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Ecosystem carbon response of an Arctic peatland to simulated permafrost thaw

Running head: Carbon fluxes of thawing permafrost peatlands

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ABSTRACT

Permafrost peatlands are biogeochemical hot spots in the Arctic as they store vast amounts of carbon. Permafrost thaw could release part of these long-term immobile carbon stocks as the greenhouse gases (GHGs) carbon dioxide (CO_2) and methane (CH_4) to the atmosphere, but how much, at which time-span and as which gaseous carbon species is still highly uncertain. Here we assess the effect of permafrost thaw on GHG dynamics under different moisture and vegetation scenarios in a permafrost peatland. A novel experimental approach using intact plant–soil systems (mesocosms) allowed us to simulate permafrost thaw under near-natural conditions. We monitored GHG flux dynamics via high-resolution flow-through gas measurements, combined with detailed

monitoring of soil GHG concentration dynamics, yielding insights into GHG production and consumption potential of individual soil layers. Thawing the upper 10–15cm of permafrost under dry conditions increased CO_2 emissions to the atmosphere (without vegetation: 0.74±0.49 vs. 0.84±0.60g CO_2–C $m^{-2}d^{-1}$; with vegetation: 1.20±0.50 vs. 1.32±0.60g CO_2–C $m^{-2}d^{-1}$, mean±SD, pre- and post-thaw, respectively). Radiocarbon dating (^{14}C) of respired CO_2, supported by an independent curve fitting approach, showed a clear contribution (9–27%) of old carbon to this enhanced post-thaw CO_2 flux. Elevated concentrations of CO_2, CH_4, and dissolved organic carbon at depth indicated not just pulse emissions during the thawing process, but sustained decomposition and GHG production from thawed permafrost. Oxidation of CH_4 in the peat column, however, prevented CH_4 release to the atmosphere. Importantly, we show here that, under dry conditions, peatlands strengthen the permafrost–carbon feedback by adding to the atmospheric CO_2 burden post-thaw. However, as long as the water table remains low, our results reveal a strong CH_4 sink capacity in these types of Arctic ecosystems pre- and post-thaw, with the potential to compensate part of the permafrost CO_2 losses over longer timescales.

1. INTRODUCTION

Permafrost soils are large carbon (C) reservoirs, storing ~1035Pg (=1035 billion tons) of organic C in the upper 3m (Hugelius *et al.*, 2014). These vast C stocks have accumulated over thousands of years in the form of frozen and seasonally thawed soil, litter and peat (Koven *et al.*, 2011). Thawing of permafrost as a result of climate warming exposes these long-term immobile belowground C stocks to microbial decomposition and remobilization, leading to the release of the greenhouse gases (GHGs) carbon dioxide (CO_2) and methane (CH_4) to the atmosphere (Hayes *et al.*, 2014). As enhanced vegetation productivity is expected to compensate little to none of this permafrost C release (Abbott *et al.*, 2016), the increased concentration of these gases within the atmosphere will further amplify warming (Dorrepaal *et al.*, 2009, Hobbie *et al.*, 2002, Schuur *et al.*, 2013). However, the magnitude

of this permafrost–C feedback is poorly constrained (McGuire *et al.*, 2018) and not included in current IPCC projections, likely underestimating the climate feedback of the Arctic (Ciais *et al.*, 2013, Koven *et al.*, 2011, Schaefer *et al.*, 2014). Recent climate simulations predict an additional warming of ~0.2°C caused by permafrost C loss by the end of this century (Burke *et al.*, 2017, Schaefer *et al.*, 2014).

Permafrost is warming across the globe (Biskaborn *et al.*, 2019) and within the last two decades upper permafrost temperatures have risen by 0.5–2.0°C (Romanovsky *et al.*, 2010). Subarctic regions, where permafrost temperatures are already close to zero, are particularly vulnerable to near-term C losses with permafrost thaw (Koven *et al.*, 2015). These areas, underlain by discontinuous and sporadic permafrost, currently experience extensive permafrost degradation (Sweden: Åkerman & Johansson, 2008, Norway: Borge *et al.*, 2017, Canada: Helbig *et al.*, 2017a, Alaska: Lara *et al.*, 2016, Russia: Romanovsky *et al.*, 2010). The Subarctic is also the region where highly sensitive, warm permafrost coincides with the occurrence of vast peatlands (Gorham, 1991). These organic soils, with their thick peat deposits, are biogeochemical hot spots in the Arctic, as they are by far the largest C reservoirs (Gorham, 1991, Hugelius *et al.*, 2014, Tarnocai *et al.*, 2009), storing ~296 Pg C (0–3m, land cover classes histosols and histels; Hugelius *et al.*, 2014) – almost one third of the total organic C stored in the upper 3m of soils in the permafrost region. About half of these C stocks (147 Pg) occur in organic soils underlain by permafrost (histels; Hugelius *et al.*, 2014). Due to their location in the rapidly warming southern Arctic, and their large ice content in the porous peat material, permafrost peatlands are vulnerable to thaw and thermokarst formation (Hugelius *et al.*, 2012, Sannel & Kuhry, 2011), and degradation of permafrost peatlands is observed in the entire subarctic region (Baltzer *et al.*, 2014, Borge *et al.*, 2017, Helbig *et al.*, 2017a, Malmer *et al.*, 2005).

Thawing of permafrost (ground that remains continuously frozen for at least two consecutive years) can occur either gradually, seen as a deepening of the active layer (annually thawing soil layer above the permafrost), or more abruptly, when thawing of ice-rich permafrost creates collapse features

and thermokarst (Hugelius *et al.*, 2011, Olefeldt *et al.*, 2016, Schuur *et al.*, 2008). Ground collapse severely alters site hydrology, leading to either drying or wetting depending on local drainage conditions. However, hydrological and landscape changes associated with permafrost thaw and associated changes in C release are difficult to predict, thereby posing a large uncertainty in predicting the future C balance in these regions. Currently, we lack sufficient understanding of the ratio of CO_2 vs. CH_4 of total gaseous C release, which will have important consequences for radiative forcing due to a ~30 times higher warming potential of CH_4 per mass unit (Knoblauch *et al.*, 2018, Myhre *et al.*, 2013, Schädel *et al.*, 2016, Schuur *et al.*, 2015). An increasing number of studies show that permafrost thaw promotes CO_2 and CH_4 production potential in soils (Hodgkins *et al.*, 2014, Schädel *et al.*, 2016). Hence, the atmospheric C release from permafrost soils is anticipated to increase substantially as permafrost thaws (Koven *et al.*, 2011, Koven *et al.*, 2015, Schneider von Deimling *et al.*, 2012, Schuur *et al.*, 2009, Zhuang *et al.*, 2006). While the largest C losses are expected to occur when thawing takes place under oxic conditions due to the proportionally larger production of CO_2 vs. CH_4 (Lee *et al.*, 2012, Schädel *et al.*, 2016, Schuur *et al.*, 2015, Treat *et al.*, 2014), recent long-term incubations predict an equally large permafrost–C feedback from anoxic soils, promoted by CH_4 production (Knoblauch *et al.*, 2018).

Despite growing evidence of enhanced gaseous C production in thawing permafrost soils, the effect of permafrost thaw on the ecosystem C balance remains poorly constrained, and field observations contradict model projections (Schädel *et al.*, 2018). Some key uncertainties of the permafrost-carbon feedback are related to 1) changes in vegetation cover and moisture conditions post-thaw, and 2) transformation of carbon in the soil profile. The major reasons for current uncertainties are of a practical nature: simulating the direct effect of permafrost thaw on biogeochemical cycling, without creating a mixed signal of thawing, soil warming, snow depth, moisture and vegetation changes (Mauritz *et al.*, 2017, Salmon *et al.*, 2016) is near to impossible under *in situ* conditions. Soil incubation studies, on the other hand, using homogenized soil samples or sub-cores taken out of context of the intact soil system, are valuable tools to assess the C decomposability and temperature

sensitivity of gaseous C production from thawed permafrost (Schädel *et al.*, 2016, Treat *et al.*, 2015). However, while soil incubation studies provide insight into soil processes and their environmental controls, they provide limited insights into the role of vegetation and the diverse transport and biogeochemical transformation processes along the soil profile. In many cases, gaseous C production at depth is decoupled from soil surface C emissions, especially in peatlands (Blodau & Moore, 2003a): even if CO_2 and CH_4 production rates in or near the permafrost are high, gases can be consumed (reduction of CO_2 to CH_4, oxidation of CH_4 to CO_2) while diffusing upwards through the soil profile (Dorodnikov *et al.*, 2013). Further, downward leaching of nutrients and dissolved C from the surface and soil rooting zone to deeper soil layers can be an important process supporting microbial activity at depth (Corbett *et al.*, 2013, Voigt *et al.*, 2017a, Wild *et al.*, 2016). All these processes determine whether permafrost thaw results in a net increase or decrease in ecosystem C emissions.

To directly assess how permafrost thaw affects the ecosystem GHG balance of permafrost peatlands, we developed an experimental set-up that allowed us to sequentially increase the thaw depth in intact plant–soil systems (mesocosms), with treatments simulating different vegetation and moisture scenarios. We used a specifically designed flow-through system combined with a laser instrument to obtain continuous measurements of CO_2 and CH_4, and complemented our flux observations with radiocarbon dating (^{14}C) of CO_2 fluxes and peat, as well as detailed auxiliary measurements: concentrations of CO_2, CH_4, dissolved organic C (DOC) and microbial biomass in the whole unfrozen part of the peat profile, as well as soil physical-chemical parameters. We hypothesize that thawing of permafrost will substantially alter the peatland C budget compared to pre-thaw conditions by increasing old C release. Specifically, we expect post-thaw release of CO_2 and CH_4 previously trapped in the permafrost layer, seen as short-term emissions peaks, but also a more sustained gaseous C production at depth via the enhanced substrate pool of freshly thawed permafrost. We further expect post-thaw C emissions to be regulated by moisture conditions in the peat profile, with wet conditions reducing CO_2 emissions but instead promoting CH_4 production and release.

2. MATERIAL AND METHODS

2.1 Study site

The intact plant-soil systems (mesocosms) used in this study were collected in a palsa mire ("Peera Palsa", 68.88°N, 21.05°E) in the discontinuous/sporadic permafrost zone of Finnish Lapland. Peat plateaus and palsas, permafrost peatlands uplifted above the surrounding mires by frost heave, are a common feature in the Subarctic (Borge *et al.*, 2017, Kuhry, 2008, Seppälä, 2006). As a result of permafrost uplift, the water table in these permafrost peatlands is low (Estop-Aragonés *et al.*, 2018a, Nykänen *et al.*, 2003, Turetsky *et al.*, 2002). The uplifted palsa surface is covered by typical palsa vegetation, dominated by *Empetrum nigrum* subsp. *hermaphroditum* and other dwarf shrubs such as *Vaccinium vitis-idaea* L., *Betula nana* L., and herbaceous plants, such as *Rubus chamaemorus* L., as well as lichens (mostly *Cladonia* spp.). Mosses (*Dicranum* spp., *Polytrichum* spp., *Pleurozium* spp, *Sphagnum spp.*) occur in the wetter parts of the palsa. The vegetated palsa surface is interspersed with patches of bare peat, naturally free of vascular plants, occurring regularly in uplifted permafrost peatlands (Marushchak *et al.*, 2011, Repo *et al.*, 2009, Seppälä, 2003, Seppälä, 2006). The site is described in greater detail in the Supporting Information.

2.2 Collection of mesocosms and experimental design

We collected 16 intact peat mesocosms (Ø = 10 cm, length ~80cm) from vegetated (8 mesocosms with typical, low-statured palsa vegetation) and naturally bare (8 mesocosms without vascular plants and only covered sporadically with lichens) parts of the palsa complex, using a custom-made steel corer (Fig. S1) (Voigt *et al.*, 2017b). Due to the comparatively small surface area, and to keep root damage during sampling to a minimum, larger vascular plants such as *Betula nana* L. were excluded from the mesocosms. However, the vegetation on the mesocosms (*Empetrum nigrum* subsp. *Hermaphroditum*, interspersed with *Vaccinium vitis-idaea* L, *Rubus chamaemorus* L., mosses and

lichens) was representative of the palsa surface (Fig. S1). The peat cores extended from the active layer (thickness ~65cm) down to the upper permafrost (thickness ~15cm). The cores were kept intact and were frozen immediately upon sampling. We used a freezer with custom-made temperature control to ensure storage in mild freezing temperatures (minimum temperature: -5°C), representing natural winter conditions beneath the snow cover. Prior to mesocosm collection we measured *in situ* flux rates of CO_2 and CH_4 from each sampling location at the study site, using the manual chamber technique (see Supporting Information for details).

After five months of storage, mimicking the winter period, the mesocosms were set up in a climate-controlled chamber (BDR16 Reach-in plant growth chamber, CONVIRON, Winnipeg, Canada), allowing regulation of air temperature (adjusted to +10°C) and light levels (PAR at full light ≤ 800 µmol m^{-2} s^{-1}). The light levels were adjusted to represent a typical diurnal rhythm of the snow-free season in the region (18h full light, 4h of darkness, 1h of reduced light when transitioning from day to night and reverse).

We applied two distinct moisture treatments: while the water table in half of the mesocosms was kept at natural level (>50cm below surface, "dry"), we artificially raised the water table level in another subset of the cores to 5–10cm below surface ("wet"). The vegetation and moisture scenarios used in this study are referred to as DB (dry, bare), DV (dry, vegetated), WB (wet, bare), and WV (wet, vegetated). Step-wise thawing was achieved by placing the mesocosms in a saltwater-filled and glycol-circulated bath at temperatures below 0°C, as described earlier (Voigt *et al.*, 2017b). In short, we sequentially unfroze the mesocosms from top to bottom in 5–20cm increments during six thawing stages, each lasting four weeks (Table S1). After unfreezing the full peat profile, measurements continued for three months, resulting in a total duration of the experiment of 32 weeks.

2.3 Flow-through system for carbon dioxide and methane fluxes

For gas flux measurements, the mesocosms were permanently covered with transparent (allowing photosynthesis to take place) plexiglas chambers (OD = 121.2mm, ID = 120mm, h = 250mm, V = 2.8L) connected to an air in- and outflow via two three-way-valves (STERITEX® 3W, CODAN Medical, Lensahn, Germany). We continuously measured fluxes of CO_2 (Net ecosystem exchange, NEE) and CH_4 by means of a flow-through system (Fig. S1, Fig. S2). This kind of flow-through system has been successfully used with up to nine monoliths (Mastepanov & Christensen, 2009), but – to our knowledge – never with this number of replicates of large, intact mesocosms including permafrost. Gas fluxes were calculated using the difference between the gas concentration in each individual chamber (i.e. of each mesocosm) and a reference line with ambient (i.e. atmospheric) gas concentration (=16+1 mesocosms). For this purpose, we installed a reference core, which was filled with sterilized sand. A pump with flow control (flow rate ~4L/min), connected to an overflow exhaust, provided stable inflow of ambient, outdoor air to each of the mesocosms and to the reference line. To reduce evapotranspiratory losses from the mesocosms, the inflow air was humidified before reaching the mesocosm headspace. To minimize pressure perturbations inside the chambers, the outflow was kept steady by seventeen downstream pumps, equipped with water traps, pumping air from the individual mesocosms with a stable flow rate of 200 mL min^{-1} to a valve system (Fig. S1). The valve system (consisting of 16+1 valves) automatically switched the gas flow between the mesocosms every five minutes, directing the flow to an infrared laser for high-resolution CO_2 and CH_4 concentration measurements (DLT-100, Los Gatos Research (LGR), CA, USA). Ten weeks into the experiment the gas analyzer was swapped with another laser instrument (G-2301, Picarro, CA, USA), since the former was required for a field experiment. However, during the swap both analyzers were running simultaneously for three days, in order to eliminate possible artefacts of using different gas analyzers on measured flux rates. Concentrations measured with the LGR were adjusted to fit the Picarro factory calibration.

Net C fluxes were derived from the difference in gas concentration between the chamber headspace of the mesocosm (outgoing air) and the reference line (incoming air) (Mastepanov & Christensen, 2009), and calculated as follows:

$$F = \frac{\Delta c \times f \times M \times p \times 60 \times 24}{R \times T \times A \times 10^6}, \quad (1)$$

where F is the net flux [mg m^{-2} d^{-1}; positive for fluxes directed towards the atmosphere], Δc the difference in gas concentration [ppm], f the flow rate [L min^{-1}], M the molar mass of the gas [g mol^{-1}], p the atmospheric pressure [Pa], R the ideal gas constant [8.314 J $K^{-1}mol^{-1}$], T the temperature in the chamber headspace [K], and A the core surface area [m^2].

2.4 Carbon dioxide and methane along the soil profile

To determine the concentration of gases along the soil profile, we installed five custom-made soil gas collectors horizontally in each core at depths 5cm, 20cm, and 40cm below the surface, 10cm above the measured thaw depth, as well as 5cm below the measured thaw depth. The soil gas collectors consisted of a perforated nylon/polyamide tube (ID = 4mm, OD = 6mm, length = 10cm) wrapped in fine nylon net and connected to another nylon tube (ID = 2mm, OD = 4mm, length ~50cm) capped with a three-way-valve (STERITEX® 3W, CODAN Medical, Lensahn, Germany).

Soil gas sampling and analysis are described in detail by Voigt et al. (2017a, 2017b). Briefly, soil gas sampling followed two different methods, depending on whether the sample was taken below or above the water table level. When samples were taken below the water table level, the gas concentrations were analyzed from a 28mL dinitrogen (N_2) headspace after equilibration with a 7mL water sample. When samples were taken above the water table level, 15mL of sample were withdrawn from the gas collector. In both cases samples were transferred to pre-evacuated 12mL screw-cap vials (Labco Exetainer®, Labco, UK). For samples taken below the water table level we

used 25mL of the headspace gas, while for samples taken above the water table level we used the 15mL of sampled gas and diluted with 10mL of N_2 in the exetainers. All gas samples were analyzed via gas chromatography (Agilent 6890N, Agilent Technologies, Santa Clara, CA, USA), equipped with a flame ionization detector (FID) for CH_4 (Voigt *et al.*, 2017a). Carbon dioxide was analyzed using an infrared gas analyzer (Uras26 continuous gas analyzer, AO2000 series, ABB Analytical Systems, Zurich, Switzerland), requiring a small (1mL) sample volume. For both gas analyzers, samples with high concentration were diluted with N_2 to fit the standard range (Voigt *et al.*, 2017a).

To determine the amount of gas dissolved in pore water from the gas concentration in the equilibrated headspace, we calculated the temperature dependent solubility k_H of the individual gases based on Henry's law, with coefficients taken from Lide and Frederikse (1995):

$$k_H = k_H^\theta \times \exp\left(\frac{-\Delta_{soln}H}{R} \times \left(\frac{1}{T} - \frac{1}{T^\theta}\right)\right), \quad (2)$$

where k_H^θ is the Henry's law constant at standard temperature [CO_2: 0.0350 mol atm^{-1}, CH_4: 0.0014 mol atm^{-1}], $\frac{-\Delta_{soln}H}{R}$ the temperature coefficient [CO_2: 2400 K, CH_4: 1600 K], T the soil temperature at the depth where the sample was taken and T^ϑ the standard temperature [298.15 K]. See Supporting Information for details.

2.5 Dissolved organic carbon in soil pore water

We used Rhizon pore water samplers (Rhizosphere, Wageningen, The Netherlands) for non-destructive weekly to biweekly soil water sampling to cover the temporal variation of DOC. Water samplers were installed in three depths in each mesocosm: 5–10cm and 35–40cm below the soil surface (in the active layer) and 0–5cm below the maximum seasonal thaw depth (~65–70cm below the soil surface). Pre-evacuated 12mL screw-cap vials (Labco Exetainer®, Labco, UK) connected to the Rhizon tubes were used to sample pore water (Voigt *et al.*, 2017b). Pore water samples were

frozen until further analysis and amounts of DOC in the pore water were determined as described by Voigt *et al.* (2017a).

2.6 Soil analyses

Basic soil properties (soil organic matter content (SOM), total C and nitrogen (N) content as well as C to N ratio, bulk density, water-filled pore space (WFPS) and pH) were determined at the end of the experiment at 5–6 depths of each peat profile. Details on analyses of soil properties are given by Marushchak et al. (2011) and Voigt et al. (2017a, 2017b). Additionally, we determined the amounts of DOC, total dissolved N (TDN), and C and N stored in the microbial biomass using the chloroform fumigation extraction method: samples were fumigated in chloroform atmosphere for 24h, after which fumigated and non-fumigated samples were extracted using 0.5M K_2SO_4. Samples were analyzed with a TOC/TN analyzer (LiquicTOC II; Elementar, Hanau, Germany), and we corrected for incomplete extraction of microbial C (K_{EC} = 0.45) and N (K_{EN} = 0.54) (Brookes *et al.*, 1985, Vance *et al.*, 1987) for microbial biomass calculations.

2.7 Radiocarbon age of soil and respired carbon

To determine the age of respired C in the CO_2 flux before and after thawing we measured the ^{14}C (radiocarbon) content of CO_2 by using the molecular sieve sampling technique (Biasi *et al.*, 2014, Palonen & Oinonen, 2013). To avoid obtaining a signal masked by the high background of recently fixed C by vegetation we limited the ^{14}C analysis to the dry, bare mesocosms (DB, n = 4). High respiration derived from a recently fixed C pool would have otherwise interfered with the accurate detection of the changes in the soil ^{14}C signal.

We took samples twice during the experiment: the first sample was taken in week 15 directly before thawing the permafrost, with the whole active layer of the mesocosms being unfrozen (thaw depth ~65cm). The second sample was taken in week 32 at the end of the experiment, after the full peat profile, including the upper ~15cm permafrost, had been unfrozen for 12 weeks. Using an adaptive sample preparation line (Palonen *et al.*, 2013), the CO_2 samples were collected from surface emissions and analyzed for their radiocarbon ^{14}C content at the AMS facility at the University of Helsinki, as described by Tikkanen et al. (2004). Briefly, CO_2 samples were collected from closed chambers by first scrubbing the chamber with CO_2-free air to remove background CO_2. Then, CO_2 derived from surface emissions was passed through the molecular sieves until a minimum of 1mg of CO_2-C was collected. Additionally, subsamples of soil were dated from five layers along the peat profile of one of the replicates (DB 4). The ^{14}C content of the respired CO_2, expressed as percent modern C (pMC), was corrected for mass-dependent fractionation using $\delta^{13}C$ values. We corrected the obtained pMC values for air contribution in the molecular sieves by using an isotope mixing model, as described by Biasi et al. (2014, 2011), assuming a $\delta^{13}C$ value of soil respiration of -26‰ as is typical for C_3 ecosystems, and using an atmospheric concentration of 103.1±0.2 pMC (mean±SE for March/April 2013, data from Hyytiälä Forestry Field Station (61°51' N, 24°17' E); M. Oinonen, personal communication). Ages were calculated as conventional radiocarbon ages (years before present (BP), AD 1950 = 0 years BP), applying a radiocarbon decay equation with -8033 as the mean lifetime of ^{14}C (Stuiver & Polach, 1977).

2.8 Contribution of permafrost-derived carbon to the post-thaw carbon dioxide flux

To estimate the contribution of permafrost-derived CO_2 to post-thaw CO_2 fluxes during our experiment, we applied two independent approaches, based on 1) the radiocarbon age of the flux, and 2) curve-fitting of an exponential decay function.

2.8.1 Permafrost carbon contribution based on radiocarbon dates

To assess the contribution of permafrost-derived CO_2 to the overall CO_2 emissions after the full peat profile had been unfrozen, we used a two-pool isotope mixing model:

$$\text{Permafrost } CO_2\ (\%) = \left(\frac{AP^{14}CO_2 - BP^{14}CO_2}{PF^{14}CO_2 - BP^{14}CO_2} \right) \times 100\,, \qquad (3)$$

where $AP^{14}CO_2$ is the ^{14}C content of CO_2 derived from the completely unfrozen core including 15cm of permafrost (week 32, 12 weeks after unfreezing the permafrost, n = 4), $BP^{14}CO_2$ is the ^{14}C content of CO_2 emitted directly before thawing the permafrost (week 15, n = 3 due to too little amount of CO_2 captured in one of the molecular sieves), and $PF^{14}CO_2$ is the estimated age of CO_2 originating from the permafrost layer alone. Since the experimental set-up did not allow us to directly measure the ^{14}C content of permafrost CO_2, we estimated the ^{14}C content of this permafrost-derived CO_2 based on the ^{14}C content of the permafrost soil (Table S2; see Supporting Information for details).

2.8.2 Permafrost carbon contribution based on exponential decay function

To estimate the contribution of permafrost-derived CO_2 from all four treatments, while accounting for the higher decay rate of the more labile surface C pool (Schädel *et al.*, 2013), we fitted a 3-parameter exponential decay function to measured daily CO_2 flux rates (normalized to g CO_2-C kgC^{-1} d^{-1}) from weeks 1–20. This time period included the complete thawing of the active layer (weeks 1–16) as well as the active layer-permafrost interface (top 5cm of permafrost, weeks 17–20). We extended the exponential fits until the end of the experiment (week 32) and calculated the permafrost C contribution by comparing values measured during the permafrost thaw period (week 21 onwards) with values predicted by the exponential decay function. Periods of water table fluctuations in the wet mesocosms were excluded from the analysis (Table S3). Curve fitting was done in SigmaPlot version 13.0 and fits had to pass tests for normality and constant variance.

2.9 Cumulative greenhouse gas budget

For the calculation of cumulative C fluxes, flux rates, measured every ~90min per mesocosm, were interpolated linearly to obtain hourly flux rates. Cumulative sums of CO_2 and CH_4 fluxes were calculated for each thawing step (lasting 28 days), as well as for the whole duration of the experiment.

To comparatively assess the post-thaw release of all three important GHGs – CO_2, CH_4, and nitrous oxide (N_2O), we used previously published N_2O flux data from the same experiment (Voigt *et al.*, 2017b). Briefly, N_2O fluxes were measured 2–3 times per week via manual chamber sampling and subsequent analysis on a gas chromatograph (GC; Agilent 6890N, Agilent Technologies, Santa Clara, CA, USA). Cumulative sums of N_2O were derived by interpolating linearly between measurement points. To compare the radiative forcing strength of all three GHGs, we applied the commonly used Global Warming Potential (GWP) approach (Myhre *et al.*, 2013), and compared this approach with Sustained-flux Global Warming and Cooling Potentials (SGWP, SGCP) (Neubauer & Megonigal, 2015).

2.10 Statistical analyses

All statistical analyses were performed in R version 3.5.1. (R Core Team, 2018). Prior to statistical tests we assessed the distribution of data via visual inspection of histograms, density plots and Q-Q plots, in combination with the Shapiro-Wilk normality test. Statistical differences between CO_2 and CH_4 fluxes during thawing of the active layer vs. thawing of the permafrost layer were determined based on the four-week periods directly before thawing the permafrost (week 13–16) and after thawing the full permafrost (week 21–24). The lower active layer (thawed during weeks 13–16) and the permafrost layer both consisted of fen type peat material (Voigt *et al.*, 2017b), allowing for comparison of layers with similar peat quality. Due to the lower frequency of sampling, statistical differences for soil profile concentration of gases were calculated based on the full period of active

layer thawing (weeks 1–16) and thawing of the permafrost (weeks 17–32). We used Student's t-test for normally distributed variables and Welch's two-sample t-test when variables were not normally distributed. To test for differences between treatments in cumulative fluxes for each thawing step (CO_2, CH_4, N_2O, and the complete GHG budget), we applied a two-way ANOVA, coupled with Tukey's HSD post-hoc test. The ANOVA included surface type (bare/vegetated) and moisture (dry/wet) as explanatory variables (GHG ~ Type + Moisture). Periods of water table fluctuations in the wet mesocosm (water table level below 10cm) were excluded from the analysis when comparing mean pre- and post-thaw flux rates. However, emission peaks related to this temporary drying and re-wetting of peat were included when assessing cumulative GHG budgets, to account for labile C losses.

3 RESULTS

3.1 Carbon dioxide fluxes

All treatments showed net CO_2 release to the atmosphere (Fig. 1a). Fluxes of CO_2 (NEE) ranged from -0.91 to 61.34g CO_2–C m^{-2} d^{-1}, (Fig. S4–S7), averaging at 0.79±0.56 (DB), 1.41±0.81 (DV), 0.67±0.59 (WB), 1.02±0.98g CO_2–C m^{-2} d^{-1} (WV, mean±SD). Fluxes were higher when vegetation was present (Fig. 1a, Fig. 2, Table S3). While wet mesocosms displayed lower CO_2 fluxes than their dry counterparts (Fig. 2), the effect of moisture was not significant (Table S4). Importantly, although the surface layers initially displayed the highest overall CO_2 emission rates, these surface emissions declined as thawing of the active layer progressed, but we again observed a pronounced increase in CO_2 emissions, particularly in the dry mesocosms, during the later stage of the experiment, when thawing reached the permafrost layer (Fig. 2, Fig. 3, Table S3).

3.2 Methane fluxes

Methane fluxes over the whole duration of the experiment ranged from high uptake rates of -17.92mg CH_4–C m^{-2} d^{-1} to short-term emission peaks of 29.75mg CH_4–C m^{-2} d^{-1} (Fig. S4–S7), however, average fluxes showed CH_4 uptake over all treatments (DB: -2.17±1.63mg CH_4–C m^{-2} d^{-1}, DV: -3.54±4.20mg CH_4–C m^{-2} d^{-1}, WB: -0.32±0.51mg CH_4–C m^{-2} d^{-1}, WV: -0.11±0.41mg CH_4–C m^{-2} d^{-1}; mean±SD). The dry mesocosms (DB and DV) acted as clear sinks for CH_4, whereas the wet mesocosms were generally CH_4 neutral (Fig. 1b) but switched to CH_4 sinks after temporary drops in water table level (Fig. S3b). Thawing of permafrost did not increase CH_4 emissions, and had, in fact, a reverse effect: gradual deepening of the active layer, increasing the oxygenated soil volume, enhanced CH_4 uptake in the dry mesocosms, causing higher rates of CH_4 uptake post-thaw (Fig. 1b, Fig. 2, Table S3), and – except for one out of 16 mesocosms – permafrost thaw did not initiate CH_4 emissions. Methane uptake was largest in dry, vegetated mesocosms (DV), with maximum uptake rates of -11.9mg CH_4–C m^{-2} d^{-1} occurring post-thaw (mean: -3.8mg CH_4–C m^{-2} d^{-1}; Table S3).

3.3 Temporal and spatial dynamics of carbon dioxide, methane, dissolved organic carbon and microbial biomass in the soil profile

The soil profile concentrations of gas and dissolved C were dynamic over time and with depth. Higher CO_2 concentrations occurred in deeper soil layers, particularly after thawing the permafrost, and the high concentrations lasted until the end of the experiment (Fig. 4a, Table S5). Carbon dioxide accumulated especially in the wet mesocosms (Fig. 4a). There, CO_2 concentrations peaked at values >60 000 ppm (ambient: ~390 ppm, Table S5), with the largest concentrations occurring in the deeper active layer, near the active layer–permafrost interface. Concentrations of CH_4, on the other hand, were clearly elevated only in the lower part of the mesocosms, and especially in the

permafrost part (>300 ppm CH_4, Fig. 4b, Table S6). While some CH_4 peaks occurred in the peat profile directly after thawing, the mid- and upper active layer of all mesocosms (bare as well as wet) seemed to be zones of CH_4 consumption (Fig. 4b, Fig. S9–S11).

Concentrations of DOC displayed a similar trend as CO_2, with the largest DOC contents measured in the middle and lower layers of the peat profiles (Fig. 4c). Detailed soil analyses after complete thawing showed significantly larger amounts of DOC (and TDN) in the permafrost peat than in the active layer (Fig. S12, Table S9). Even though the largest amounts of microbial biomass C (and N) occurred in the surface soil (5cm below surface), microbial biomass C was larger in the permafrost compared to the lower active layer, especially in the wet mesocosms (Fig. S12).

3.4 Permafrost-derived carbon dioxide fluxes and age of respired carbon

Except for wet, vegetated mesocosms, the increase in CO_2 emissions post-thaw was significant across treatments compared to thawing of the active layer (weeks 21–24 vs. weeks 13–16, Fig. 2, Table S3). On average, post-thaw CO_2 fluxes were 15% higher (mean of all treatments, Table S3). When accounting for the different amounts of C exposed with each thaw stage (Fig. S13, S14), our curve fitting approach revealed a permafrost contribution (thawing of the upper 10–15cm of permafrost) to measured post-thaw CO_2 emissions of 22–31% (bare, DB) and 5–10% (vegetated, DV) when thawing occurs under dry conditions, and a small or no detectable permafrost contribution under wet conditions (Table 1, Fig. S15, Table S10)

Radiocarbon dating of soil and respired C of dry, bare mesocosms (DB) confirmed the permafrost contribution obtained via the curve fitting approach: a higher age of the post-thaw CO_2 flux of 1895±191yr BP (mean±SE) compared to the pre-thaw age (1542±158yr BP) (Fig. 3) suggests a maximum permafrost contribution of 23–27±5% (mean±SE, Table S10). Not accounting for the age

difference between bulk soil and respired C (Table S2) still resulted in a permafrost contribution of 16±4%.

3.5 Cumulative greenhouse gas budgets

Wet bare mesocosms displayed the lowest cumulative GHG emissions, expressed as global warming potential (GWP), on a 100yr time horizon (WB: 464g CO_2–eq m^{-2}, Fig. 5a). Dry conditions promoted GHG release (DB: 682g CO_2–eq m^{-2}), and the highest emissions occurred in vegetated mesocosms (WV: 763g CO_2–eq m^{-2}, DV: 837g CO_2–eq m^{-2}). The cumulative CH_4 fluxes were higher (P=0.050) under wet conditions, but neither the GHG balance (P=0.264) nor the CO_2 fluxes (P=0.351) differed significantly between moisture treatments (Table S4). In contrast, the vegetation cover played a role in regulating the cumulative CO_2 emissions, with significantly higher CO_2 emissions from vegetated mesocosms under both moisture regimes (P=0.045), affecting also the total GHG balance (P=0.081, Table S4).

4 DISCUSSION

The main goal of this study was to directly assess how permafrost thaw, simulated on intact mesocosms under near-field conditions, affects the atmospheric C balance of permafrost peatlands under various moisture and vegetation scenarios. We expected increased post-thaw CO_2 release under dry conditions, but enhanced CH_4 release if permafrost thaw results in a raised water table. Our results revealed a contribution of the exposed permafrost layer to post-thaw CO_2 fluxes under dry conditions (9–27%). Contrary to our expectations we did not observe enhanced CH_4 release from this type of peatland, despite elevated post-thaw CH_4 concentrations in the peat profile at depth. Instead, deeper active layers promoted the ecosystem's CH_4 sink function.

4.1 Gaseous carbon production and release from permafrost in post-thaw peatlands

We observed a detectable signal of permafrost C release from dry mesocosms, seen as sustained GHG production and increased CO_2 emissions post-thaw (Fig. 3, Fig. S15, Table S10). Due to the presence of more recalcitrant material at depth, surface soil generally accounts for the largest proportion of CO_2 production (Hicks Pries *et al.*, 2015, Walz *et al.*, 2017, Wang & Roulet, 2017), and CO_2 production rates often show a depth-dependent decline (Christensen *et al.*, 1999, Estop-Aragonés *et al.*, 2018a, Treat *et al.*, 2014). Peatlands, however, display a high organic C availability (Treat *et al.*, 2016) and the deep peat layers, preserved in the permafrost for centuries, can be relatively labile and produce a considerable amount of GHGs (Treat *et al.*, 2014, Wang & Roulet, 2017), showing a long-lasting sensitivity to warming (Dorrepaal *et al.*, 2009).

The higher radiocarbon age of respired C after permafrost thaw (Fig. 3) suggests, that this increase in post-thaw emissions was due to the contribution of older C pools, originating from the permafrost layers. The temporal and spatial dynamics of gases, DOC (Fig. 4a–c) and microbial biomass C and N (Fig. S12) in the peat column support the conclusion of enhanced permafrost C release: in both scenarios, dry and wet, CO_2 accumulated to a greater extent after thawing the permafrost, and both, CO_2 and DOC concentrations at depth increased with time after thaw and were largest at the end of the experiment, three months after thawing the permafrost (Fig. 4a, Fig. 4c). Together, these results clearly suggest not only the release of gaseous C previously trapped in permafrost, but a sustained decomposition at depth post-thaw, and on-going CO_2 production from the thawed permafrost peat material.

Our two independent estimates of the permafrost contribution to post-thaw CO_2 fluxes (curve-fitting: ~10% (vegetated), ~22% (bare), ^{14}C: ~23% (bare), dry scenario) fall within the range of those few studies presenting quantified estimates of old C contribution to soil respiration (11–28%: Estop-Aragonés *et al.*, 2018a, 4–22% (burned and unburned peat plateau): Estop-Aragonés *et al.*, 2018b, 4–23%: Schuur *et al.*, 2009). Unlike previous studies, however, our experimental design allows us to

provide a first, tentative estimate of the magnitude of changing C cycling patterns from a thawing permafrost peatland, with and without vegetation cover, immediately upon thaw. By directly linking enhanced CO_2 emissions to permafrost thaw, our study attests for the contribution of permafrost-derived C not only to respiration, but to ecosystem-scale CO_2 emissions.

Although our study was laboratory based, our mesocosm approach simulating *in situ* conditions allows us to draw conclusions on the post-thaw C balance of permafrost peatlands: first of all, the peat stratigraphy of the sampling site (bog peat underlain by fen-type peat material; Voigt *et al.*, 2017b) is representative for the majority (~80%) of uplifted permafrost peatlands in the Northern Hemisphere (Treat *et al.*, 2016). Second, measured C flux rates agreed well with *in situ* C fluxes at the study site, as well as CO_2 and CH_4 fluxes measured across a range of Eurasian permafrost peatlands (Fig. 6). While the studied palsa and other permafrost peatlands likely show larger *in situ* C uptake than we observed here due to better plant performance under field conditions, the vegetation on the mesocosms was active throughout the experiment, and CO_2 fluxes were showing diurnal variation following the established light cycle (Fig. S16–S17). Additionally, permafrost peatlands and other Arctic ecosystems frequently show net C losses during summer, and increasingly so as soils continue to warm (Grogan & Chapin, 2000, Lund *et al.*, 2012, Lundin *et al.*, 2016, Nykänen *et al.*, 2003, Oechel *et al.*, 1993, Voigt *et al.*, 2017a, Zamolodchikov *et al.*, 2000). Hence, recent climate change has weakened the cooling effect northern peatlands have exerted on our climate for the past ~10000 years (Frolking & Roulet, 2007). Recent field observations report C losses and a weakened CO_2 sink strength from peatlands spanning the Pan-Arctic, including boreal peatland landscapes (Euskirchen *et al.*, 2014, Helbig *et al.*, 2017a, Jones *et al.*, 2017, O'Donnell *et al.*, 2012).

We provide evidence that thawing peatlands may strengthen the permafrost–C feedback of the Arctic, especially if thawing occurs under dry conditions, or if enhanced vegetation growth is not able to compensate for increased belowground CO_2 losses. Our results highlight the vulnerability of deep, previously frozen peat to decomposition. Climate models neglecting the permafrost–C

feedback, particularly from peatlands, are thus likely underestimating CO_2 emissions from Arctic ecosystems as it continues to warm (Burke *et al.*, 2017, Schaefer *et al.*, 2014).

4.2 Effects of moisture conditions on post-thaw carbon fluxes

Wet sites are generally growing season sinks for CO_2 and sources of CH_4, resulting in an overall net C sink across ecosystem types, such as wet parts of palsa mires (Christensen *et al.*, 2012), wet sedge and tussock tundra (Lafleur *et al.*, 2012), and wetlands in permafrost peatland landscapes in tundra (Heikkinen *et al.*, 2002) and boreal regions (Helbig *et al.*, 2017a). Soil oxic conditions are a key regulator of soil CO_2 production (Schädel *et al.*, 2016, Treat *et al.*, 2014, Walz *et al.*, 2017), and the position of the water table level therefore critically governs the rate and magnitude of C emissions from peatlands (Blodau & Moore, 2003b, Moore & Knowles, 1989, Nykänen *et al.*, 2003, Regina *et al.*, 1999). Yet, whether the Arctic will become wetter or drier in a future climate is highly uncertain (Schuur *et al.*, 2015), and the patchiness of the mosaic-like Arctic landscape makes it difficult to predict future, and even current landscape-level C balances (Schneider von Deimling *et al.*, 2012, Shaver *et al.*, 2007, Sturtevant & Oechel, 2013).

The majority of studies currently predict a larger permafrost C feedback when thawing occurs under oxic conditions (Schädel *et al.*, 2016, Schuur *et al.*, 2015), with old C release from dry peat soils, but no old C contribution to the surface CO_2 flux from wet, thermokarst-affected areas (Estop-Aragonés *et al.*, 2018a, Estop-Aragonés *et al.*, 2018b). Interestingly, even though our study finds the permafrost C contribution to post-thaw CO_2 fluxes under wet conditions minor (Table 1), the cumulative CO_2 emissions in our study were not significantly lower in the wet mesocosms (Fig. 5, Table S4). We attribute the similarity among moisture treatments to two reasons: first, the important contribution of the well oxygenated upper 0–10cm of the soil profile to total respiration. Second, the cumulative CO_2 fluxes in the wet mesocosms were partly determined by short-term

emission peaks, associated with a temporarily lowered water table during the thawing process (Fig. S3a) and associated changes in peat redox chemistry caused by these water table fluctuations. These emission peaks show a reoxygenation of electron acceptors (Knorr & Blodau, 2009), but also indicate the presence of a labile C pool and active microbial community, well adapted to anaerobic conditions, as has been shown earlier for old peat soils (Diakova *et al.*, 2016). Hence, the timing and magnitude of CO_2 emissions from wet mesocosms was governed by the position of the water table which, when lowered, enabled rapid out-diffusion of CO_2. Water table fluctuations are a common phenomenon in northern peatlands (Komulainen *et al.*, 1998, Tuittila *et al.*, 1999). Thus, even though CO_2 emissions from thaw-affected peatlands might be small as long as the peat column stays well water saturated, our results show that seasonally or annually varying moisture conditions occurring post-thaw must clearly be considered when drawing conclusions on ecosystem-scale C emissions associated with permafrost thaw. Not only can labile C be released via on-site CO_2 emissions, but it can further be relocated to aquatic systems via leaching and runoff processes (Olefeldt & Roulet, 2012). Due to the tight coupling of the hydrological and the C cycle, and associated relocation of C emissions (Vonk & Gustafsson, 2013), predicting and quantifying post-thaw C emissions under wet conditions poses an even larger challenge than estimating the permafrost-C feedback in comparatively dry settings.

Unexpectedly, despite evident CH_4 accumulation at depth after permafrost thaw (Fig. 4b), wet conditions did not cause net CH_4 release to the atmosphere. Incubation experiments have shown that previously well-aerated soils that are exposed to sudden anoxic conditions display long lag-times in CH_4 production (Knoblauch *et al.*, 2018, Knoblauch *et al.*, 2013, Treat *et al.*, 2015), and even under field conditions thawed permafrost peat layers may contribute only little to surface CH_4 emissions (Cooper *et al.*, 2017). In comparably dry soils such as permafrost peatlands, where the soil microbial communities are well adapted to oxic conditions, methanogen populations are small, and only establish with time (McCalley *et al.*, 2014). Such well oxygenated sites display a high oxidation potential, and methanogenesis is additionally suppressed by drying and rewetting cycles (Knorr &

Blodau, 2009) and the presence of alternative electron acceptors like sulfate, nitrate and iron (Bridgham *et al.*, 2013, Neubauer *et al.*, 2005). We observed an accumulation of CH_4 only in the lower part of the peat profile (Fig 4b), consisting of fen-type peat material (Voigt *et al.*, 2017b), likely an active CH_4 source before permafrost uplift. These results show that, to predict future CH_4 release from permafrost, understanding permafrost aggradation history is highly important, as the site hydrologic conditions during permafrost aggradation determine the initial activity, presence, or absence of methanogens and methanotrophs upon thaw.

4.3 Short- and long-term peatland carbon response and post-thaw greenhouse gas balance

We observed comparatively high CO_2 emissions derived from the seasonally-thawing active layer (Fig. 1, Fig. 2). We attribute the initially high CO_2 fluxes to the presence of labile substrates in the undecomposed bog peat in the upper peat profile (Voigt *et al.*, 2017b), plant and root respiration, as well as fresh litter inputs from vegetation that stimulated microbial growth (Fig. S12) and thus heterotrophic respiration. The top 5cm of the vegetated peat profiles (both, dry and wet) exhibited the largest microbial biomass C (Fig. S12), indicating high microbial activity in the surface soil rooting zone. These surface emissions decreased over time (Fig. 3) with depletion of the labile surface C pool as litter and other recent plant inputs decomposed. The presence of vegetation, however, likely fueled microbial activity at depth, thus promoting decomposition of this more persistent C pool: we observed larger dissolved C and N pools at depth in vegetated mesocosms than in bare mesocosms (Fig. S12), indicating downward transport of C. Also, microbial biomass C and N pools in the peat profile were significantly larger when vegetation was present (C: P = 0.006, N: P = 0.003, Fig. S12, Table S9). The input of fresh, plant-derived organics can lead to a positive priming effect, actively driving the decomposition of old organic matter (Kuzyakov, 2010) and GHG production at depth (Corbett *et al.*, 2013, Voigt *et al.*, 2017a, Wild *et al.*, 2016, Wild *et al.*, 2014).

As our mesocosms approach indicates both C pools, young and old, are tightly linked. In field observations, with annual vegetation dynamics and rapid C turnover, the labile surface C pool may thus well dominate short-term, seasonal C emissions, thereby masking the permafrost-C feedback. But, even if small compared to seasonal vegetation C dynamics, permafrost thaw provides an additional, persistent C pool at depth, with the potential to affect the peatland C balance over long timescales. Depending on the thickness of the organic layer, a gradually increasing thaw depth (current rate in Northern Scandinavia: ~1cm yr^{-1}; Åkerman & Johansson, 2008), together with warming of soils, could fuel microbial decomposition at depth for centuries.

While our study demonstrates that permafrost thaw in Arctic peatlands will likely release an additional CO_2 burden to the atmosphere, the future GHG balance of thawing permafrost peatlands depends on moisture and vegetation changes, as well as on the dynamics of the other major greenhouse gases CH_4 and N_2O, both of which have a stronger potential to warm our climate than CO_2. Besides releasing CO_2, the dry mesocosms acted as sinks for CH_4, and as reported in our earlier study (Voigt *et al.*, 2017b), the bare mesocosms were a source for N_2O, and increasingly so with permafrost thaw. Commonly, the GWP approach (Myhre *et al.*, 2013) is used to compare the warming effect caused by different GHGs, projected to a 100yr time scale. However, the applicability of the GWP metrics to project long-term radiative forcing of peatlands is limited, as this approach assumes one-time pulse emissions (Neubauer & Megonigal, 2015) rather than sustained GHG production from steadily increasing permafrost C and N pools made accessible as thaw deepens. Additionally, the direction of gas transport has major implications for net radiative forcing, requiring different metrics when projecting GHG uptake and emissions (Neubauer & Megonigal, 2015).

Although the overall GHG budget of all four treatments was governed by CO_2 fluxes (Fig. 5), N_2O emissions from dry, bare mesocosms accounted for 14% of CO_2 emissions (GWP100; Fig. 5). The same approach places CH_4 uptake at 2–3% (bare vs. vegetated) of CO_2 emissions, and slightly higher (7–8%) when applying a shorter time span (20yr, Fig. S18). When considering the pronounced CH_4

sink capacity in dry mesocosms via the SGWP/SGCP approach (Neubauer & Megonigal, 2015), we show here that CH_4 uptake can compensate post-thaw ecosystem CO_2 emissions by 14%–19%, (20yr vs. 100yr time horizon), and up to 27% on a 500yr time scale (Fig. 5, Fig. S19).

Methane oxidation frequently occurs in ecosystems of the northern high latitudes (dry upland tundra: Bartlett & Harriss, 1993, Jørgensen *et al.*, 2015, Lau *et al.*, 2015, Christiansen *et al.*, 2015, D'Imperio *et al.*, 2017, Arctic peatlands: Flessa *et al.*, 2008, Malhotra & Roulet, 2015, upland forests: Olefeldt *et al.*, 2013). Methane fluxes are the balance between CH_4 production by methanogens under anoxic conditions, and CH_4 consumption under oxic conditions (Lai, 2009). Even though we observed enhanced CH_4 concentrations at depth after thaw (>300 ppm vs. ~1.9 ppm ambient concentration), a thick oxidative layer prevented CH_4 release to the atmosphere in both dry and wet mesocosms (Fig S8–S11). While CH_4 production may increase under long-term anoxic conditions and inflow of surrounding fen waters containing methanogens, our study emphasizes the need to consider transport and transformation pathways of CH_4 in the soil column when attempting to project the role of permafrost CH_4 release.

Current models predict increased CH_4 release from Arctic ecosystems as permafrost thaws, due to increased surface wetness (Anisimov, 2007, Deng *et al.*, 2014, Koven *et al.*, 2015, Wilson *et al.*, 2017), and field observation show increased CH_4 emissions from wet, thermokarst-affected sites (Christensen *et al.*, 2004, Helbig *et al.*, 2017b, Johnston *et al.*, 2014, Olefeldt *et al.*, 2013, Turetsky *et al.*, 2002). In contrast, our study emphasizes the important role CH_4 uptake may play in offsetting the permafrost-C feedback caused by CO_2 emissions, as long as conditions stay dry. This is an important finding, considering that, in fact, mounting evidence suggests that permafrost degradation will lead to a reduction in wetland extent (Avis *et al.*, 2011) by increasing runoff and drainage (Haynes *et al.*, 2018, Liljedahl *et al.*, 2016, Malmer *et al.*, 2005, Swindles *et al.*, 2015). Considering the vast Arctic landmasses, enhanced surface drying and deeper thaw is likely to increase the Arctic CH_4 sink, with potential repercussions on the global CH_4 budget. In light of the current overestimation of CH_4

emissions from northern wetlands (Saunois *et al.*, 2016), our study highlights the relevance of CH_4 uptake from well drained Arctic soils, such as uplifted permafrost peatlands, considering the potential of these dry surfaces to counterbalance wetland CH_4 emissions (D'Imperio *et al.*, 2017, Treat *et al.*, 2018). Overall, improving our understanding of local hydrological settings and vegetation dynamics will be key to predicting changes of the carbon cycle in a warming Arctic.

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Fig. 1: Carbon dioxide (CO_2) (a) and methane (CH_4) fluxes (b) from the four treatments (mean±SE, n = 4): DB = dry bare, WB = wet bare, DV = dry vegetated, WV = wet vegetated. Seasonal thaw = thawing of the active layer (0–65cm), permafrost = thawing of permafrost (65–80cm). To exclude the effect of a temporarily lowered water table level, CO_2 and CH_4 flux values in the wet mesocosms were discarded for the three days following initiation of each thawing stage, and when the water table dropped below 10cm during the experiment. Measured (hourly) flux rates (light green line) are shown with data gaps, whereas daily mean flux rates (dark green line) for these time

periods were interpolated linearly. The time series including periods with water table fluctuations are shown in Fig. S3. Thawing steps, week 1: Thawing down to ~20 cm, week 5: thawing down to ~40 cm, week 9: thawing down to 5 cm above the maximum seasonal thaw depth; week 13: thawing down to the maximum seasonal thaw depth; week 17: thawing down to 5 cm below the maximum seasonal thaw depth; week 21: thawing of the full core (15 cm below the maximum seasonal thaw depth). Flux rates of individual replicates are provided as Supporting Information (Fig. S4–S7).

Fig. 2: Mean daily fluxes of CO_2 and CH_4 for the four-week period before thawing the permafrost (week 13–16, thawing of the whole active layer) and the four week period after thawing the deeper permafrost (week 21–24, thawing of the whole core). Note deviating scaling of y-axis for CO_2 and CH_4. Flux peaks related to a thawing-induced, temporarily lowered water table in the wet mesocosms were removed from the analysis; see Table S3 for details. Data are shown for bare and vegetated mesocosms with natural ("dry") and artificially raised (5–10 cm below surface, "wet")

water table, referred to as DB = dry bare, DV = dry vegetated, WB = wet bare, WV = wet vegetated. Boxplots show mean (thick black line), median (dotted black line), upper and lower quartile, as well as the smallest and largest value. n = 4 for all treatments except for DV post-thaw (n = 2). Levels of significance: ***significant at $P \leq 0.001$, **significant at $P \leq 0.01$, *significant at $P \leq 0.05$.

Fig. 3: Cumulative carbon dioxide (CO_2) and methane (CH_4) fluxes, calculated as CO_2–eq during each thawing step (lasting four weeks each). Seasonal thaw = thawing of the active layer (0–65cm), permafrost = thawing of permafrost (65–80cm). Data are shown for bare and vegetated mesocosms with natural ("dry") and artificially raised (5–10 cm below surface, "wet") water table, referred to as DB = dry bare, DV = dry vegetated, WB = wet bare, WV = wet vegetated. Boxplots show median (thick black line), upper and lower quartile, as well as the smallest and largest value. n = 4 unless otherwise specified. Arrows used to emphasize increasing trend in CO_2 emissions when thawing the permafrost layer. Inset in DB: Radiocarbon (^{14}C) age of C respired. Thick black line in boxplots for ^{14}C age represents mean, dotted black line is the median.

Fig. 4: Soil profile concentrations of gaseous and dissolved carbon dioxide (CO_2), methane (CH_4) and dissolved organic carbon (DOC) in mesocosms for the duration of the experiment. Seasonal thaw = thawing of the active layer (0–65cm), permafrost = thawing of permafrost (65–80cm). Data are shown for bare and vegetated mesocosms with natural ("dry") and artificially raised (5–10 cm below surface, "wet") water table, referred to as DB = dry bare, DV = dry vegetated, WB = wet bare, WV = wet vegetated. Contour plots were created by linear interpolation between measurement points. For CO_2 and CH_4 the number of measurement points per mesocosm was 26 and for DOC the figure includes 15 measurement points. White areas: no data available due to frozen soil conditions. Thick red line indicates thaw depths over time, dashed lines indicate thawing steps, and thick grey line

marks a zone of below ambient CH_4 concentration. Thawing steps, week 1: Thawing down to ~20 cm, week 5: thawing down to ~40 cm, week 9: thawing down to 5 cm above the maximum seasonal thaw depth; week 13: thawing down to the maximum seasonal thaw depth; week 17: thawing down to 5 cm below the maximum seasonal thaw depth; week 21: thawing of the full core (15 cm below the maximum seasonal thaw depth). Note logarithmic scaling of colour scale for CH_4. Gas concentrations of individual replicates are provided as Supporting Information (Fig. S8-S11).

Fig. 5: Cumulative fluxes of carbon dioxide (CO_2), methane (CH_4), nitrous oxide (N_2O), and total greenhouse gas (GHG) emissions expressed as (a) global warming potential (GWP) and (b) sustained-flux global warming/cooling potentials (SGWP/SGCP) from the four treatments mean±SE, n = 4): DB = dry bare, WB = wet bare, DV = dry vegetated, WV = wet vegetated. Seasonal thaw = thawing of the active layer (0–65cm), permafrost = thawing of permafrost (65–80cm). The cumulative sum of total GHG emissions (dashed black line) and of CO_2 (light blue line) are indicated on the y-axis. Grey areas show uncertainty (SE) of CO_2, CH_4 and N_2O fluxes. Data for N_2O fluxes are taken from Voigt *et al.*, 2017. Conversion factors for (a) CH_4: 28, N_2O: 265, (b) CH_4 emissions: 45, CH_4 uptake: 203, N_2O emissions: 270, N_2O uptake: 349. Thawing steps, week 1: Thawing down to ~20 cm, week 5: thawing down to ~40 cm, week 9: thawing down to 5 cm above the maximum seasonal thaw depth; week 13: thawing down to the maximum seasonal thaw depth; week 17: thawing down to 5 cm below the maximum seasonal thaw depth; week 21: thawing of the full core (15 cm below the maximum seasonal thaw depth).

Fig. 6: Mean measured flux rates of carbon dioxide (CO_2) and methane (CH_4) from bare and vegetated mesocosms (weeks 1–16, thawing of the active layer) and *in situ* measurements at the sampling site ("Peera Palsa" near Kilpisjärvi, 68.88°N, 21.05°E), as well as published, *in situ* flux rates

from a range of permafrost peatlands in northern Finland (palsa mires) (Marushchak *et al.*, 2011, Nykänen *et al.*, 2003) and western Russia (peat plateau) (Voigt *et al.*, 2017a). Spring: June, summer: July and August, autumn: September, n. d.= not determined. Boxplots show median (thick black line), upper and lower quartile, as well as the smallest and largest value.

Table 1: Permafrost contribution to carbon dioxide (CO_2) flux in the weeks following permafrost thaw for each experimental treatment. Flux peaks related to a thawing-induced, temporarily lowered water table in the wet mesocosms were removed from the analysis; see Table S3 for details. Flux values are shown as mean±SD for the four-week period after thawing the permafrost part of the mesocosms (week 21–24); further time periods are presented in Table S10.

Treatment	$\Delta_{measured - predicted}$ ($g\ CO_2–C\ m^{-2}\ d^{-1}$)	Permafrost contribution
dry bare (DB)	0.20 ± 0.17	22 %
dry vegetated (DV)	0.16 ± 0.22	10 %
wet bare (WB)	0.02 ± 0.08	4 %
wet vegetated (WV)	-0.01 ± 0.01	-2 %