. 5000 cal yr BP at Indico BS I and 3700 cal yr BP at Indico BS II) (Figs. 3, 4 Supplementary
6 Table 1). In the VS peat core, the depth of 24 cm yielded an age of 675 cal yr BP, and as in Seida,
7 there was a considerable gap in the chronology between 4600 and 675 cal yr BP. In Indico, only the
8 peat sections overlying the permanently frozen peat/soil was studied and dated (Figs. 3, 4). Indico BS
9 I plant data shows a succession towards wetter conditions as indicated by a change from dry *S. fuscum*
10 dominance to prevalence of wet *Sphagna*, dated to ca. 6000 cal yr BP (Fig 3). The Indico VS I plant
11 data, both bryophytes and vascular plants, suggest relatively dry habitat conditions throughout (Fig
12 3). The ages of active layer bottom peats, representing depths of 38–50 cm, were ca. 7000 (Indico BS
13 I), 6300 (Indico BS II) and 7250 (Indico VS I) cal yr BP. These ages agree with those derived for
14 Seida for corresponding depths (Figs. 3, 4). A bare peat surface BS I, from Rogovaya, yielded similar
15 age of ca. 5170 cal yr BP compared to Seida and Indico. The other bare peat surface age was younger,
16 ca. 465 cal yr BP (Rogovaya BS II) (Fig. 4).

17 More detailed plant data and chronologies from Tavvavuoma peat records were published in
18 Sannel et al. (2017), but new information was that the bare peat surfaces at Tavvavuoma were also
19 old: 5170 and 5800 cal yr BP (Supplementary Table 1). As a probable result of erosion, extensive late
20 Holocene hiatuses in peat accumulation have been recorded in the VS peat cores from this site (Figs.
21 3, 4), and old peat ages around 3000–4000 cal yr BP are common at relatively shallow depths (~30
22 cm) (Sannel et al., 2017). These VS chronologies indicate revegetation processes after periods of peat
23 erosion, similar to the Seida study sites. In contrast to the chronological patterns detected for Russia
24 and Sweden, the bare peat surfaces in Finnish Lapland represented the present time, with ages of 2007
25 CE at Kevo BS I and 2006 CE at Kilpisjärvi BS I. The plant data from Kevo do not indicate any clear

1 succession, although after 19 cm the plant remains were more intact and the amount of UOM
2 decreased. This might be related to the young age and incomplete decomposition process (Fig. 3). In
3 the Kilpisjärvi record, there seems to be a clear change from wet to dry conditions at 23 cm. Below
4 this depth, wet fen *Sphagna* prevail (Fig 3). The bottommost peat layers overlying the frozen peat
5 yielded ages of 1485 cal yr BP (30 cm) and 4540 cal yr BP (30 cm) at Kevo and Kilpisjärvi,
6 respectively (Figs. 3, 4). Slow accumulation rates/hiatus occur in the Kilpisjärvi record between 1570
7 and 4540 cal yr BP.

8

9 Reconstructed changes in greenhouse gas fluxes and radiative forcing

10

11 According to the habitat-specific GHG flux data, the permafrost aggradation and the subsequent
12 large-scale formation of bare peat surface area had a clear impact on GHG dynamics and the
13 associated radiative forcing in Seida, our intensive study site in western Russia (Figs. 2, 5). Likely,
14 the improved drainage enhanced decomposition, and CO₂ uptake ceased in the absence of vegetation,
15 resulting in a large increase in net CO₂ emissions (Marushchak et al., 2013). Similarly, the increase
16 in bare peat surface area enhanced N₂O emissions (Fig. 2D). At the same time, CH₄ emissions ceased
17 when the previously wet habitats became drier (Marushchak et al., 2016). These changes in GHG
18 fluxes between the Seida peatland and the atmosphere, especially the emissions of CO₂ and N₂O,
19 resulted in a positive RF, i.e. net warming effect on climate (Fig. 5).

20

21 Development of bare peat surfaces based on remote sensed data

22

23 High-resolution satellite data analyses show that within the analyzed area covering 1085 ha, of which
24 342 ha is uplifted peat bog, the bare peat surfaces have reduced during the last decades. The 2007
25 data show that bare surface areas covered 5.7 (4.3–8.4) ha in 410 (286–616) separate patches, while

1 in 2015 they only covered 4.4 (3.1–5.2) ha in 318 (236–375) patches (mean of five different image
2 classification methods, the range of different methods in parentheses) (Räsänen et al., 2019).

3

4 Discussion

5

6 Past permafrost peatland dynamics

7

8 Cryoturbation has been previously suggested as a possible mechanism behind the formation of bare
9 surfaces (Repo et al., 2009). Our peat records revealed features contradicting this theory. Firstly, the
10 consistent chronologies, which show no age reversals (Figs. 3, 4), suggest that cryoturbation is not
11 the main reason for the creation of the bare peat surfaces, although small-scale frost action is likely
12 important for maintaining the surfaces bare (Kaverin et al., 2014). Comparable data are available
13 from Canada, where bare peat surfaces are mostly dated to late Holocene ages with no reversals in
14 the stratigraphy (Bhiry et al., 2007; Lamarre et al., 2012).

15 Secondly, our data highlight the important role of another mechanism behind the occurrence of
16 bare peat surfaces: the drastic changes in hydrology, vegetation and susceptibility to erosion
17 associated with permafrost aggradation and uplifting of the peat surface. Neoglacial insolation-driven
18 cooling of summers after 4000 cal yr BP (Marsicek et al., 2018) initiated the landscape-level
19 permafrost aggradation over the circumarctic and sub-arctic belt and had an important impact on
20 vegetation communities and peat accumulation. The impact of cooling and the subsequent
21 aggradation of permafrost is widely detectable as a slow-down in the peat accumulation in sub-arctic
22 records from North America (Arlen-Pouliot and Bhiry, 2005; Kuhry, 2008; Sannel and Kuhry, 2009;
23 Vardy et al., 2000), Siberia (Kremenetski et al., 2003) and Fennoscandia (Kokfelt et al., 2010). The
24 onset of permafrost formation has occurred over the whole post-glacial time period, but it increased

1 3000 years ago, and the major aggradation has been dated to occur from 1000 BP onwards (Treat and
2 Jones, 2018).

3 In general, permafrost aggradation involves peatland surface upheaval that results in drying of
4 the peat surface (Seppälä, 2011). The radical habitat changes from water-logged to dry conditions
5 lead to a rapid disappearance of wet-adapted vegetation, but plants adapted to drier conditions, such
6 as lichens and dwarf shrubs, colonize only with a delay (Seppälä, 2011). In the meanwhile, the
7 uplifted peat surfaces are subjected to enhanced decomposition due to oxic soil conditions and wind
8 erosion (Seppälä, 2003). These processes could logically explain the old bare peat surface ages in
9 Seida, Indico and Tavvavuoma, including the bark age of 5965 cal yr BP on top of the Seida BS I
10 surface. Yet, profound understanding of the initiation and enduring process of these surfaces remained
11 unresolved. Erosion dynamics provide a likely explanation for the chronological gaps observed within
12 the studied VS profiles. Our palaeoecological data from locations currently covered by vegetation
13 provide evidence that at some point in time vegetation started to re-colonize the bare and eroded peat
14 surfaces while peat accumulation resumed, and the bare peat surface area shrank. In the Seida region,
15 bare surfaces currently cover ca. 1% of the uplifted peat bog area (Marushchak et al., 2013; Räsänen
16 et al., 2019).

17

18 Implications of permafrost dynamics on GHG emissions and radiative forcing.

19

20 According to our reconstruction for Seida, permafrost aggradation started to reduce CH₄ emissions
21 about 3000 yr ago (Fig. 2C) and thus induced a negative RF, i.e. had a cooling effect (Fig. 5). The
22 cooling effect increased for 1000 yr as non-permafrost fens, which are strong CH₄ emitters (Table 1),
23 were replaced by permafrost bog (Fig. 2A). Due to the short atmospheric perturbation lifetime of CH₄
24 (ca. 12 yr; IPCC, 2013), this RF component remained relatively constant after the concentration
25 change reached the level at which the surface flux and atmospheric decay rates were in equilibrium

1 (Fig. 5), i.e. soon after the flux change stabilized at 2000 cal yr BP (Fig. 2C). The gradual CH₄-RF
2 change after this was not related to Seida but the global decrease in the atmospheric CH₄ concentration
3 (Köhler et al., 2017). Similarly, the recent decrease of CH₄-RF resulted from the increasing
4 concentration since the pre-industrial times, because RF was calculated here as a marginal effect of
5 the local-scale contribution to the global concentration, which was assumed to follow a predefined
6 trajectory (Köhler et al., 2017). Due to spectral saturation effects, radiative efficiency, i.e. the RF
7 change per unit change in atmospheric mixing ratio, is progressively reduced with increasing
8 background concentrations (IPCC, 2013; Etminan et al., 2016).

9 As the mean CO₂ flux within the Seida region changed substantially due to the peatland type
10 change from fen to permafrost bog (Fig. 2A, B), and because CO₂ has a very long residence time in
11 the atmosphere, the CO₂-induced RF increased until about 200 cal yr BP; it outweighed the CH₄-
12 induced cooling already at 2000 cal yr BP (Fig. 5). The rapid decline of CO₂-RF after 200 cal yr BP
13 predominantly results from the increase of the background atmospheric CO₂ concentration since the
14 pre-industrial times, as explained above.

15 Although significantly smaller than the RF due to increased CO₂ emissions, the enhanced N₂O
16 emissions from bare peat surfaces, resulting from the improved reactive N availability in well-drained
17 conditions and the lack of plant N uptake, had a temporary warming effect on the climate system,
18 which started to decline 2000 cal yr BP, when the bare surface areas started to diminish (Figs. 2, 5).

19 Overall, our study highlights the importance of sub-arctic peatlands for atmospheric GHG
20 dynamics, affecting both the past and future climate. A recent modelling exercise suggests an
21 increased C uptake capacity for high-latitude peatlands in the future (Gallego-Sala et al., 2018). This
22 may substantially compensate for the predicted positive climate forcing impact from thawing
23 permafrost, which is suggested to trigger a landscape change towards wetter conditions (Swindles et
24 al., 2015) and a consequent increase in the CH₄-induced forcing (Hugelius et al., 2020). Our data
25 support these assumptions and suggest further that a decreasing trend in the extent of bare peat

1 surfaces reduces the climate warming feedback effect of thawing permafrost peatlands. However,
2 large spatial variations can be expected for permafrost development pathways, which may also lead
3 to landscape drying when new drainage channels open (Liljedahl et al., 2016; Loisel et al., 2020).
4 Furthermore, it should be acknowledged that permafrost thawing leads to the release of volatile
5 organic compounds (Li et al., 2020), as well as dissolved C and nutrients, whose radiative forcing
6 and ultimate impact on climate remain unresolved.

7

8 Conclusions

9

10 Our data suggest that the landscape changes associated with permafrost initiation in the studied sub-
11 arctic peatlands had a significant impact on GHG fluxes and the related RF over the late Holocene.
12 The data confirm that sub-arctic peatlands are effective C sinks that globally act as cooling landscape
13 elements. The modelled long-term RF pattern for the Seida is negative for the fen phase sustaining
14 until the permafrost initiation at ca. 2000 cal yr BP, when the surface was lifted up resulting in
15 replacement of wet fen by dry bog surfaces with bare peat and consequently leading to a substantial
16 increase in the positive RF component. This was mainly due to the large CO₂ emissions originating
17 from uplifted dry and abundant bare peat surfaces and the decreased productivity accompanied by
18 erosion processes and disappearance of the plant cover. This landscape development, while
19 decreasing CH₄ emissions, dramatically increased CO₂ and N₂O emissions. Our case studies from
20 Russia, Finland and Sweden provide evidence for a large-scale formation of bare peat surfaces around
21 3000 cal yr BP due to the late Holocene permafrost aggradation. Palaeoecological data from Seida
22 suggest larger-than-today biogenic N₂O emissions for the late Holocene due to formation of bare peat
23 surfaces, which have since diminished due to revegetation. Paradoxically it seems that the insolation-
24 driven late Holocene summer cooling in the Northern Hemisphere likely induced a widespread,

1 compensating warming effect through CO₂ and N₂O emissions from permafrost peatlands that
2 opposed the general cooling trend.

3

4

5 Author contributions

6

7 MV, CB, MM, AP and DK were responsible for the fieldwork campaigns in Russia, MV, SP and HZ
8 for Finnish Lapland and MV, SP and BS for Swedish Lapland. HZ and SP analysed fossil plant data
9 under MV supervision. AL and J-PT developed the radiative forcing scenarios. AR and TV carried
10 out the satellite image analysis. MV had the main responsibility for the design and writing of the
11 manuscript together with J-PT and MM. All co-authors participated and provided contribution with
12 regard to their own field of scientific expertise.

13

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23

24 Declaration of competing interest

25

1 This manuscript has not been published, nor is under consideration for publication elsewhere. We
2 have no conflicts of interest and the manuscript has been approved by all co-authors. All authors have
3 made substantial contributions to the submission.

4

5 References

6

- 7 Appleby, P.G., Oldfield, F., 1978. The calculation of lead-210 dates assuming a constant rate of
8 supply of unsupported ^{210}Pb to the sediment. *CATENA* 5, 1-8.
- 9
- 10 Arlen-Pouliot, Y., Bhiry, N., 2005. Palaeoecology of a palsa and a filled thermokarst pond in a
11 permafrost peatland, subarctic Québec, Canada. *The Holocene* 15, 408-419.
- 12
- 13 Bäckstrand, K., Crill, P.M., Jackowicz-Korczyński, M., Mastepanov, M., Christensen, T.R.,
14 Bastviken, D., 2010. Annual carbon gas budget for a subarctic peatland, Northern Sweden.
15 *Biogeosciences* 7, 95-108.
- 16
- 17 Bhiry, N., Payette, S., Robert, É.C., 2007. Peatland development at the arctic tree line (Québec,
18 Canada) influenced by flooding and permafrost. *Quat. Res.* 67, 426-437.
- 19
- 20 Biasi, C., Jokinen, S., Marushchak, M.E., Hämäläinen, K., Trubnikova, T., Oinonen, M., Martikainen,
21 P.J., 2014. Microbial Respiration in Arctic Upland and Peat Soils as a Source of Atmospheric Carbon
22 Dioxide. *Ecosystems* 17, 112-126.
- 23
- 24 Borge, A.F., Westermann, S., Solheim, I., Etzelmüller, B., 2017. Strong degradation of palsas and
25 peat plateaus in northern Norway during the last 60 years. *Cryosphere* 11, 1-16.
- 26
- 27 Brown, J., O. Ferrians, J. A. Heginbottom, and E. Melnikov. 2002. Circum-Arctic Map of Permafrost
28 and Ground-Ice Conditions, Version 2. Boulder, Colorado USA. NSIDC: National Snow and Ice Data
29 Center. doi: <https://doi.org/10.7265/skbg-kf16>.
- 30
- 31 Deng, J., Li, C., Frohking, S., Zhang, Y., Bäckstrand, K., Crill, P., 2014. Assessing effects of
32 permafrost thaw on C fluxes based on multiyear modeling across a permafrost thaw gradient at
33 Stordalen, Sweden. *Biogeosciences* 11, 4753-4770.
- 34
- 35 Etminan, M., Myhre, G., Highwood, E.J., Shine, K.P., 2016. Radiative forcing of carbon dioxide,
36 methane, and nitrous oxide: a significant revision of the methane radiative forcing.
37 *Geophys. Res. Lett.* 43, 614-623.
- 38
- 39 Frohking, S., Roulet, N., 2007. Holocene radiative forcing impact of northern peatland carbon
40 accumulation and methane emissions. *Glob. Change Biol* 13, 1079-1088.
- 41
- 42 Gallego-Sala, A.V., Charman, D.J., Brewer, S., Page, S.E., Prentice, I.C., Friedlingstein, P., Moreton,
43 S., Amesbury, M.J., Beilman, D.W., Björck, S., Blyakharchuk, T., Bochicchio, C., Booth, R.K.,
44 Bunbury, J., Camill, P., Carless, D., Chimner, R.A., Clifford, M., Cressey, E., Courtney-Mustaphi,

- 1 C., De Vleeschouwer, F., de Jong, R., Fialkiewicz-Koziel, B., Finkelstein, S.A., Garneau, M.,
2 Githumbi, E., Hribljan, J., Holmquist, J., Hughes, P.D.M., Jones, C., Jones, M.C., Karofeld, E., Klein,
3 E.S., Kokfelt, U., Korhola, A., Lacourse, T., Le Roux, G., Lamentowicz, M., Large, D., Lavoie, M.,
4 Loisel, J., Mackay, H., MacDonald, G.M., Makila, M., Magnan, G., Marchant, R., Marcisz, K.,
5 Martínez Cortizas, A., Massa, C., Mathijssen, P., Mauquoy, D., Mighall, T., Mitchell, F.J.G., Moss,
6 P., Nichols, J., Oksanen, P.O., Orme, L., Packalen, M.S., Robinson, S., Roland, T.P., Sanderson,
7 N.K., Sannel, A.B.K., Silva-Sánchez, N., Steinberg, N., Swindles, G.T., Turner, T.E., Uglow, J.,
8 Väiliranta, M., van Bellen, S., van der Linden, M., van Geel, B., Wang, G., Yu, Z., Zaragoza-Castells,
9 J., Zhao, Y., 2018. Latitudinal limits to the predicted increase of the peatland carbon sink with
10 warming. *Nat. Clim. Change* 8, 907-913.
- 11
- 12 Gorham, E., 1991. Northern Peatlands: Role in the Carbon Cycle and Probable Responses to Climatic
13 Warming. *Ecol. Appl* 1, 182-195.
- 14
- 15 Hugelius, G., Bockheim, J.G., Camill, P., Elberling, B., Grosse, G., Harden, J.W., Johnson, K.,
16 Jorgenson, T., Koven, C.D., Kuhry, P., Michaelson, G., Mishra, U., Palmtag, J., O'Donnell, J.,
17 Schirrmeister, L., Schuur, E.A.G., Sheng, Y., Smith, L.C., Strauss, J., Yu, Z., 2013. A new data set
18 for estimating organic carbon storage to 3 m depth in soils of the northern circumpolar permafrost
19 region. *Earth Syst. Sci. Data* 5, 393-402.
- 20
- 21 Hugelius, G., Loisel, J., Chadburn, S., Jackson, R.B., Jones, M., MacDonald, G., Marushchak, M.,
22 Olefeldt, D., Packalen, M., Siewert, M.B., Treat, C., Turetsky, M., Voigt, C., Yu, Z., 2020. Large
23 stocks of peatland carbon and nitrogen are vulnerable to permafrost thaw. *PNAS* 117, 20438.
- 24
- 25 Hugelius, G., Strauss, J., Zubrzycki, S., Harden, J.W., Schuur, E.A.G., Ping, C.L., Schirrmeister, L.,
26 Grosse, G., Michaelson, G.J., Koven, C.D., O'Donnell, J.A., Elberling, B., Mishra, U., Camill, P., Yu,
27 Z., Palmtag, J., Kuhry, P., 2014. Estimated stocks of circumpolar permafrost carbon with quantified
28 uncertainty ranges and identified data gaps. *Biogeosciences* 11, 6573-6593.
- 29
- 30 IPCC, 2013. IPCC Climate Change 2013: The Physical Science Basis. Contribution of Working
31 Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change.
32 Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA,.
- 33 Johnston, C.E., Ewing, S.A., Harden, J.W., Varner, R.K., Wickland, K.P., Koch, J.C., Fuller, C.C.,
34 Manies, K., Jorgenson, M.T., 2014. Effect of permafrost thaw on CO₂ and CH₄ exchange in a western
35 Alaska peatland chronosequence. *Environ. Res. Lett* 9.
- 36
- 37 Jeglum, J.K., Rothwell, R.I., Berry, G.J., Smith, G.K.M., 1992. A peat sampler for rapid survey.
38 Technical note. *Canadian Forest Service* 13: 921-932.
- 39
- 40 Joos, F., Roth, R., Fuglestedt, J.S., Peters, G.P., Enting, I.G., Von Bloh, W., Brovkin, V., Burke,
41 E.J., Eby, M., Edwards, N.R., Friedrich, T., Frölicher, T.L., Halloran, P.R., Holden, P.B., Jones, C.,
42 Kleinen, T., Mackenzie, F.T., Matsumoto, K., Meinshausen, M., Plattner, G.K., Reisinger, A.,
43 Segschneider, J., Shaffer, G., Steinacher, M., Strassmann, K., Tanaka, K., Timmermann, A., Weaver,
44 A.J., 2013. Carbon dioxide and climate impulse response functions for the computation of greenhouse
45 gas metrics: a multi-model analysis. *Atmos. Chem. Phys.* 13, 2793-2825.
- 46
- 47 Kaverin, D.A., Pastukhov, A.V., Lapteva, E.M., Biasi, C., Marushchak, M., Martikainen, P., 2016.
48 Morphology and properties of the soils of permafrost peatlands in the southeast of the
49 Bol'shezemel'skaya tundra. *Eurasian Soil Sci* 49, 498-511.
- 50

- 1 Kaverin, D.A., Pastukhov, A.V., Mazhitova, G.G., 2014. Temperature regime of tundra soils and
2 underlying permafrost (Northeastern European Russia). *Earth's Cryosphere* 18, 23-32.
- 3
- 4 Köhler, P., Nehrbass-Ahles, C., Schmitt, J., Stocker, T.F., Fischer, H., 2017. A 156 kyr smoothed
5 history of the atmospheric greenhouse gases CO₂, CH₄, and N₂O and their radiative forcing. *Earth*
6 *Syst. Sci. Data* 9, 363-387.
- 7
- 8 Kokfelt, U., Reuss, N., Struyf, E., Sonesson, M., Rundgren, M., Skog, G., Rosén, P., Hammarlund,
9 D., 2010. Wetland development, permafrost history and nutrient cycling inferred from late Holocene
10 peat and lake sediment records in subarctic Sweden. *J. Paleolimnol* 44, 327-342.
- 11
- 12 Kremenetski, K.V., Velichko, A.A., Borisova, O.K., MacDonald, G.M., Smith, L.C., Frey, K.E.,
13 Orlova, L.A., 2003. Peatlands of the Western Siberian lowlands: current knowledge on zonation,
14 carbon content and Late Quaternary history. *Quat. Sci. Rev.* 22, 703-723.
- 15
- 16 Kuhry, P., 2008. Palsa and peat plateau development in the Hudson Bay Lowlands, Canada: timing,
17 pathways and causes. *Boreas* 37, 316-327.
- 18
- 19 Lamarre, A., Garneau, M., Asnong, H., 2012. Holocene paleohydrological reconstruction and carbon
20 accumulation of a permafrost peatland using testate amoeba and macrofossil analyses, Kuujuarapik,
21 subarctic Québec, Canada. *Rev. Palaeobot. Palynol.* 186, 131-141.
- 22
- 23 Li, H., Väiliranta, M., Mäki, M., Kohl, L., Sannel, A.B.K., Pumpanen, J., Koskinen, M., Bäck, J.,
24 Bianchi, F., 2020. Overlooked organic vapor emissions from thawing Arctic permafrost. *Environ.*
25 *Res. Lett* 15, 104097.
- 26
- 27 Liljedahl, A.K., Boike, J., Daanen, R.P., Fedorov, A.N., Frost, G.V., Grosse, G., Hinzman, L.D.,
28 Iijma, Y., Jorgenson, J.C., Matveyeva, N., Necsoiu, M., Reynolds, M.K., Romanovsky, V.E., Schulla,
29 J., Tape, K.D., Walker, D.A., Wilson, C.J., Yabuki, H., Zona, D., 2016. Pan-Arctic ice-wedge
30 degradation in warming permafrost and its influence on tundra hydrology. *Nature Geosci* 9, 312-318.
- 31
- 32 Lohila, A., Minkkinen, K., Laine, J., Savolainen, I., Tuovinen, J.-P., Korhonen, L., Laurila, T.,
33 Tietäväinen, H., Laaksonen, A., 2010. Forestation of boreal peatlands: impacts of changing albedo
34 and greenhouse gas fluxes on radiative forcing.
35 *J. Geophys. Res. Biogeosciences* 115, 1-15.
- 36
- 37 Loisel, J., Gallego-Sala, A.V., Amesbury, M.J., Magnan, G., Anshari, G., Beilman, D.W., Benavides,
38 J.C., Blewett, J., Camill, P., Charman, D.J., Chawchai, S., Hedgpeth, A., Kleinen, T., Korhola, A.,
39 Large, D., Mansilla, C.A., Müller, J., van Bellen, S., West, J.B., Yu, Z., Bubier, J.L., Garneau, M.,
40 Moore, T., Sannel, A.B.K., Page, S., Väiliranta, M., Bechtold, M., Brovkin, V., Cole, L.E.S., Chanton,
41 J.P., Christensen, T.R., Davies, M.A., De Vleeschouwer, F., Finkelstein, S.A., Frolking, S., Gałka,
42 M., Gandois, L., Girkin, N., Harris, L.I., Heinemeyer, A., Hoyt, A.M., Jones, M.C., Joos, F., Juutinen,
43 S., Kaiser, K., Lacourse, T., Lamentowicz, M., Larmola, T., Leifeld, J., Lohila, A., Milner, A.M.,
44 Minkkinen, K., Moss, P., Naafs, B.D.A., Nichols, J., O'Donnell, J., Payne, R., Philben, M., Piilo, S.,
45 Quillet, A., Ratnayake, A.S., Roland, T.P., Sjögersten, S., Sonnentag, O., Swindles, G.T., Swinnen,
46 W., Talbot, J., Treat, C., Valach, A.C., Wu, J., 2020. Expert assessment of future vulnerability of the
47 global peatland carbon sink. *Nat. Clim. Change*.
- 48
- 49 Mack, B., Roscher, R., Waske, B., 2014. Can I Trust My One-Class Classification? *Remote Sensing*
50 6.

- 1
2 Marsicek, J., Shuman, B.N., Bartlein, P.J., Shafer, S.L., Brewer, S., 2018. Reconciling divergent
3 trends and millennial variations in Holocene temperatures. *Nature* 554, 92.
4
- 5 Marushchak, M.E., Friberg, T., Biasi, C., Herbst, M., Johansson, T., Kiepe, I., Liimatainen, M., Lind,
6 S.E., Martikainen, P.J., Virtanen, T., Soegaard, H., Shurpali, N.J., 2016. Methane dynamics in the
7 subarctic tundra: combining stable isotope analyses, plot- and ecosystem-scale flux measurements.
8 *Biogeosciences* 13, 597-608.
9
- 10 Marushchak, M.E., Kiepe, I., Biasi, C., Elsakov, V., Friberg, T., Johansson, T., Soegaard, H.,
11 Virtanen, T., Martikainen, P.J., 2013. Carbon dioxide balance of subarctic tundra from plot to regional
12 scales. *Biogeosciences* 10, 437-452.
13
- 14 Marushchak, M.E., Pitkämäki, A., Koponen, H., Biasi, C., Seppälä, M., Martikainen, P.J., 2011. Hot
15 spots for nitrous oxide emissions found in different types of permafrost peatlands. *Glob. Change Biol.*
16 17, 2601-2614.
17
- 18 Mathijssen, P.J.H., Kähkölä, N., Tuovinen, J.P., Lohila, A., Minkkinen, K., Laurila, T., Välranta,
19 M., 2017. Lateral expansion and carbon exchange of a boreal peatland in Finland resulting in 7000
20 years of positive radiative forcing. *Journal of Geophysical Research: Biogeosciences*.
21
- 22 Nadelhoffer, K.J., Giblin, A.E., Shaver, G.R., Laundre, J.A., 1991. Effects of Temperature and
23 Substrate Quality on Element Mineralization in Six Arctic Soils. *Ecology* 72, 242-253.
24
- 25 Nykänen, H., Heikkinen, J.E.P., Pirinen, L., Tiilikainen, K., Martikainen, P., 2003. Annual CO₂
26 exchange and CH₄ fluxes on a subarctic palsa mire during climatically different years. *Global*
27 *Biogeochemical Cy* 17, 18-11.
28
- 29 Ogneva, O.A., Matyshak, G.V., Goncharova, O.Y., Bobrik, A.A., Ponomareva, O.E., 2016. Soils of
30 peat spots of frozen peatlands in the north of western siberia. *Earth's cryosphere* 2, 55–61.
31
- 32 Olefeldt, D., Goswami, S., Grosse, G., Hayes, D., Hugelius, G., Kuhry, P., McGuire, A.D.,
33 Romanovsky, V.E., Sannel, A.B.K., Schuur, E.A.G., Turetsky, M.R., 2016. Circumpolar distribution
34 and carbon storage of thermokarst landscapes. *Nat. Commun.* 7.
35
- 36 Piilo, S.R., Korhola, A., Heiskanen, L., Tuovinen, J.-P., Aurela, M., Juutinen, S., Marttila, H., Saari,
37 M., Tuittila, E.-S., Turunen, J., Välranta, M.M., 2020. Spatially varying peatland initiation, Holocene
38 development, carbon accumulation patterns and radiative forcing within a subarctic fen. *Quat. Sci.*
39 *Rev* 248, 106596.
40
- 41 Räsänen, A., Elsakov, V., Virtanen, T., 2019. Usability of one-class classification in mapping and
42 detecting changes in bare peat surfaces in the tundra. *Int. J. Remote Sens.* 40, 4083-4103.
43
- 44 Repo, M.E., Susiluoto, S., Lind, S.E., Jokinen, S., Elsakov, V., Biasi, C., Virtanen, T., Martikainen,
45 P.J., 2009a. Large N₂O emissions from cryoturbated peat soil in tundra. *Nature Geosci* 2, 189-192.
46
- 47 Ronkainen, T., Välranta, M., McClymont, E., Biasi, C., Salonen, S., Fontana, S., Tuittila, E.S., 2015.
48 A combined biogeochemical and palaeobotanical approach to study permafrost environments and
49 past dynamics. *J. Quat. Sci.* 30, 189-200.
50

- 1 Sannel, A.B.K., Hempel, L., Kessler, A., Prékienis, V., 2017. Holocene development and permafrost
2 history in sub-arctic peatlands in Tavvavuoma, northern Sweden. *Boreas* 47, 1-15.
- 3
- 4 Sannel, A.B.K., Kuhry, P., 2009. Holocene peat growth and decay dynamics in sub-arctic peat
5 plateaus, west-central Canada. *Boreas* 38, 13-24.
- 6
- 7 Schuur, E.A.G., McGuire, A.D., Schadel, C., Grosse, G., Harden, J.W., Hayes, D.J., Hugelius, G.,
8 Koven, C.D., Kuhry, P., Lawrence, D.M., Natali, S.M., Olefeldt, D., Romanovsky, V.E., Schaefer,
9 K., Turetsky, M.R., Treat, C.C., Vonk, J.E., 2015. Climate change and the permafrost carbon
10 feedback. *Nature* 520, 171-179.
- 11
- 12 Seppälä, M., 2003. Surface abrasion of palsas by wind action in Finnish Lapland. *Geomorphology*
13 52, 141-148.
- 14
- 15 Seppälä, M., 2011. Synthesis of studies of palsa formation underlining the importance of local
16 environmental and physical characteristics. *Quat. Res.* 75, 366-370.
- 17
- 18 Stenzel, S., Fassnacht, F.E., Mack, B., Schmidlein, S., 2017. Identification of high nature value
19 grassland with remote sensing and minimal field data. *Ecol. Indic.* 74, 28-38.
- 20
- 21 Stuiver, M., Reimer, P.J., 1993. Extended ¹⁴C Data Base and Revised CALIB 3.0 ¹⁴C Age Calibration
22 Program. *Radiocarbon* 35, 215-230.
- 23
- 24 Swindles, G.T., Morris, P.J., Mullan, D., Watson, E.J., Turner, T.E., Roland, T.P., Amesbury, M.J.,
25 Kokfelt, U., Schoning, K., Pratte, S., Gallego-Sala, A., Charman, D.J., Sanderson, N., Garneau, M.,
26 Carrivick, J.L., Woulds, C., Holden, J., Parry, L., Galloway, J.M., 2015. The long-term fate of
27 permafrost peatlands under rapid climate warming. *Sci. Rep.* 5, 17951.
- 28
- 29 Treat, C.C., M.C. Jones., 2018. Near-surface permafrost aggradation in Northern Hemisphere
30 peatlands shows regional and global trends during the past 6000 years. *The Holocene*
31 10.1177/0959683617752858.
- 32
- 33 Turetsky, M.R., Kotowska, A., Bubier, J., Dise, N.B., Crill, P., Hornibrook, E.R.C., Minkkinen, K.,
34 Moore, T.R., Myers-Smith, I.H., Nykänen, H., Olefeldt, D., Rinne, J., Saarnio, S., Shurpali, N.,
35 Tuittila, E.S., Waddington, J.M., White, J.R., Wickland, K.P., Wilmking, M., 2014. A synthesis of
36 methane emissions from 71 northern, temperate, and subtropical wetlands. *Glob. Change Biol.* 20,
37 2183-2197.
- 38
- 39 Väiliranta, M., Korhola, A., Seppä, H., Tuittila, E.-S., Sarmaja-Korjonen, K., Laine, J., Alm, J., 2007.
40 High-resolution reconstruction of wetness dynamics in a southern boreal raised bog, Finland, during
41 the late Holocene: a quantitative approach. *The Holocene* 17, 1093-1107.
- 42
- 43 Vardy, S.R., Warner, B.G., Turunen, J., Aravena, R., 2000. Carbon accumulation in permafrost
44 peatlands in the Northwest Territories and Nunavut, Canada. *Holocene* 10, 273-280.
- 45
- 46 Voigt, C., Lamprecht, R.E., Marushchak, M.E., Lind, S.E., Novakovskiy, A., Aurela, M.,
47 Martikainen, P.J., Biasi, C., 2017. Warming of subarctic tundra increases emissions of all three
48 important greenhouse gases - carbon dioxide, methane, and nitrous oxide. *Glob Chang Biol* 23, 3121-
49 3138.
- 50

- 1 Voigt, C., Marushchak, M.E., Abbott, B.W., Biasi, C., Elberling, B., Siciliano, S.D., Sonnentag, O.,
 2 Stewart, K.J., Yang, Y., Martikainen, P.J., 2020. Nitrous oxide emissions from permafrost-affected
 3 soils. *Nat. Rev. Earth Environ.* 1, 420-434.
 4
 5 Zhang, H., Gallego-Sala, A.V., Amesbury, M.J., Charman, D.J., Piilo, S.R., Väiliranta, M.M., 2018a.
 6 Inconsistent Response of Arctic Permafrost Peatland Carbon Accumulation to Warm Climate Phases.
 7 *Global Biogeochem Cy* 32, 1605-1620.
 8
 9 Zhang, H., Piilo, S.R., Amesbury, M.J., Charman, D.J., Gallego-Sala, A.V., Väiliranta, M.M., 2018b.
 10 The role of climate change in regulating Arctic permafrost peatland hydrological and vegetation
 11 change over the last millennium. *Quat. Sci. Rev.* 182, 121-130.
 12
 13 Zoltai, S.C., Tarnocai, C., 1975. Perennially Frozen Peatlands in the Western Arctic and Subarctic of
 14 Canada. *Can J Earth Sci* 12, 28-43.

15

16 Table 1. Present-day habitat-specific greenhouse gas fluxes from the Seida study region (mean with
 17 standard deviation). ¹Marushchak et al. (2013), ²Marushchak et al. (2016), ³Marushchak et al. (2011)

18

	CO ₂ flux	CH ₄ flux	N ₂ O flux
	(g CO ₂ m ⁻² yr ⁻¹)	(g CH ₄ m ⁻² yr ⁻¹)	(g N ₂ O m ⁻² yr ⁻¹)
SEIDA REGION			
Vegetated permafrost bog	-164 ± 183 ¹	0.18 ± 0.17 ²	0.02 ± 0.02 ³
Bare permafrost bog	307 ± 32 ¹	0.66 ± 1.07 ²	1.34 ± 0.28 ³
Non-permafrost fen	-392 ± 351 ¹	34.38 ± 15.94 ²	-0.02 ± 0.02 ³

19

20 Figure captions

21

22 Fig. 1. **Color figure** (A) Circumpolar permafrost distribution. (B) Peatland coverage within the
 23 discontinuous and sporadic permafrost zones and the study site locations. Permafrost extent is based
 24 on a circumpolar map of permafrost and ground ice conditions (Brown et al., 2002). Peatland
 25 classification includes histosols and histels according to Hugelius et al. (2013 and 2014) (Hugelius et

1 al., 2013; Hugelius et al., 2014). Seida (67°07'N, 62°57'E), Rogovaya (68°27'N, 20°54'E) and Indico
 2 (67°15'N, 49°48'E) are located in sub-arctic NE European Russia, in the discontinuous permafrost
 3 zone. Kevo (69°49'N, 27°10'E) and Kilpisjärvi (68°53'N, 21°3'E) are located in Finnish Lapland in
 4 the sporadic permafrost zone. Tavvavuoma peatlands (68°28'N, 20°54'E) are located in Swedish
 5 Lapland in the sporadic permafrost zone. (C) A photo of a typical bare peat surface in Seida at a
 6 location where the BS cores were collected. (D) A photo of remains of birch (*Betula* sp.) bark on the
 7 surface of bare peat.

8
 9 Fig 2. **Color figure** A) Permafrost aggradation-induced development of different land cover types
 10 assumed for the flux upscaling and radiative forcing calculations. B-D) Up-scaled late Holocene CO₂,
 11 CH₄ and N₂O fluxes for the Seida peatland.

12
 13 Fig. 3. Plant macrofossil diagrams showing fossil plant assemblage data for Seida1, Indico, Kevo and
 14 Kilpisjärvi peat cores: bare surface peat site BS and vegetated peat site VS. Only selected taxa are
 15 presented. Combined taxonomic units include the following species: Cyperaceae sl.: *Eriophorum* and
 16 *Carex* remains and unidentified Cyperaceae remains, such as roots. Brown mosses: *Calliergon*,
 17 *Staminergon* and *Cinclidium* species. Dwarf shrubs: *Rubus chamaemorus*, *Betula nana*, *Empetrum*
 18 *nigrum*, *Rhododendron tomentosum* (syn. *Ledum palustre*). Dry Sphagna: *Sphagnum fuscum* and *S.*
 19 *capillifolium*. # = number of remains, + = remains present, black bars = proportion in percentages.
 20 UOM=Unidentified Organic Matter means that plant material was highly decomposed and
 21 taxonomical identification could not be achieved.

22
 23 Fig 4. **Color figure** Chronological information for the studied peat records in Russia, Finland and
 24 Sweden. All pre-bomb radiocarbon ages are expressed as calibrated radiocarbon years, a mean of 2-
 25 sigma range is indicated. Post-bomb radiocarbon ages are isotopic-corrected CE ages. The surface

1 ^{210}Pb ages originate from the CRS model. The Tavvavuoma long-core data are from Sannel et al.
2 (2017). Uncalibrated BP ages are presented in Supplementary Table 1.

3

4 Fig. 5. **Color figure** Radiative forcing due to development of permafrost bogs within the Seida study
5 region (23.2 km²), calculated with greenhouse gas fluxes shown in Fig. 2.

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