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

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Highlights:

- permafrost aggradation triggered by late Holocene cooling led to warming climate forcing
- bare peat surfaces were more extensive in the past and led to stronger N_2O forcing, towards modern times the bare surface area has diminished
- sub-arctic peatlands have strong impact on atmospheric greenhouse gas dynamics but predictions for future development pathways remain uncertain

Abstract

Effects of permafrost aggradation on greenhouse gas (GHG) dynamics and climate forcing have not been previously quantified. Here, we reconstruct changes in GHG balances over the late Holocene for a sub-arctic peatland by applying palaeoecological data combined with measured GHG flux data, focusing on the impact of permafrost aggradation in particular. Our data suggest that permafrost initiation around 3000 years ago resulted in GHG emissions, thereby slightly weakening the general long-term peatland cooling impact. As a novel discovery, based on our chronological data of bare peat surfaces, we found that current sporadic bare peat surfaces in subarctic regions are probably remnants of more extensive bare peat areas formed by permafrost initiation. Paradoxically, our data suggest that permafrost initiation triggered by the late Holocene cooling climate generated a positive radiative forcing and a short-term climate warming feedback, mitigating the general insolation-driven late Holocene summer cooling trend. Our work with historical data demonstrates the importance of permafrost peatland dynamics for atmospheric GHG concentrations, both in the past and future. It suggests that, while thawing permafrost is likely to initially trigger a change towards wetter conditions and consequent increase in CH_4 forcing, eventually the accelerated C uptake capacity under warmer climate may overcome the thaw effect when a new hydrological balance becomes established.

Introduction

The carbon (C) stock stored in currently frozen peatlands is large, nearly 200 Pg (Hugelius et al., 2020), and is vulnerable to permafrost thaw (Borge et al., 2017). However, there are complex, poorly understood interactions between peat accumulation, hydrology and vegetation changes (Hugelius et al., 2014; Olefeldt et al., 2016; Schuur et al., 2015; Zhang et al., 2018b). Ecosystem-atmosphere flux measurements of the key GHGs, i.e. carbon dioxide (CO_2), methane (CH_4) and nitrous oxide (N_2O), from sub-arctic areas have shown considerable differences between different habitat microforms, such as the dry uplifted permafrost mounds, vegetated or bare, and the subsided non-permafrost fen habitats (Bäckstrand et al., 2010; Voigt et al., 2017). Permafrost initiation involves peatland surface upheaval that results in drying of the peat surface, which is often prone to abrasion and erosion processes (Seppälä, 2011). In general, all vegetated surfaces, wet or dry, act as net sinks of C (Gorham, 1991) in contrast to bare peat surfaces which do not sequester C due to absence of plants but are substantial net sources of CO_2 because of high rate of organic matter decomposition of the dry oxic surface peat and small sources of CH_4 to the atmosphere (Marushchak et al., 2013, 2016; Voigt et al., 2017). These bare peat surfaces on uplifted permafrost peatlands are typical landscape features in permafrost environments in Canada (Zoltai and Tarnocai, 1975), Scandinavia (Seppälä, 2003), European Russia (Kaverin et al., 2016) and Siberia (Kaverin et al., 2016; Seppälä 2003; Ogneva, 2016; Zoltai 1995). The non-permafrost fens have a dual effect on climate: they are generally stronger CO_2 sinks than ombrotrophic peatland surfaces due to higher productivity and slow decomposition in wet, anoxic conditions, but at the same time their CH_4 emissions are high (Marushchak et al., 2016; Nykänen et al., 2003; Turetsky et al., 2014). Typically, the net climatic forcing of the fens is positive (warming) at century scales because the CH_4 emissions offset the CO_2 uptake (Hugelius et al., 2020; Johnston et al., 2014). Consequently, the predicted changes in environmental conditions leading to changes in distributions of landscape components will largely determine the magnitude and direction of sub-arctic carbon-feedbacks to climate change (Deng et al., 2014; Johnston et al., 2014; Swindles et al., 2015; Zhang et al., 2018a).

Compared to C, studies on nitrogen (N) processes and, particularly, emissions of N_2O are rare in the sub-arctic, although currently N_2O is contributing ca. 6% to the global warming due to well-mixed GHGs (IPCC, 2013), and N_2O emissions from permafrost-affected soils could contribute as much as 7.1% to the global N_2O budget (Voigt et al., 2020). Due to the low availability of reactive N in cold soils with low N mineralization rates (Nadelhoffer et al., 1991), N_2O-related climate feedbacks have so far been considered unimportant for the sub-arctic, but Voigt et al. (2020) showed that climate change related disturbances increase N_2O emissions in permafrost regions. Contrary to expectations, bare peat surfaces on permafrost peatlands, where reactive N availability for microbial processes is enhanced by well-drained conditions and absence of plant N uptake have been identified as N_2O emission hotspots (Marushchak et al., 2011; Repo et al., 2009). At the same time, the adjacent vegetated peat surfaces do not emit N_2O (Marushchak et al., 2011; Repo et al., 2009). As a first back-of-the-envelope calculation, the global source strength of N_2O from the current bare peat surfaces in the sub-arctic was estimated to be ca. 0.1 Tg N_2O yr^{-1} (Repo et al., 2009) which falls within the range estimated for current industrial processes (IPCC, 2013).

Valuable information is stored in thick sub-arctic peat deposits, which can help to unravel how the GHG flux dynamics of these peatlands in the past responded to changing climate, thus providing us means to predict the future. To our knowledge, none of the previous studies has quantified the long-term post-glacial radiative forcing (RF) of sub-arctic peatlands, in particular, while future RF trajectories following permafrost thaw were recently estimated and modelled (Hugelius et al., 2020). Previous Holocene RF reconstructions are available for non-permafrost peatlands, and accordingly they do not take into account permafrost dynamics or initiation of bare peat surfaces; also the N_2O emission component is missing (Frolking and Roulet, 2007; Mathijssen et al., 2017; Piilo et al., 2020). Thus, to fill this gap, we carried out detailed case studies for permafrost peat cores collected from six locations, three from NE European Russia (Seida, Rogovaya, Indico), two from northernmost Finland (Kevo, Kilpisjärvi) and two peatlands in northern Sweden (Tavvavuoma) (Fig. 1). For Tavvavuoma, previously published chronological data exist for the habitats covered by vegetation (Sannel et al., 2017). To complement these, we dated two additional surface samples from Tavvavuoma and Rogovaya, but now collected on the bare peat surfaces. Chronological data from Russia and Finland were supplemented with subfossil plant data. These studies, with Seida as the key site, provided us detailed background information of past and present permafrost peatland dynamics. All study sites are characterised by a mixture of shrub–lichen–moss tundra vegetation including taxa such as *Betula nana*, *Empetrum nigrum*, *Rubus chamaemorus* and, on lawns, *Eriophorum* spp., *Sphagnum fuscum*, *Polytrichum strictum* and *Dicranum elongatum* are the dominant bryophytes on hummocks, while on wetter depressions *Sphagnum lindbergii* is common. Bare peat surfaces are lacking all living flora (Fig. 1). To model the past RF pattern for the Seida site over the last 3000 years, we used locally obtained palaeoecological data in combination with on-site measured GHG fluxes. In addition, we used high-resolution spatial satellite images from the Seida site to capture possible changes in the bare peat surface distribution and area over the last decade.

Methods

Sediment coring

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

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

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

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

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

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

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

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

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

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

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

Plant macrofossil analysis

Plant macrofossils were analysed for Seida BS I and Seida VS I, for Indico BS I and Indico VS I, and for Kevo BS and Kilpisjärvi BS. The plant macrofossil subsample size was 5 cm^3. The subsamples were rinsed under running water and the material retained on a 140-µm sieve was examined under a stereomicroscope. The species were identified using a high power light microscope. The proportions of the different plant remains were visually estimated according to the protocol described by Väliranta et al. (2007).

Greenhouse gas flux data

Present-day habitat-specific GHG fluxes at the Seida study site were used to represent the peatland GHG fluxes before and after permafrost initiation (Table 1). We used the annual GHG flux estimates for permafrost bogs (vegetated and bare surfaces) and non-permafrost fens measured at the site in October 2007 – October 2008. The CO_2 (Marushchak et al., 2013), CH_4 (Marushchak et al., 2016) and N_2O (Marushchak et al., 2011) fluxes were monitored by chamber techniques and a snow-gradient method as a part of a regional GHG balance assessment. To our knowledge, this is the only available dataset from sub-arctic peatlands with year-round flux estimates for all three GHGs.

Reconstruction of the habitat changes and radiative forcing calculations

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

RF was calculated for the difference in the emission/uptake rates of CO_2, CH_4 and N_2O that occurred within the present permafrost peatland area as a result of the habitat-type changes described above. The temporal variation of mean fluxes within this area (Fig. 2B, C, D) was estimated by multiplying the areal development of habitats (Fig. 2A) by the present-day habitat-specific flux densities measured within the study area (Table 1). The GHG flux dynamics directly related to climate, such as those linked to variations in temperature, precipitation and ground water level, were not explicitly accounted for. However, they were included in the analysis indirectly through the habitat-type changes considered.

RF was calculated annually for CO_2, CH_4 and N_2O with a sustained impulse–response model (Lohila et al., 2010; Piilo et al. 2020). This RF model includes a parameterization of the atmospheric lifetime and radiative efficiency for each gas. The model input data consist of the fluxes of CO_2, CH_4 and N_2O within the study area (Fig. 2B, C, D) and the atmospheric background concentrations of these gases (Köhler et al., 2017), both estimated annually during the study period. RF was calculated as a marginal effect with respect to the varying background concentration assuming instantaneous atmospheric mixing and globally uniform concentration distribution (Lohila et al., 2010). The annual atmospheric GHG pulses were modelled to decay according to characteristic perturbation time scales corresponding to global biogeochemical cycles. For CO_2, this was implemented as a weighted sum of four exponential functions (Joos et al., 2013), whereas for CH_4 and N_2O a first-order decay was assumed (IPCC, 2013). In each year, the effect of all preceding pulses was integrated to obtain the time series of atmospheric concentration changes. The instantaneous RF resulting from these concentration changes was calculated with the parameterization of Etminan et al. (2016), which takes into account the spectral interactions between CO_2, CH_4 and N_2O. For more details of the RF model employed here, see Lohila et al. (2010) and Piilo et al. (2020).

Satellite image analysis

To determine the dynamics of bare peatland surface in the recent past, we compared a QuickBird image acquired on 6 July 2007 and a WorldView-3 image from 9 August 2015. Both images were resampled to the 2.4-m pixel size, and the same bands (blue, green, red, near-infrared) were used for both images. The images were first segmented using full lambda schedule segmentation and then classified using one-class and binary approaches. The satellite image classifications and their accuracy depend on the classification procedure applied (Mack et al., 2014; Stenzel et al., 2017). To reduce a potential bias due to method selection, the bare peat areas were classified using four different classification methods: random forest, rotation forest, one-class support vector machine and biased/binary support vector machine classifiers. Each of these was applied in two settings: fully supervised and with the help of positive and un-labeled samples. In the training of the classifiers, field data from the summers 2007 and 2016 were used. Different methods produced to some extent differing results, but as there is no simple criterion to select the best method, we reported the consensus of five methods, while the consensus of three and seven methods were used as the upper and lower range of the uncertainty estimate, respectively (Räsänen et al., 2019).

Results

Reconstructed permafrost peatland dynamics and initiation of bare peat formations

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

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

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

More detailed plant data and chronologies from Tavvavuoma peat records were published in Sannel et al. (2017), but new information was that the bare peat surfaces at Tavvavuoma were also old: 5170 and 5800 cal yr BP (Supplementary Table 1). As a probable result of erosion, extensive late Holocene hiatuses in peat accumulation have been recorded in the VS peat cores from this site (Figs. 3, 4), and old peat ages around 3000–4000 cal yr BP are common at relatively shallow depths (~30 cm) (Sannel et al., 2017). These VS chronologies indicate revegetation processes after periods of peat erosion, similar to the Seida study sites. In contrast to the chronological patterns detected for Russia and Sweden, the bare peat surfaces in Finnish Lapland represented the present time, with ages of 2007 CE at Kevo BS I and 2006 CE at Kilpisjärvi BS I. The plant data from Kevo do not indicate any clear succession, although after 19 cm the plant remains were more intact and the amount of UOM decreased. This might be related to the young age and incomplete decomposition process (Fig. 3). In the Kilpisjärvi record, there seems to be a clear change from wet to dry conditions at 23 cm. Below this depth, wet fen *Sphagna* prevail (Fig 3). The bottommost peat layers overlying the frozen peat yielded ages of 1485 cal yr BP (30 cm) and 4540 cal yr BP (30 cm) at Kevo and Kilpisjärvi, respectively (Figs. 3, 4). Slow accumulation rates/hiatus occur in the Kilpisjärvi record between 1570 and 4540 cal yr BP.

Reconstructed changes in greenhouse gas fluxes and radiative forcing

According to the habitat-specific GHG flux data, the permafrost aggradation and the subsequent large-scale formation of bare peat surface area had a clear impact on GHG dynamics and the associated radiative forcing in Seida, our intensive study site in western Russia (Figs. 2, 5). Likely, the improved drainage enhanced decomposition, and CO_2 uptake ceased in the absence of vegetation, resulting in a large increase in net CO_2 emissions (Marushchak et al., 2013). Similarly, the increase in bare peat surface area enhanced N_2O emissions (Fig. 2D). At the same time, CH_4 emissions ceased when the previously wet habitats became drier (Marushchak et al., 2016). These changes in GHG fluxes between the Seida peatland and the atmosphere, especially the emissions of CO_2 and N_2O, resulted in a positive RF, i.e. net warming effect on climate (Fig. 5).

Development of bare peat surfaces based on remote sensed data

High-resolution satellite data analyses show that within the analyzed area covering 1085 ha, of which 342 ha is uplifted peat bog, the bare peat surfaces have reduced during the last decades. The 2007 data show that bare surface areas covered 5.7 (4.3–8.4) ha in 410 (286–616) separate patches, while in 2015 they only covered 4.4 (3.1–5.2) ha in 318 (236–375) patches (mean of five different image classification methods, the range of different methods in parentheses) (Räsänen et al., 2019).

Discussion

Past permafrost peatland dynamics

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

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

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

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

Implications of permafrost dynamics on GHG emissions and radiative forcing.

According to our reconstruction for Seida, permafrost aggradation started to reduce CH_4 emissions about 3000 yr ago (Fig. 2C) and thus induced a negative RF, i.e. had a cooling effect (Fig. 5). The cooling effect increased for 1000 yr as non-permafrost fens, which are strong CH_4 emitters (Table 1), were replaced by permafrost bog (Fig. 2A). Due to the short atmospheric perturbation lifetime of CH_4 (ca. 12 yr; IPCC, 2013), this RF component remained relatively constant after the concentration change reached the level at which the surface flux and atmospheric decay rates were in equilibrium

(Fig. 5), i.e. soon after the flux change stabilized at 2000 cal yr BP (Fig. 2C). The gradual CH_4-RF change after this was not related to Seida but the global decrease in the atmospheric CH_4 concentration (Köhler et al., 2017). Similarly, the recent decrease of CH_4-RF resulted from the increasing concentration since the pre-industrial times, because RF was calculated here as a marginal effect of the local-scale contribution to the global concentration, which was assumed to follow a predefined trajectory (Köhler et al., 2017). Due to spectral saturation effects, radiative efficiency, i.e. the RF change per unit change in atmospheric mixing ratio, is progressively reduced with increasing background concentrations (IPCC, 2013; Etminan et al., 2016).

As the mean CO_2 flux within the Seida region changed substantially due to the peatland type change from fen to permafrost bog (Fig. 2A, B), and because CO_2 has a very long residence time in the atmosphere, the CO_2-induced RF increased until about 200 cal yr BP; it outweighed the CH_4-induced cooling already at 2000 cal yr BP (Fig. 5). The rapid decline of CO_2-RF after 200 cal yr BP predominantly results from the increase of the background atmospheric CO_2 concentration since the pre-industrial times, as explained above.

Although significantly smaller than the RF due to increased CO_2 emissions, the enhanced N_2O emissions from bare peat surfaces, resulting from the improved reactive N availability in well-drained conditions and the lack of plant N uptake, had a temporary warming effect on the climate system, which started to decline 2000 cal yr BP, when the bare surface areas started to diminish (Figs. 2, 5).

Overall, our study highlights the importance of sub-arctic peatlands for atmospheric GHG dynamics, affecting both the past and future climate. A recent modelling exercise suggests an increased C uptake capacity for high-latitude peatlands in the future (Gallego-Sala et al., 2018). This may substantially compensate for the predicted positive climate forcing impact from thawing permafrost, which is suggested to trigger a landscape change towards wetter conditions (Swindles et al., 2015) and a consequent increase in the CH_4-induced forcing (Hugelius et al., 2020). Our data support these assumptions and suggest further that a decreasing trend in the extent of bare peat surfaces reduces the climate warming feedback effect of thawing permafrost peatlands. However, large spatial variations can be expected for permafrost development pathways, which may also lead to landscape drying when new drainage channels open (Liljedahl et al., 2016; Loisel et al., 2020). Furthermore, it should be acknowledged that permafrost thawing leads to the release of volatile organic compounds (Li et al., 2020), as well as dissolved C and nutrients, whose radiative forcing and ultimate impact on climate remain unresolved.

Conclusions

Our data suggest that the landscape changes associated with permafrost initiation in the studied sub-arctic peatlands had a significant impact on GHG fluxes and the related RF over the late Holocene. The data confirm that sub-arctic peatlands are effective C sinks that globally act as cooling landscape elements. The modelled long-term RF pattern for the Seida is negative for the fen phase sustaining until the permafrost initiation at ca. 2000 cal yr BP, when the surface was lifted up resulting in replacement of wet fen by dry bog surfaces with bare peat and consequently leading to a substantial increase in the positive RF component. This was mainly due to the large CO_2 emissions originating from uplifted dry and abundant bare peat surfaces and the decreased productivity accompanied by erosion processes and disappearance of the plant cover. This landscape development, while decreasing CH_4 emissions, dramatically increased CO_2 and N_2O emissions. Our case studies from Russia, Finland and Sweden provide evidence for a large-scale formation of bare peat surfaces around 3000 cal yr BP due to the late Holocene permafrost aggradation. Palaeoecological data from Seida suggest larger-than-today biogenic N_2O emissions for the late Holocene due to formation of bare peat surfaces, which have since diminished due to revegetation. Paradoxically it seems that the insolation-driven late Holocene summer cooling in the Northern Hemisphere likely induced a widespread, compensating warming effect through CO_2 and N_2O emissions from permafrost peatlands that opposed the general cooling trend.

Author contributions

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

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Declaration of competing interest

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

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

	CO_2 flux (g CO_2 m^{-2} yr^{-1})	**CH_4 flux (g CH_4 m^{-2} yr^{-1})**	**N_2O flux (g N_2O 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]

Figure captions

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

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

Fig 2. **Color figure** A) Permafrost aggradation-induced development of different land cover types assumed for the flux upscaling and radiative forcing calculations. B-D) Up-scaled late Holocene CO_2, CH_4 and N_2O fluxes for the Seida peatland.

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

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

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

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