Global Change Biology

Global Change Biology (2015), doi: 10.1111/gcb.12875

A pan-Arctic synthesis of CH_4 and CO_2 production from anoxic soil incubations

CLAIRE C. TREAT[1,*], SUSAN M. NATALI[2], JESSICA ERNAKOVICH[3,†], COLLEEN M. IVERSEN[4], MASSIMO LUPASCU[5], ANTHONY DAVID MCGUIRE[6], RICHARD J. NORBY[4], TANIYA ROY CHOWDHURY[7], ANDREAS RICHTER[8,9], HANA ŠANTRŮČKOVÁ[10], CHRISTINA SCHÄDEL[11,‡], EDWARD A. G. SCHUUR[11,‡], VICTORIA L. SLOAN[4], MERRITT R. TURETSKY[12] and MARK P. WALDROP[13]

[1]*Earth Systems Research Center, Institute for the Study of Earth, Oceans & Space, University of New Hampshire, 8 College Road, Durham, 03824 NH, USA,* [2]*Woods Hole Research Center, 149 Woods Hole Road, Falmouth, 02540 MA, USA,* [3]*Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, CO, USA,* [4]*Environmental Sciences Division and Climate Change Science Institute, Oak Ridge National Laboratory, One Bethel Valley Road, Building 1062, Oak Ridge, 37831-6422 TN, USA,* [5]*Department of Earth System Science, University of California, Croul Hall, Irvine, 92697 CA, USA,* [6]*U.S. Geological Survey, Alaska Cooperative Fish and Wildlife Research Unit, University of Alaska Fairbanks, 214 Irving I Builidng, Fairbanks, 99775 AK, USA,* [7]*Biosciences Division, Oak Ridge National Laboratory, 1 Bethel Valley Road, MS 6038, Oak Ridge, 37830 TN, USA,* [8]*Department of Microbiology and Ecosystem Science, University of Vienna, Althenstrasse 14, 1090, Vienna, Austria,* [9]*Austrian Polar Research Institute, Althenstrasse 14, 1090, Vienna, Austria,* [10]*Department of Ecosystem Biology, University of South Bohemia, Branisovska 31, České Budějovice 37005, Czech Republic,* [11]*Department of Biology, University of Florida, 421 Carr Hall, PO Box 118525, Gainesville, FL 32611, USA,* [12]*Department of Integrative Biology, University of Guelph, Science Complex, Guelph, N1G 1G2 ON, Canada,* [13]*U.S. Geological Survey, 345 Middlefield Rd, MS 962, Menlo Park, 94025 CA, USA*

Abstract

Permafrost thaw can alter the soil environment through changes in soil moisture, frequently resulting in soil saturation, a shift to anaerobic decomposition, and changes in the plant community. These changes, along with thawing of previously frozen organic material, can alter the form and magnitude of greenhouse gas production from permafrost ecosystems. We synthesized existing methane (CH_4) and carbon dioxide (CO_2) production measurements from anaerobic incubations of boreal and tundra soils from the geographic permafrost region to evaluate large-scale controls of anaerobic CO_2 and CH_4 production and compare the relative importance of landscape-level factors (e.g., vegetation type and landscape position), soil properties (e.g., pH, depth, and soil type), and soil environmental conditions (e.g., temperature and relative water table position). We found fivefold higher maximum CH_4 production per gram soil carbon from organic soils than mineral soils. Maximum CH_4 production from soils in the active layer (ground that thaws and refreezes annually) was nearly four times that of permafrost per gram soil carbon, and CH_4 production per gram soil carbon was two times greater from sites without permafrost than sites with permafrost. Maximum CH_4 and median anaerobic CO_2 production decreased with depth, while CO_2:CH_4 production increased with depth. Maximum CH_4 production was highest in soils with herbaceous vegetation and soils that were either consistently or periodically inundated. This synthesis identifies the need to consider biome, landscape position, and vascular/moss vegetation types when modeling CH_4 production in permafrost ecosystems and suggests the need for longer-term anaerobic incubations to fully capture CH_4 dynamics. Our results demonstrate that as climate warms in arctic and boreal regions, rates of anaerobic CO_2 and CH_4 production will increase, not only as a result of increased temperature, but also from shifts in vegetation and increased ground saturation that will accompany permafrost thaw.

Keywords: anaerobic incubation, arctic, boreal, carbon dioxide, climate change, methane, permafrost

Received 18 June 2014; revised version received 7 January 2015 and accepted 8 January 2015

[*]Current address: Water and Environmental Research Center, University of Alaska Fairbanks, Fairbanks, AK, USA

[†]Current address: Agriculture Flagship, CSIRO, Adelaide, SA, Australia

[‡]Current address: Center for Ecosystem Science and Society, Northern Arizona University, Flagstaff, AZ, USA

Correspondence: Claire Treat, tel. 650 329 5232, fax 650 329 4920, e-mail: ctreat@usgs.gov

Introduction

The northern permafrost region contains ~1300 Pg soil carbon (C) (Tarnocai *et al*., 2009; Hugelius *et al*., 2014), some of which has been stored in permafrost (ground that remains at or below 0° C for ≥2 years) for millennia. Climate warming in northern high latitudes will reduce the areal extent of permafrost (Zhang *et al*., 2008; Koven *et al*., 2012; Lawrence *et al*., 2012), making

the large pool of permafrost C vulnerable to mineralization following thaw (Dutta *et al.*, 2006; Schuur *et al.*, 2009, 2013). Permafrost thawing in arctic and boreal regions has brought about changes in ecosystem C balance, often resulting in a net loss of C to the atmosphere (Johansson *et al.*, 2006; O'Donnell *et al.*, 2012; Natali *et al.*, 2014). The magnitude, timing, and form of C release as a result of permafrost thaw will depend not only on changes in air and soil temperature, but also on associated landscape-level changes that can affect soil redox state, organic matter quality, environmental conditions, and plant and microbial community dynamics. While carbon dioxide (CO_2) is the primary decomposition product in oxic soils, when soils are saturated, anaerobic decomposition results in the production of both methane (CH_4) and CO_2; the proportion of these anaerobic products is dependent upon methanogenic pathways that generate both CH_4 and CO_2 and other anaerobic pathways that generate CO_2 (e.g., denitrification, sulfate reduction). Quantifying the relative amount of C released as CO_2 or CH_4 is essential for determining biological feedbacks from permafrost ecosystems to climate change because CH_4 has a 28–34 times larger global warming potential (GWP) on the 100-year time horizon (Myhre *et al.*, 2013).

Once permafrost thaws, the fate of soil C is determined in large part by soil moisture (e.g., Elberling *et al.*, 2013), which can change abruptly following thaw due to collapse of surface soils, resulting in saturated conditions (Halsey *et al.*, 1995; Jorgenson *et al.*, 2001; Payette *et al.*, 2004; Jorgenson & Osterkamp, 2005). Areas of permafrost thaw frequently become hotspots of CH_4 flux to the atmosphere due to anaerobic decomposition (Christensen *et al.*, 2004; Johansson *et al.*, 2006; Walter *et al.*, 2006; Wickland *et al.*, 2006; Myers-Smith *et al.*, 2007; Turetsky *et al.*, 2007; Olefeldt *et al.*, 2013). However, in some areas, permafrost thaw may result in soil drying, where CH_4 emissions are reduced (Olefeldt *et al.*, 2013), or in soils that can fluctuate between saturated and dry conditions. Fluctuations in soil saturation can inhibit CH_4 production as a result of the oxidation and regeneration of alternate electron acceptors, or the depletion of substrate for methanogenesis due to consumption in more kinetically favorably reactions (Schlesinger, 1997; Knorr & Blodau, 2009).

In addition to changes in soil moisture, permafrost thaw can also impact the amount and composition of organic matter inputs to the anoxic zone, thereby altering substrate availability for fermentation and methanogenesis. Organic matter composition is driven by plant community composition and the form of organic matter inputs (e.g., roots vs. leaf litter) (Bergman *et al.*, 1998; Kuder & Kruge, 2001; Hines *et al.*, 2008; Nilsson & Oquist, 2009; Hodgkins *et al.*, 2014). In permafrost regions, in addition to newly assimilated C from vegetation, there also can be inputs of organic material from thawing permafrost (Dutta *et al.*, 2006; Waldrop *et al.*, 2010; Lee *et al.*, 2012; Schädel *et al.*, 2014), which may be partly responsible for high rates of CH_4 emissions observed following permafrost thaw (Olefeldt *et al.*, 2013). Ultimately, microbial communities control both the production of substrates for methanogenesis from fermentation (e.g., acetate, hydrogen, formate, and possibly ethanol) and rates of methanogenesis itself, both of which have low energy yields and slow rates (c.f. Conrad, 1999) that can in turn limit CH_4 production (Chanton *et al.*, 1995; Bergman *et al.*, 1998; Duddleston *et al.*, 2002; Hines *et al.*, 2008; McCalley *et al.*, 2014).

Field and laboratory studies have also highlighted the importance of environmental conditions such as temperature, pH, anoxia, and redox potential on anaerobic decomposition. Methane production and anaerobic CO_2 production positively relate to temperature in incubations of organic soils from the permafrost zone (Svensson, 1984; Yavitt *et al.*, 2006; Lupascu *et al.*, 2012; Treat *et al.*, 2014). Methane production is also dependent on pH (Svensson, 1984; Valentine *et al.*, 1994; Bergman *et al.*, 1998), and while the exact mechanism is unclear, it is likely that fermentation products such as organic acids lower pH and inhibit methanogen growth. The pH optima of methanogens vary from acidic to neutral (Williams & Crawford, 1985; Dunfield *et al.*, 1993).

A synthesis of CH_4 emissions from the permafrost region identified plant community composition, water table depth, soil moisture, and soil temperature as key drivers of CH_4 emissions (Olefeldt *et al.*, 2013). These net CH_4 emissions reflect CH_4 production, transport, and oxidation processes. In this study, we examined how environmental and ecological drivers affect CH_4 and anaerobic CO_2 *production* through a synthesis of anaerobic incubation studies of soils from the permafrost region (Table 1, Fig. 1). We hypothesized that CH_4 and CO_2 production from permafrost region soils could be predicted by environmental controls (e.g., incubation temperature, relative water table position), soil characteristics (e.g., soil type, depth, active layer/permafrost layer, pH, and C:N ratio), and site characteristics (e.g., mean annual temperature, mean annual precipitation, biome, landscape position, vegetation type, and permafrost presence/absence). While CH_4 and anaerobic CO_2 production rates from incubations will not necessarily reflect field fluxes due to the concurrent processes of CH_4 oxidation, alternative transport pathways, and plant–soil interactions, laboratory incubations allow the examination of soil properties and environmental conditions that control CH_4 and CO_2 production rates. We synthesized CH_4 and anaerobic CO_2 production rates across 20 independent studies from northern latitude sites in Alaska, Canada, Sweden, and

Table 1 Summary of anaerobic incubation studies included in this synthesis

Author	Latitude	Longitude	Country	Permafrost zone	MAAT (°C)*	Biome	Landscape position	Soil type	pH	Depths (cm)†	Incubation temp. (°C)	Days measured	CO_2‡
Bellisario *et al.* (1999)	55.67°N	97.87°W	Canada	Discontinuous	−3.1	Boreal	Wetland	Organic	4.0–6.8	0–40 (10)	21	5	
Blazewicz *et al.* (2012)	64.80°N	147.90°W	USA	Discontinuous	−2.8	Boreal	Wetland	Organic	5.1	0–15	25	14–71	
Capek[U1]	72.49°N	101.65°E	Russia	Continuous	−13.4	Tundra	Upland	Organic	6.2	5–20	4, 12, 20	16–139	x
Ernakovich[U2]	69.40°N	148.70°W	USA	Continuous	−13.5	Tundra	Upland	Mineral	5.4–6.3	0–25	1, 15	1–91	x
Ganzert *et al.* (2007)	72.37°N	126.47°E	Russia	Continuous	−14.7	Tundra	Flood plain Wetland	Organic, mineral	No data	0–52 (2–9)	5, 18	7	
	73.60°N	117.33°E	Russia	Continuous	−14.7	Tundra	Wetland	Organic, mineral	No data	0–45 (5) 0–44 (5–8)	5, 18	7	
Holland (1992)	58.64°N	93.82°W	Canada	Discontinuous	−7.6	Boreal	Wetland	Organic	7.0–7.8	0–25	15	5	
	58.68°N	93.84°W		Discontinuous	−7.6	Boreal	Wetland	Organic	7.0–7.8	0–25	15	5	
	58.66°N	93.83°W		Discontinuous	−7.6	Boreal	Wetland	Organic	7.0–7.8	0–25	15	5	
	58.77°N	93.86°W		Discontinuous	−7.6	Boreal	Wetland	Organic	7.0–7.8	0–25	15	5	
Iversen[U3]	71.28°N	156.61°W	USA	Continuous	−12.3	Tundra	Wetland	Organic mineral	4.3–5.8	0–27 (2–5)	2, 12	1–28	x
Kane *et al.* (2013)	64.82°N	147.87°W	USA	Discontinuous	−2.8	Boreal	Wetland	Organic	5.3	5–25	22	2–38	x
Knoblauch *et al.* (2013)	72.33°N	126.28°E	Russia	Continuous	−14.7	Tundra	Upland	Mineral	4.0–8.1	58–2000§	4	16–1248	x
	72.37°N	126.48°E		Continuous	−14.8								
Lee *et al.* (2012)	63.88°N	149.25°W	USA	Discontinuous	−4.1	Boreal	Upland	Organic Mineral	3.6–4.8	5–15	15	7–493	x
	64.85°N	149.72°W	USA	Discontinuous	−4.0	Boreal	Upland	Mineral	5.1	65–80	15	7–493	x
	68.63°N	149.72°W	USA	Continuous	−11.4	Tundra	Upland	Mineral	7.2	1000	15	7–493	x
	68.80°N	161.38°E	Russia	Continuous	−12.6	Tundra	Upland	Mineral	6.6 No data	42–57, 100 1000	15	7–493	x
Lipson *et al.* (2012)	71.32°N	156.62°W	USA	Continuous	−12.3	Tundra	Drained lake	Mineral	4.6–5.2	0–15	4	1	x
Lupascu *et al.* (2012)	68.35°N	18.82°E	Sweden	Discontinuous	−0.1	Tundra	Wetland	Organic	3.8–6.0	2–47§	4, 14, 24	1	x
Moore *et al.* (1994)	51.18°N	80.38°W	Canada	Discontinuous	−1	Boreal	Wetland	Organic	No data	0–10, 15–20	15	5	
	51.28°N	80.37°W		Discontinuous	−1	Boreal	Wetland	Organic	5.5	0–10, 15–20	15	5	
	51.29°N	80.28°W		Discontinuous	−1	Boreal	Wetland	Organic	5.7	0–10, 15–20	15	5	
	51.31°N	80.27°W		Discontinuous	−1	Boreal	Wetland	Organic	5.2	0–10, 15–20	15	5	
	51.50°N	81.02°W		Discontinuous	−1	Boreal	Wetland	Organic	3.2	0–10, 15–20	15	5	
Svensson (1984)	68.37°N	19.05°E	Sweden	Discontinuous	−0.7	Tundra	Wetland	Organic	4.2–4.9	10–15	2, 5,10, 12, 15, 20, 24, 28, 37	30, 75	

 Global Change Biology, doi: 10.1111/gcb.12875

Table 1 (continued)

Author	Latitude	Longitude	Country	Permafrost zone	MAAT (°C)*	Biome	Landscape position	Soil type	pH	Depths (cm)†	Incubation temp. (°C)	Days measured	CO_2‡
Treat *et al.* (2014)	63.57°N	157.73°W	USA	Discontinuous	−3.6	Boreal	Lowland	Organic	3.8–4.9	35–45, 90–100	−0.5, 20	3–27	x
	64.88°N	147.78°W	USA	Discontinuous	−2.9	Boreal	Lowland	Organic	5.5	29–39, 83–92	−0.5, 20	3–27	x
	68.61°N	149.20°W	USA	Continuous	−11.5	Tundra	Flood plain	Organic	5.1–5.3	30–40, 90–100	−0.5, 20	3–27	x
Waldrop *et al.* (2010)	64.87°N	147.86°W	USA	Discontinuous	−2.8	Boreal	Upland	Organic	No data	35–50, 85–100	5	30	
	65.67°N	149.08°W	USA	Discontinuous	−4.9	Boreal	Lowland	Organic	No data	35–50, 65–80	5	30	
	67.20°N	150.27°W	USA	Continuous	−7.8	Boreal	Upland	Mineral	No data	35–50, 65–80	5	30	
Waldrop [U4]	64.69°N	148.32°W	USA	Discontinuous	−2.8	Boreal	Lowland	Mineral	No data	26–41, 81–96	5, 23	0–378	x
	64.70°N	148.32°W	USA	Discontinuous	−2.8	Boreal	Wetland	Organic	No data	5–25, 20–35, 33–48, 40–60	5, 23	0–378	x
	65.35°N	146.92°W	USA	Discontinuous	No data	Boreal	Lowland	Mineral	4.7, 5.7	10–20	5, 23	0–378	x
										50–60, 90–100	5, 23	0–378	x
Whalen & Reeburgh (2000)	64.88°N	147.50°W	USA	Discontinuous	−3.3	Boreal	Wetland	Organic	4.0	0–40 (5)	1–12	2.5	
Yavitt *et al.* (2006)	55.85°N	107.68°W	Canada	Discontinuous	−0.6	Boreal	Wetland	Organic	3.6–4.0	24–95§	10, 22, 25	7, 54	x
Zona *et al.* (2012)	71.29	156.60°W	USA	Continuous	−12.3	Tundra	Drained lake	Organic	No data	0–15	4	1–56	x
								mineral	No data	15–30			

*Mean annual air temperature (MAAT) from WorldClim database (Hijmans *et al.*, 2005).

†Depth ranges used in incubation; parentheses indicate depth increments used if consecutive depths were incubated. CO_2 and CH_4 measurements were made for samples bulked over the sampling increment or depth.

‡Studies that also measured anaerobic CO_2 production noted with 'x'.

§Multiple or irregular sampling depths were incubated; please consult reference for further information.

Unpublished anaerobic incubation studies:

[U1]Capek, C., H. Santruckova, K. Diakova, J.-E. Dickopp, J. Barta, B. Wild, J. Schnecker, G. Guggenberg, N. Gentsch, G. Hugelius, P. Kuhry, N. Lashchinsky, A. Gittel, C. Schleper, R. Mikutta, J. Palmtag, O. Shibistova, T. Urich, S. Zimov, A. Richter: Soil organic matter transformation in cryoturbated horizons of permafrost affected soils (in prep).

[U2]Ernakovich, J. Sagwon Hills, Alaska; Ernakovich *et al.* (2014)

[U3]Iversen, C.M., V. Sloan & R.J. Norby. Barrow Experimental Observatory, AK.

[U4]Waldrop, M.W. *et al.* Interior Alaska.

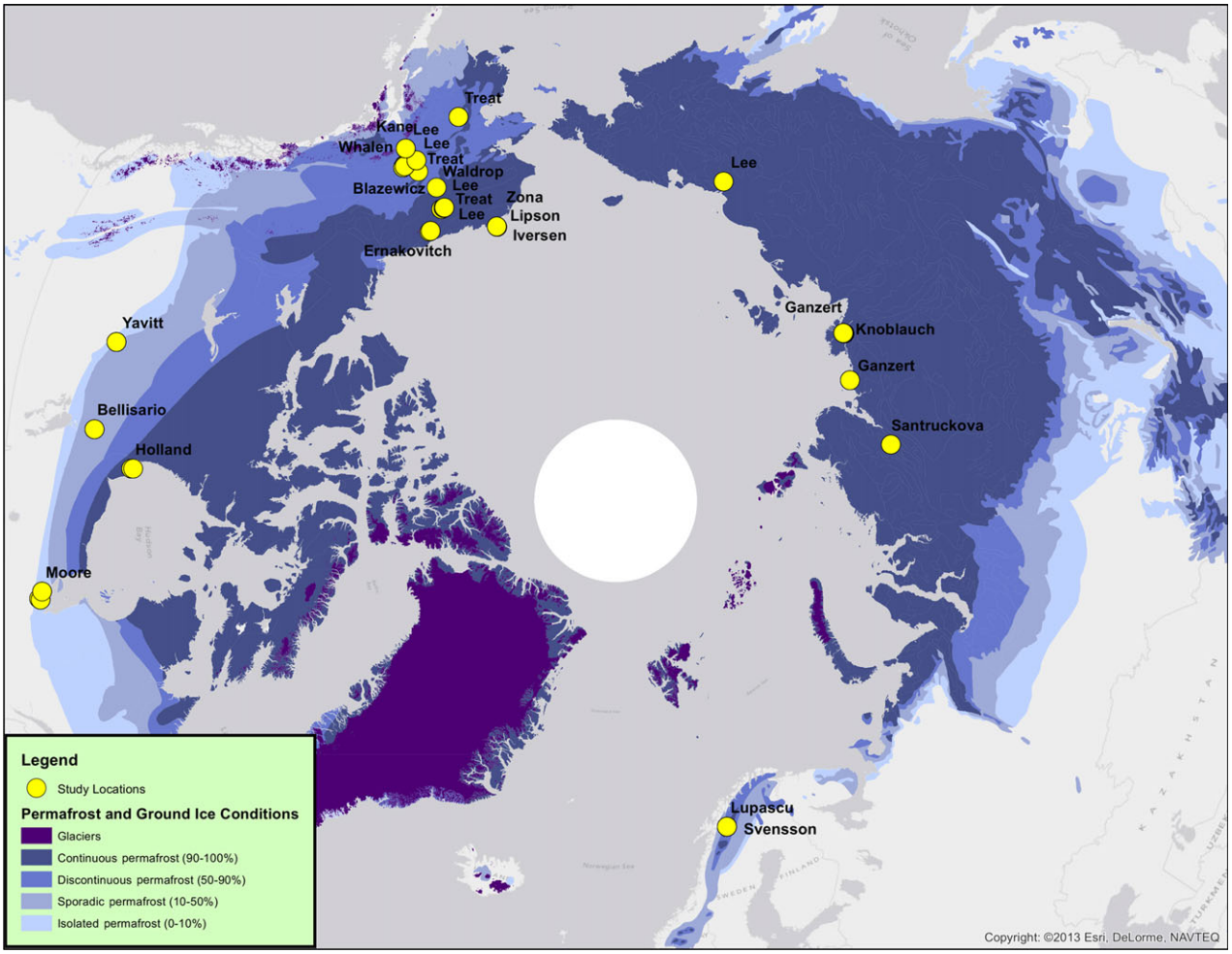

Fig. 1 Sites included in anaerobic incubation synthesis labeled by study author. The study domain was limited to the northern geographic permafrost region as identified by this map (Brown *et al*., 1998; revised 2001). Colors correspond with different permafrost zones. The full list of studies can be found in Table 1.

Siberia to quantify effects of known controls on anaerobic processes that operate throughout the permafrost zone. Finally, we identify and discuss promising areas for future research.

Materials and methods

Data collection and site classification

We compiled a database of anaerobic incubations that were conducted on soil samples within the geographic permafrost area (Fig. 1, Table 1; Brown *et al*. 1998, revised 2001). We identified potential published studies for inclusion in the database using Web of Science with the keywords 'anaerobic or anoxic or methane or incubation' and 'arctic or boreal or permafrost', and we actively solicited contributions of published and unpublished studies through the NSF-funded Vulnerability of Permafrost Carbon Research Coordination Network as a parallel study to Schädel *et al*. (2014). Twenty studies (16 published, 4 unpublished) fell within the northern high-latitude permafrost area and met the following criteria: (i) created anaerobic headspace using oxygen-free gas (most commonly N_2 or He); (ii) measured CH_4 on a per gram soil dry weight or per gram C basis; (iii) reported sample depth and incubation temperature. We included soils with either intact or homogenized soil structure but excluded soil slurries and incubations of lake sediments due to difficulties of comparing methods. These efforts resulted in a dataset of 2270 CH_4 production measurements across 54 sites in Alaska (USA), Canada, Sweden, and Siberia (Russia) between 1984 and 2013 (Fig. 1). We extracted CH_4 and CO_2 production data from published studies using a data extraction program (Plot Digitizer), calculated the molar CO_2:CH_4 production ratio, and collected ancillary data that were commonly reported across studies.

We extracted information about site type and local conditions from the published studies and unpublished datasets. We classified sites by biome (tundra or boreal) and landscape position (drained lake basin, active floodplain, wetland, lowland, upland) based on site descriptions. The wetland

classification included bogs, fens, mires, marshes, swamps, and polygonal tundra, while the lowland classification included low-lying black spruce forests without standing water. We classified dominant vascular vegetation within each landscape position at each site into graminoid, shrub, and tree categories using vegetation descriptions. Moss cover for each site was classified into three categories: no moss, dominance of *Sphagnum* mosses, or dominance by other mosses (e.g., *Polytrichum* spp., *Drepanocladus* spp.), based on site-level vegetation description. We also categorized water table position of each soil sample based on sample depth relative to reported water table depth. The three water table categories were dry (>2.5 cm above the mean water table depth), fluctuating (mean water table fell within 2.5 cm of the sample depth), and inundated (mean water table depth was within the sample depth). We classified soil type according to % soil C; soils with >20% C were classified as organic soil, while soils with <20% C were classified as mineral. Two samples with cryoturbation features were classified as a mix of organic and mineral soil (O/M). We also classified sites using two categories for permafrost: permafrost present/absent and active layer/permafrost layer. Permafrost present/absent included measurements only from active layer soils when permafrost was present, and the active layer/permafrost layer comparison excluded measurements from sites without permafrost. Finally, we extracted mean annual air temperature and mean annual precipitation (1950–2000) from WorldClim database (Hijmans *et al.*, 2005). Vascular vegetation, moss cover, and water table position were not classified for samples from >1 m depth, and these samples were omitted from the vegetation and water table position analyses ($N = 18$).

Data assimilation and data processing

The anaerobic laboratory incubation studies ranged in incubation length from 1 to 1238 days, incubation temperatures ranged from −0.5 °C to 35 °C, and sample depth ranged from the soil surface to 10 m. There were often multiple C production measurements collected during an incubation for each sample (i.e., a unique site × depth × incubation temperature combination). Instead of using multiple production measurements taken over multiple days in the analysis, maximum CH_4, mean CO_2 production rates, and mean daily CO_2:CH_4 production ratios prior to 150 days were used as a single measurement for each sample (see Supplemental Materials), hereafter referred to as the aggregated dataset. We used maximum CH_4 production rate from each sample instead of mean production (as we did for CO_2) because different environmental conditions and potential differences in microbial communities resulted in varying lag times for CH_4 production that, in part, drove mean CH_4 differences. Similarly, lag time effects precluded us from obtaining relevant cumulative CH_4 production rates. We excluded daily production measurements that showed CH_4 uptake (consumption) from our calculations of the mean daily CO_2:CH_4 production. After finding mean and maximum CH_4 and CO_2 production rates for each sample, we identified 44 samples in the aggregated dataset that showed no CH_4 production over the course of the incubation; all of these samples were removed from our study either because the incubation time (<7 days) was too short (33 samples) to recover from disturbance to the microbial communities due to sampling, transport, and handling (Nilsson & Oquist, 2009) or due to insufficient replication to validate the zero measurement (11 samples). This resulted in 303 measurements of CH_4 production and 219 anaerobic CO_2 production measurements in the aggregated dataset.

The dataset was highly unbalanced with regard to temperature, a known control on CH_4 and CO_2 production rates. We did not standardize measurements for incubation temperature using a Q_{10} derived from the full dataset because of the high variability associated with the calculation; Q_{10} derived from individual studies with multiple incubation temperatures (Table 1) ranged from 0.96 to 3.10 for CH_4 production (median: 1.16) and from 0.67 to 4.10 for anaerobic CO_2 production (median: 1.39). Instead, we included temperature as a covariate in our statistical analysis.

To directly compare the potential radiative forcing of CH_4 and CO_2 production, we calculated the CO_2 equivalent (CO_2e) of CH_4 production using a GWP of 28 kg CO_2 equivalents kg^{-1} CH_4 over a 100-year time horizon (Myhre *et al.*, 2013). While some of the CH_4 produced under field conditions is oxidized before reaching the atmosphere (and thus has a GWP of 0), the calculation of CO_2e allows us to compare the warming potential of these two greenhouse gases.

We estimated % C and bulk density values using an empirical relationship and calculated CO_2 and CH_4 production per gram soil C. Percent C was not reported for ~ 30% of measurements, and bulk density was not reported for ~ 70% of measurements. We estimated missing % C and bulk density values using an empirical relationship between depth, soil type, and % C or bulk density (Table S3, Fig. S5). We calculated missing CH_4 or CO_2 production per gram C from the reported C production per gram dry weight to investigate the relative differences in C quality among samples. We use the term, C quality, to refer to decomposability as determined from laboratory incubations, as has been performed in a recent synthesis of aerobic soil incubations (Schädel *et al.*, 2014). While we mainly present results on a per gram C basis, results per gram dry weight followed similar trends. Carbon production rates on an areal basis were calculated to a 1 m depth using maximum CH_4 and mean CO_2 production per gram dry weight soil from the aggregated dataset and measured or estimated bulk density (see Supplemental Methods).

Lag analysis of CH_4 production

To understand dynamics of CH_4 production over time, we analyzed the lag time from the start of the incubation to maximum rates of CH_4 production, hereafter referred to as lag time. Lag time integrates both redox potential and microbial community dynamics within the soils, as maximum rates of CH_4 production are achieved under conditions when alternate electron acceptors are depleted and methanogen communities are established (Knorr & Blodau, 2009; Nilsson & Oquist, 2009). Microbial communities, and thus lag times, can be affected by disturbance when sampling, handling, and

processing during the experimental setup. While the level of disturbance may vary across studies as a result of methodological differences, we do not expect systematic differences across sample or site types, which is the focus of our analyses. Lag time was calculated using a subset of the data with three or more CH_4 production measurements during the incubation experiment (n = 120; Fig. S3).

K-value decay rate calculation

In addition to quantifying lag times, we calculated the exponential decay rate (k) of CH_4 production following maximum rates of CH_4 production using the same dataset. The exponential decay rate (k) represents the rate of relative decrease in CH_4 production rates from maximum production rates over time to better understand potential changes in CH_4 production due to substrate depletion of the labile C pool. We calculated relative decrease in CH_4 production following maximum rates using the percentage of daily CH_4 production relative to the maximum CH_4 production among samples, which had several orders of magnitude of variation in maximum production rates (Fig. S1, Fig. S3). We then fit a log-linear regression to obtain k, the exponential decay rate of CH_4 production over time. We tested for interactions between time and incubation temperature, vegetation, sample depth, and relative water table position that would indicate differences in the rate of labile C consumption among groups within those factors. In field conditions, substrate for methanogenesis is generally highly labile C compounds and recent photosynthates (King *et al.*, 2002; Prater *et al.*, 2007). k represents the depletion of labile C pool due to anaerobic metabolism. This approach assumes that CH_4 is only derived from the labile C rather than multiple C pools of varying quality, as has previously been performed for CO_2 production during incubations (Schädel *et al.*, 2014). However, k provides little information on the absolute size of the labile C pool or about methanogenic substrate shifts from recently fixed plant photosynthates and highly labile C compounds to more recalcitrant compounds.

Temperature sensitivity analysis

We performed a temperature sensitivity analysis to better understand the response of CH_4 and CO_2 production to temperature for each soil sample. Apparent temperature sensitivity (Q_{10}) was calculated using the equation: $Q_{10} = (R_2/R_1)^{10/(T_2 - T_1)}$, where T_1 and T_2 represent two temperatures and R_2 and R_1 represent C production rates at temperatures T_1 and T_2. We calculated Q_{10} using the subset of data with incubations conducted at multiple temperatures as well as the entire dataset using the regression between incubation temperature and log-transformed mean CO_2 and maximum CH_4 production. We compared differences in apparent temperature sensitivity among groups using one-way ANOVAs. There were insufficient data to evaluate differences in Q_{10} due to incubation temperature range (Hamdi *et al.*, 2013).

Statistical analyses

We investigated differences in maximum CH_4 production, mean CO_2 production, CO_2:CH_4 production, CO_2e, and lag times among environmental controls (incubation temperatures, relative water table position, pH), substrate controls (vegetation type, depth, permafrost, soil type), and landscape patterns (biomes and landscape position). We used mixed effects modeling (lmer, R package: lme4, Bates *et al.*, 2014) with maximum likelihood estimation to account for the random effects of site and fixed effects of incubation temperature, pH, and depth. While we could have included these fixed effects as blocking factors in a linear modeling approach, the dataset was highly unbalanced and the mixed modeling approach was preferable. We tested for differences among groups using a chi-squared test against a null model including only fixed and random effects (incubation temperature, pH, and site). The chi-squared test is known to be conservative and agreed with model comparisons using AIC.

We hypothesized that CH_4 and CO_2 production could be predicted by a combination of environmental controls, soil characteristics, and site characteristics. We used a forward-selection stepwise multiple regression to identify which predictors explained the most variance among rates of maximum CH_4 production, mean CO_2 production, anaerobic CO_2:CH_4 production, and lag times based on AIC scores (stepAIC, R package: MASS, Venables & Ripley, 2002). Variables were selected for the model in the order of largest improvement in AIC scores from the null model with only an intercept and calculated the relative importance of the accepted predictors (calc.relimp, R package: Relaimpo, Grömping, 2006). Variables that resulted in higher AIC scores (i.e., poorer model fit) than the null model were rejected. Prior to running the stepwise regression, we tested for correlation among predictor variables and found that all correlations were <0.4. An additional ordination analysis was used for data visualization (Figs S8 and S9).

Data were log-transformed (+1 μg C gC^{-1} day^{-1}) to meet assumption of normality for all statistical analyses. All statistical analyses were conducted using R (R Development Core Team, 2008). We were unable to use meta-analysis techniques on this dataset because there was no common incubation temperature or length across all incubations (i.e., no 'control' treatment; Table 1).

Results

General trends

The median value of the maximum CH_4 production rates from incubations of northern permafrost zone soils was 0.6 μg CH_4-C g $soil^{-1}$ day^{-1} and normalized per gram soil C was 3.2 μg CH_4-C gC^{-1} day^{-1}. Maximum CH_4 production per gram soil was positively related to % C in the soil ($F_{1,205}$ = 36.7, P < 0.001, R^2 = 0.15; Fig. S6). On an areal basis, median of the maximum CH_4 production rates from laboratory incubations was 0.05 g CH_4-C m^{-2} day^{-1}.

The median rate of anaerobic CO_2 production from incubations of northern permafrost zone soils was 18.0 μg CO_2-C g $soil^{-1}$ day^{-1} and normalized per gram C was 58.3 μg CO_2-C gC^{-1} day^{-1}. As with CH_4 production, anaerobic CO_2 production per gram soil was positively related to % C in the soil ($F_{1,172}$ = 36.7, $P < 0.001$, R^2 = 0.18; Fig. S6). On an areal basis, median anaerobic CO_2 production from laboratory incubations was 1.5 g CO_2-C m^{-2} day^{-1}. Hereafter, we report all results for anaerobic CO_2 and CH_4 production as per gram soil C to account for differences in the amount of soil C among samples, unless otherwise noted.

CO_2 and CH_4 production rates varied among hierarchical landscape units. The CO_2:CH_4 production ratio was >50 times higher in boreal sites (median = 387) than tundra sites (median = 7; χ^2 = 18.5, df = 1, $P < 0.001$), and while CO_2 production was higher in the boreal biome than the tundra biome (153 ± 17 and 109 ± 16 μg CO_2-C gC^{-1} day^{-1}), these differences were not statistically significant (χ^2 = 0.45, df = 1, P = 0.50). Anaerobic CO_2 production and the CO_2:CH_4 production ratio differed among landscape positions ($\chi^2 > 14$, df = 4, $P < 0.01$; Table 2). Anaerobic CO_2 production was largest from the wetlands while the CO_2:CH_4 production ratio was largest from the lowland forests and smallest from the wetlands (Table 2). Maximum CH_4 production did not differ significantly between boreal and tundra sites (χ^2 = 2.36, df = 1, P = 0.12) or among landscape positions (χ^2 = 6.6, df = 4, P = 0.16; Table 2). However, the decay rates (k) of CH_4 production differed significantly among landscape positions (Table 2).

Effects of substrate

Maximum CH_4 and mean CO_2 production rates per gram soil C were significantly different among mineral and organic soils and across soil depths. Maximum CH_4 production was more than five times greater in organic soils than mineral soils (χ^2 = 3.6, df = 1, P = 0.06; Table 3), and anaerobic CO_2 production was three times greater in organic soils than mineral soils (χ^2 = 20.5, df = 1, $P < 0.001$; Table 3). There was a trend toward lower anaerobic CO_2:CH_4 in mineral soils (median = 11.6) than in organic soils (median = 19.0; χ^2 = 2.3, df = 1, P = 0.13). The decay rate (k) of CH_4 production was significantly higher in organic soils than mineral soils (14.6 and 2.9 × 10^{-4} day^{-1}, respectively; $F_{3,748}$ = 51.8, $P < 0.001$). Lag times were significantly longer in mineral soils than organic soils

Table 2 Category means (SE) of maximum rates of CH_4 production, mean anaerobic CO_2 production, median daily CO_2:CH_4 production, mean and median lag times before maximum CH_4 production rates, exponential decay rate (k) of CH_4 production rates following maximum CH_4 production, and number of samples (n)

Category	Max. CH_4 production (μg CH_4-C gC^{-1} day^{-1})	n_{CH4}	Mean CO_2 production (μg CO_2-C gC^{-1} day^{-1})	n_{CO2}	Median CO_2:CH_4 production	Lag time (days)			Mean incubation temp. (°C)	k (% day^{-1})
						Mean	Median	n_{lag}		
Incubation temperature										
<10 °C	3.8 (0.5)*	114	67 (16)*	83	98*	341 (65)	28	56	3.6	0.14 (0.02)
10–20 °C	14.1 (2.6)*	102	146 (27)*	72	59*	37 (8)	20	54	15.1	0.10 (0.02)
>20 °C	30.5 (4.5)*	87	172 (17)*	64	100*	21 (14)	0	10	24.4	0.09 (0.02)
Relative water table position										
Dry	2.4 (0.4)*	48	68 (8)*	45	153*	49 (13)*	20	28	12.6	0.07 (0.02)*
Fluctuating	13.6 (3.3)*	56	364 (60)*	31	57*	20 (2)*	27	23	12.0	0.23 (0.05)*
Inundated	20.3 (2.7)*	165	105 (11)*	115	32*	11 (2)*	10	31	15.6	0.11 (0.04)*
Depth										
0–20 cm	23.7 (3.5)*	124	181.0 (29.6)	76	18*	41 (9)*	28	38	12.8	0.18 (0.04)*
20–100 cm	9.3 (1.4)*	161	100.6 (10.3)	125	153*	95 (36)*	17	54	14.6	0.09 (0.01)*
>100 cm	5.0 (1.2)*	18	42.6 (13.0)	18	1635*	765 (110)*	880	18	5.8	0.03 (0.03)*
Landscape position										
Drained Lake	0.6 (0.3)	7	125 (47)*	7	34*	19 (9)	7	3	4.0	1.16 (0.37)*
Flood plain	1.5 (0.5)	18	41.7 (10.6)*	8	353*	17 (3)	28	8	10.7	2.33 (1.19)*
Lowland	0.7 (0.3)	24	47.8 (9.5)*	21	2336*	37 (12)	NA	21	10.8	0.06 (0.74)*
Upland	8.2 (3.0)	42	52.1 (9.2)*	38	710*	513 (83)	10	38	8.2	0.03 (0.74)*
Wetland	19.5 (2.2)	212	159 (17)*	81	19*	15 (2)	43	40	15.3	0.13 (0.74)*

*Indicates significant differences ($P < 0.05$) among groups.

Table 3 Mean (SE) of maximum daily rates of CH_4 production and mean anaerobic CO_2 production by soil type (mineral; organic; cryoturbated mineral/organic, OM) and depth

			Maximum CH_4 production			Mean anaerobic CO_2 production		
	% C	% N	μg CH_4-C g C^{-1} day^{-1}	μg CH_4-C g DW^{-1} day^{-1}	mg CH_4-C m^{-2} day^{-1}	μg CO_2-C g C^{-1} day^{-1}	μg CO_2-C g DW^{-1} day^{-1}	mg CO_2-C m^{-2} day^{-1}
Soil Type								
Mineral	6.8 (0.8)*	0.3 (0.0)*	3.3 (0.5)*	0.2 (0.0)*	71 (13)	47.2 (7.4)*	2.78 (0.47)*	1070 (310)
Organic	39.6 (0.8)*	1.4 (0.0)*	18.7 (12.1)*	4.5 (0.7)*	657 (102)	145.8 (15.2)*	57.1 (6.3)*	5890 (690)
OM	4.9 (1.7)*	2.1 (1.9)*	1.3 (1.0)*	0.1 (0.0)*	NA			
Depth (cm)								
0–20	39.0 (1.6)*	1.3 (0.1)*	15.4 (2.7)*	5.9 (1.1)*	139 (24)*	181 (30)	74.6 (12.8)	970 (110)
20–100	30.1 (1.6)*	1.1 (0.1)*	3.2 (0.5)*	0.9 (0.2)*	833 (137)*	101 (10)	33.2 (3.7)	7840 (890)
>100	4.2 (0.5)*	0.3 (0.0)*	5.0 (1.2)*	0.2 (0.1)*	NA	42.6 (13.0)	1.2 (0.1)	NA

*Indicates significant differences among groups ($P < 0.05$).

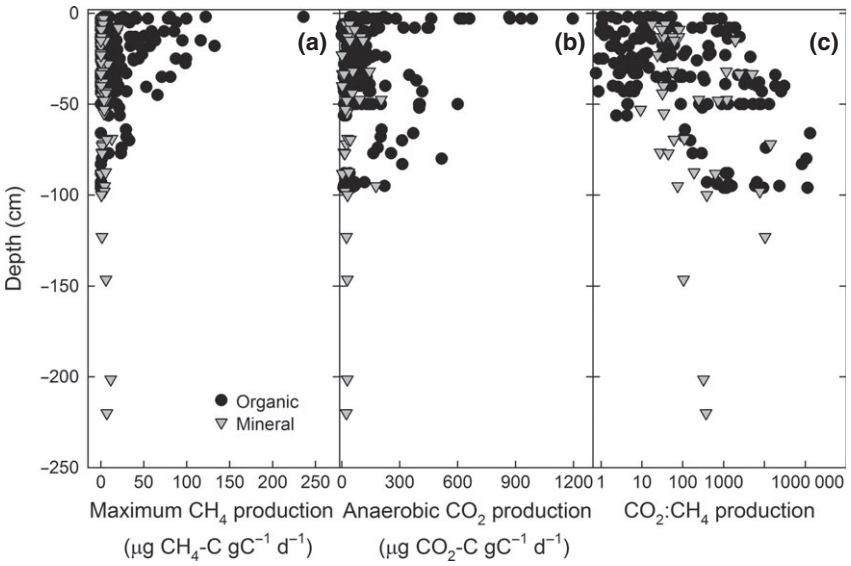

Fig. 2 (a) Maximum CH_4 production rates, (b) mean CO_2 production, and (c) and CO_2:CH_4 production for organic (dark circles) and mineral (gray triangles) soil types. Note log-scale for CO_2:CH_4 production. Data points for all depths up to 2000 cm can be found in Fig. S4.

(403 ± 72 days and 27 ± 5 days, respectively; $\chi^2 = 4.5$, df = 1, $P = 0.03$).

Both CH_4 and anaerobic CO_2 production decreased as a function of soil depth (Fig. 2). Maximum CH_4 production was significantly higher in soil from the top 20 cm than deeper soils (>20 cm; $\chi^2 = 17.0$, df = 2, $P < 0.001$; Table 2). Anaerobic CO_2 production also decreased at depth ($\chi^2 = 6.5$, df = 2, $P = 0.04$; Table 2), while CO_2:CH_4 production ratio increased with depth (Fig. 2c; Table 2). Soil depth also affected lag time, which was less than 45 days for surface soils and over 2 years for soils from >1 m depth ($\chi^2 = 13.0$, df = 2, $P = 0.001$; Table 2). The CO_2e of anaerobic decomposition was largest from 20 to 100 cm depth soils, followed by surface soils (<20 cm), and then by deep soils (>100 cm) (1530, 680, and 340 μg CO_2e g C^{-1} day^{-1}, respectively; $\chi^2 = 26.6$, df = 2, $P < 0.0001$). The decay rate (k) of CH_4 production significantly decreased with depth (Table 2; $F_{5,746} = 35.3$, $P < 0.0001$).

Rates of CH_4 production and anaerobic CO_2 production differed significantly among vegetation types. Maximum CH_4 production was more than five times greater in soils from graminoid- and shrub-dominated sites compared to soils from treed sites (Fig. 3a; $\chi^2 = 32.2$, df = 2, $P < 0.001$). Maximum rates of CH_4 production from sites with *Sphagnum* and other moss species were more than double sites without moss (Fig. 3b; $\chi^2 = 21.1$, df = 2, $P < 0.001$). The CO_2:CH_4

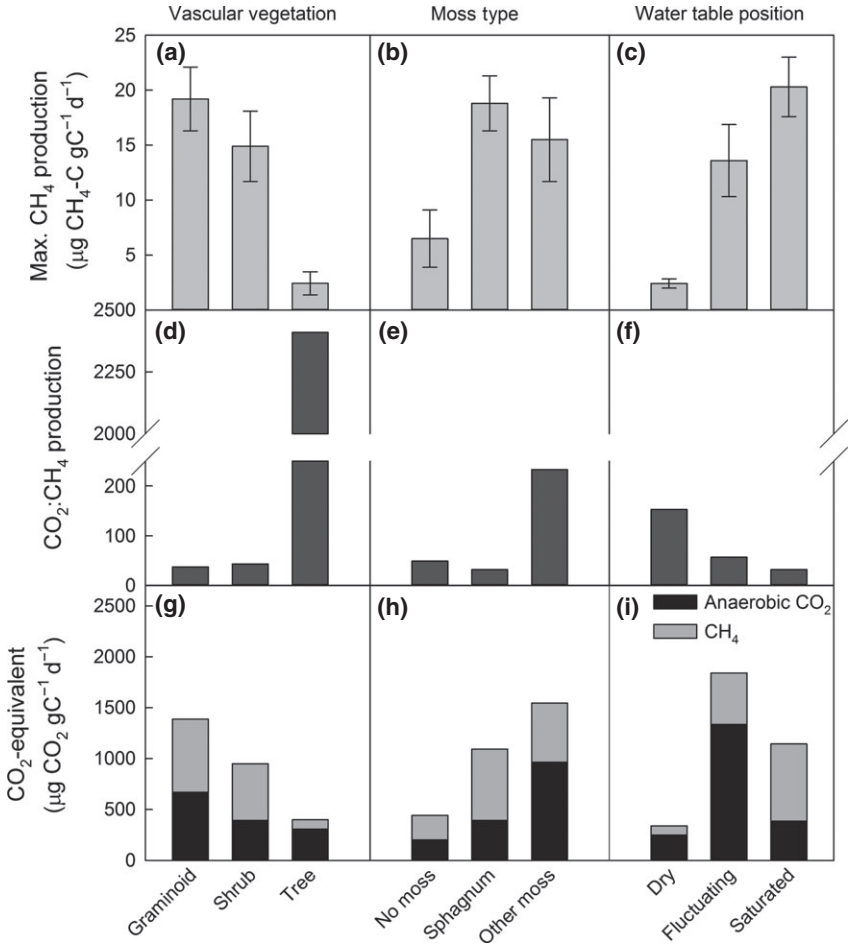

Fig. 3 Maximum CH_4 production (a–c), median anaerobic CO_2:CH_4 production ratio (d–f), and CO_2 equivalent (CO_2e) (g–i) differed significantly between vascular plant type (left), moss type (center), and water table status (right). Error bars represent standard error. CO_2e calculated using a GWP of 28 kg CO_2 equivalents kg^{-1} CH_4 and a 100-year time horizon (Myhre *et al.*, 2013).

production ratio differed significantly among vascular plant types (Fig. 3d; $\chi^2 = 188$, df = 2, $P < 0.001$) and moss cover (Fig. 3e; $\chi^2 = 78.4$, df = 2, $P < 0.001$), as did CO_2e (Fig. 3g–h; $\chi^2 > 325$, df = 2, $P < 0.001$). Lag times between the beginning of the incubation and day of maximum CH_4 production were <30 days for graminoid- and tree-dominated sites, but were ~7 months for shrub-dominated sites ($\chi^2 = 64.8$, df = 2, $P < 0.001$). Decay rates (k) of CH_4 production were larger in graminoid and shrub sites than treed sites (0.12 ± 0.02 and 0.04 ± 0.05 day^{-1}, respectively).

Effects of environmental conditions

Environmental conditions – both within the incubation experiments themselves (i.e., temperature) and site-level conditions (pH and water table status) – significantly affected rates of CO_2 and CH_4 production. Incubation temperature significantly and positively related to CH_4 and anaerobic CO_2 production but explained relatively little variability compared to all variables considered (Table 4). The temperature sensitivities of anaerobic CH_4 and CO_2 production differed among studies with multiple incubation temperatures and across the whole synthesized dataset. The median apparent Q_{10} for CH_4 production across all sites, depths, and temperatures was 1.18, and the median apparent Q_{10} for anaerobic CO_2 production was 1.41. Lag times and decay rates (k) of CH_4 production did not differ among incubation temperatures (Table 2).

The relative water table position of a soil sample in the field also affected CO_2 and CH_4 production during the incubation experiments. Maximum CH_4 production was more than five times higher from inundated samples than from dry samples (Fig. 3c, Table 2; $\chi^2 = 43.8$, df = 2, $P < 0.001$). Mean anaerobic CO_2 production was more than three times higher in fluctuating water table samples than from inundated samples and more than five times higher in fluctuating samples than from dry soils (Table 2; $\chi^2 = 77.3$, df = 2, $P < 0.001$). The CO_2:

Table 4 Best predictors of maximum CH_4, mean anaerobic CO_2, mean daily CO_2:CH_4 production ratio, and lag time. Predictor variables were selected by stepwise linear regression using forward selection and were accepted/rejected from the model using AIC values. Active layer/permafrost layer was also included but rejected for all models; zeroes indicate rejected predictor variables. Categorical predictor variable levels used were as follows: biome (boreal, tundra), landscape position (drained lake, flood plain, lowland forest, upland forest or tundra, and wetland), vascular vegetation type (graminoid, shrub, or tree), moss type (none, Sphagnum, other moss), water table position (dry, fluctuating, inundated)

	Total % variance explained			
Predictor	CH_4	CO_2	CO_2:CH_4	Lag time
Landscape-level				
Biome	11	5	32	6
Landscape position	7	9	8	20
Permafrost: presence/absence	3	0	0	0
Mean annual precipitation (mm)	0	0	3	9
Mean annual air temp. (°C)	0	5	0	12
Substrate and soil characteristics				
Vascular vegetation type	5	3	0	0
Moss type	4	12	0	0
Soil type (organic/mineral)	2	4	0	0
Soil C:N ratio	0	4	0	0
pH	0	5	19	0
Depth	0	0	8	10
Soil environment				
Incubation temperature	7	13	0	0
Water table position	0	16	0	0
Regression statistics				
Total variance explained (r^2)	0.40	0.75	0.70	0.58
F-value	6.96	23.29	42.3	10.89
Degrees of freedom	12, 128	16, 122	7, 129	7, 56
P	<0.001	<0.001	<0.001	<0.001
Number of measurements	141	139	137	64

CH_4 production ratio differed significantly among water table positions (Fig. 3f; $\chi^2 = 123$, df = 2, $P < 0.001$). Lag time was <20 days for inundated saturated samples or periodically inundated soils but >45 days for dry unsaturated soils (Table 2; $\chi^2 = 113$, df = 2, $P < 0.001$). Decay rates (k) of CH_4 production rates were greatest in the zone of fluctuating water table followed by inundated samples (Table 2; Fig. S3).

Soil pH was significantly and positively correlated with CH_4 production. Furthermore, the relationship between CH_4 production and pH was dependent on incubation temperature ($\chi^2 = 35$, df = 4, $P < 0.001$; Fig. S7). The CO_2:CH_4 production ratio was negatively correlated with pH (slope = -0.64 ± 0.18, $\chi^2 = 84$, df = 1, $P < 0.001$).

Effects of permafrost

Presence of permafrost, both within and across sites, affected anaerobic CO_2 and CH_4 production. Maximum CH_4 production rates from sites without permafrost were nearly double those from sites with permafrost (Fig. 4a; $\chi^2 = 4.3$, df = 1, $P = 0.04$). In sites with permafrost, maximum CH_4 production rates from the active layer were nearly four times greater than from the permafrost layer (Fig. 4a; $\chi^2 = 1.7$, df = 1, $P = 0.20$). Anaerobic CO_2 production was also higher from sites without permafrost than with permafrost (Fig. 4b; $\chi^2 = 8.5$, df = 1, $P = 0.004$) and was more than twice as large from the active layer than from the permafrost layer at sites that contained permafrost (Fig. 4b; $\chi^2 = 3.1$, df = 1, $P = 0.08$). In sites with permafrost, anaerobic CO_2:CH_4 production was significantly larger in the permafrost layer than the active layer (median = 1163 and 37, respectively; $\chi^2 = 6.6$, df = 1, $P = 0.01$). Lag times did not differ among any permafrost classification ($P = 0.8$, $P = 0.28$).

Relative importance of substrate, environmental, and landscape controls

The relative importance of substrate, environmental, and landscape controls differed for anaerobic CH_4 and CO_2 production. All variables considered explained 39% of CH_4 production rates, with the highest amount of variance explained by landscape-level categorization (21%), followed by substrate controls (i.e., moss type,

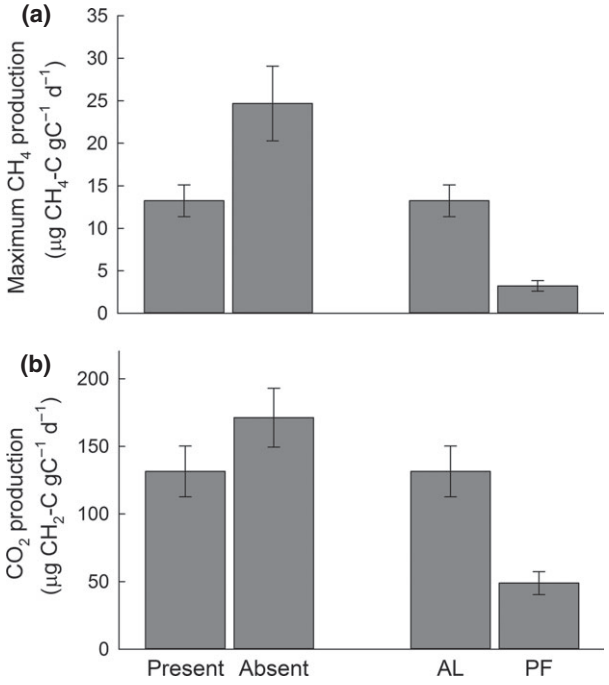

Fig. 4 Rates of (a) maximum CH_4 production and (b) mean CO_2 production in sites with permafrost presence/absence (left), and between active layer and permafrost layer in sites with permafrost present (right).

vascular vegetation type, and soil type) (11%) and incubation temperature (7%; Table 4). All variables considered explained 75% of anaerobic CO_2 production. Environmental controls including incubation temperature (13%) and relative water table position (16%) explained 29% of variance, followed by substrate controls (moss type, vascular vegetation, pH, C:N ratio, and soil type) (28%) and landscape factors such as biome (5%), landscape position (9%), and mean annual air temperature (MAAT, 5%; Table 4). Site-level and landscape factors, such as biome, landscape position, and precipitation, explained most of the relative variance in CO_2:CH_4 production ratio (43%), followed by substrate controls (27%; Table 4). Lag time was best predicted by landscape factors (47% of total variance), followed by substrate controls, specifically depth (10% of total variance; Table 4). Permafrost, both within and across sites, was not a significant predictor of anaerobic CO_2 production, CO_2:CH_4 production ratio, or lag time.

Discussion

Methane production in permafrost soils: insights from the synthesis

This synthesis of anaerobic incubations studies showed the complexities and also the generalizable patterns in CH_4 and anaerobic CO_2 production rates in soils across the permafrost region. Production of methane and anaerobic CO_2, as observed from laboratory incubation studies, is largely controlled by factors that can be grouped into a few general categories: (i) substrate, (ii) environmental conditions, (iii) landscape-level factors, and (iv) microbial community dynamics (not examined in this synthesis; Table 4). The relative importance of environmental, substrate, and landscape controls differed for CH_4 production and anaerobic CO_2 production. We observed numerous legacy effects on CH_4 production and anaerobic CO_2 production from site factors such as landscape position, biome, relative water table position, and vegetation type (Fig. 3). These observed differences in CH_4 and CO_2 production among sites, under common incubation conditions, highlight the importance of soil and substrate composition for greenhouse gas production.

Substrate controls on CH_4 production

Substrate composition controls the overall decomposability of soil organic matter, and therefore, substrate is a primary determinant of potential CH_4 and CO_2 production. Substrate quality often differs between depths due to fresh litter inputs from leaves and stems at the surface, and roots belowground. Because all soils were incubated under a strict anoxic atmosphere, we were able to examine the effect of organic matter quality at different depths on CH_4 and CO_2 production. Differences in organic matter quality on gas production rates were evident among depths and vegetation types. We observed higher CH_4 and anaerobic CO_2 production from surface soils as well as higher decay rates (k) of CH_4 production, indicating higher organic carbon quality in this zone (Fig. 2, Table 2). Generally, higher quality organic C is expected closer to the ground surface due to root and litter inputs (Agren & Bosatta, 1996; Nilsson & Oquist, 2009); however, high-quality organic matter can be preserved under some permafrost formation conditions (e.g., Schuur *et al.*, 2008).

Substrate controls on CH_4 production are especially important in the permafrost zone because labile C can be added to soils not only from recently fixed plant inputs, but also as a result of permafrost thaw. Results from our synthesis show that vegetation type was a better predictor of CH_4 production than sample depth (Table 4), that CH_4 production generally decreased with depth (Fig. 3), and that production was higher from active layer soils than from permafrost. Previous studies have found relatively high rates of C production at depth (Waldrop *et al.*, 2010; Treat *et al.*, 2014) due to relatively high soil C lability, which depends on permafrost formation history (Waldrop *et al.*, 2010;

Harden *et al*., 2012; Lee *et al*., 2012; Treat *et al*., 2014) and processes such as cryoturbation that can mix undecomposed, relatively labile organic matter in mineral soils (Schuur *et al*., 2008) or in patterned tundra (Repo *et al*., 2009). Finally, landscape factors such as biome and landscape position affect substrate through vegetation composition, C and N inputs, and losses through leaching, as well as through permafrost formation history. For example, soil organic matter in permafrost was much more labile in tundra soils than boreal soils due, in part, to a legacy of more decomposition prior to permafrost formation in boreal soils (Treat *et al*., 2014), which may explain why landscape factors were strong predictors of anaerobic C production in this synthesis rather than depth and environmental conditions (Table 4).

Vegetation type also influenced CH_4 production rates from incubations, similar to trends from field emissions (Olefeldt *et al*., 2013). Our synthesis results show that maximum CH_4 production rates occurred in graminoid-dominated sites followed by shrub-dominated sites, while little to no CH_4 production occurred in tree-dominated sites (Fig. 3). Similar patterns have been observed along a thaw gradient from thawed, wet, graminoid-dominated areas to dry palsa with intact permafrost due to changes in organic matter chemistry (Hodgkins *et al*., 2014). A synthesis of field measurements of CH_4 fluxes showed similar trends with highest CH_4 fluxes observed in graminoid-dominated sites and substantially lower CH_4 fluxes from shrub- and tree-dominated sites (Olefeldt *et al*., 2013), which may be a function both of differences in organic matter composition and vascular transport of CH_4 in sedge-dominated ecosystems. Tundra decomposition studies have shown that graminoid species decompose most quickly, followed by shrubs and finally mosses, a pattern tied to the high lignin:N ratios of woody tissues (Hobbie, 1996); our synthesis results show that k-values for CH_4 production were largest in graminoid- and shrub-dominated sites and smallest in treed sites. Thus, dominant site vegetation resulted in differing substrate favorability for CH_4 production in incubations through differences in the labile C pool, and this mechanism may be partially responsible for differences in CH_4 fluxes among vegetation types in field measurements (e.g., Olefeldt *et al*., 2013). However, field measurements also capture effects of vegetation on gas exchange that are not reflected in laboratory incubations. For example, the proliferation of sedges can enhance CH_4 emissions to the atmosphere through transport of CH_4 through aerenchymous tissue (King *et al*., 1998) and also enhance CH_4 oxidation through transport of oxygen to roots (Strom *et al*., 2005).

Favorable environmental conditions and microbial processes

Favorable environmental conditions for CH_4 production include temperature, pH, and deficiency of oxygen and alternate electron acceptors (not addressed in this analysis); these factors act as a secondary control on CH_4 production. Environmental conditions explained the most variance among CO_2 production rates, but were less important for CH_4 production rates (Table 4). Higher temperatures result in increased rates of CH_4 and anaerobic CO_2 production (Table 2), as has been shown in previous studies (Dunfield *et al*., 1993; Bergman *et al*., 1998; Whalen & Reeburgh, 2000; Yavitt *et al*., 2006; Lupascu *et al*., 2012). Previously, CH_4 production had been found to be positively and negatively correlated with pH (c.f. Bergman *et al*., 1998), perhaps due to interactions between pH, temperature, and substrate type (Valentine *et al*., 1994; Bergman *et al*., 1998) or due to a pH optima of methanogenesis (Dunfield *et al*., 1993). This synthesis found a positive relationship between CH_4 production and pH, and that relationship differed among incubation temperatures; pH can affect multiple processes simultaneously, including methanogenic pathway (Kotsyurbenko *et al*., 2007), and so although the specific mechanisms may be complex and interactive, pH is seen as a key variable controlling anaerobic metabolism across multiple landscape units.

Redox conditions play an important role for C cycling in anoxic soils. Dry, aerobic conditions or drying and re-wetting can result in a substantial lag time prior to CH_4 production due to regeneration of alternate electron acceptors (Dise & Verry, 2001; Knorr & Blodau, 2009). In this synthesis of incubation studies, the lag time before maximum CH_4 production was shortest in inundated sites, intermediate in fluctuating water table sites, and longest in dry sites (Table 2). Additionally, in chronically dry soils, methanogen populations may be substantially smaller than soils that experience inundation (Tveit *et al*., 2013) and require longer periods for population size to grow prior to measurable CH_4 production. Observations of lag times suggest that environmental conditions, such as temperature and redox status, as well as methanogen populations, may limit CH_4 production in fluctuating water table zones that can change over the course of a growing season in permafrost areas due to perched water tables. Furthermore, landscape changes associated with permafrost thaw, such as inundation, may not result in CH_4 production until environmental conditions are suitable and methanogen communities are present.

Recommendations, scaling up, and climate change effects

Climate change in northern regions is affecting ecosystems in multiple ways, including deepening active layer depths, shifting vegetation dynamics, growing season length, and hydrology (Serreze *et al.*, 2000; Hinzman *et al.*, 2005; Myers-Smith *et al.*, 2011; Overland *et al.*, 2013). All of these factors have the potential to affect CH_4 and anaerobic CO_2 production. Our synthesis results show both direct effects of temperature on CH_4 and anaerobic CO_2 production (Table 2), as well as indirect effects of ecosystem shifts that may be associated with climate change.

CH_4 production rates were more than twice as high in active layer soils compared to permafrost as well as from sites without permafrost compared to those underlain by permafrost, both of which suggest that CH_4 production will increase as permafrost thaws. However, there are also important indirect effects of permafrost that will have profound impacts on anaerobic CO_2 and CH_4 production and emissions. Thermokarst thaw and permafrost thaw frequently result in wetter soils, especially in lowlands. This synthesis suggests that flooding and periodic inundation of surface soils due to permafrost thaw may result in higher CH_4 fluxes, as has been observed in field CH_4 emission studies (e.g., Olefeldt *et al.*, 2013 and references therein). Vegetation changes, such as a transition from dry, treed sites to wet, graminoid sites, or from graminoid tundra sites to shrub or tree tundra, may also alter anaerobic CO_2 and CH_4 production rates (e.g., Hodgkins *et al.*, 2014), although the effects of vegetation on CH_4 production via substrate quality will operate at timescales of a growing season to decades while the environmental controls on CH_4 production operate on daily to seasonal scales.

There is substantial uncertainty in the spatial and temporal variability of estimates of CH_4 fluxes and CO_2 exchange in the permafrost region (McGuire *et al.*, 2009, 2012). This synthesis has several implications for modeling anaerobic CH_4 and CO_2 fluxes from permafrost region. Our results indicate that models of greenhouse gas emissions from thawing permafrost should consider several sources of variability in methanogenesis that are generally not taken into account: variation (i) between organic and mineral horizons, (ii) with depth within soil horizons, (iii) between active layer and thawed permafrost layer of soils in sites with permafrost, (iv) between permafrost sites and sites without permafrost, and (v) among plant functional types. Models generally consider some of the effects of water table position, but this study indicates that it is important to distinguish between chronically dry surface soil horizons and seasonally or chronically inundated soil horizons (e.g., Zhuang *et al.*, 2004; Wania *et al.*, 2010; Riley *et al.*, 2011; Bohn *et al.*, 2013). Similarly, models generally have different parameterizations for different anaerobic ecosystems, but there is no generally accepted scheme as to how those parameterizations should be developed. This synthesis indicates that parameterizations should be hierarchically organized by biome, landscape position, and vascular/moss vegetation types (Table 4). While models generally consider the effects of pH and temperature on methanogenesis, this study provides some additional insight into the relative importance of these effects on anaerobic metabolism (Table 4). The information on lag times in methanogenesis provided by this study can inform models that simulate the effects of thermokarst disturbance (e.g., from forested permafrost plateau to collapse scar bog) on methanogenesis because of possible lags in microbial colonization and population dynamics, which are ultimately shorter than the persistence of thermokarst wetlands. Finally, most models do not consider anaerobic CO_2 production in modeling methane dynamics, and this study provides substantial insight into the variability in the ratio of anaerobic CO_2 to CH_4 production.

To improve estimates of CH_4 production from soils across the permafrost zone, future incubation study designs should be modified to include longer incubations, a wider variety of sites, additional measurement parameters, and to include methane oxidation. The substantial lag times before maximum rates of CH_4 production (Table 2) suggest that longer duration anaerobic incubation experiments are required to assess maximum CH_4 production from permafrost soils; we suggest 30-day minimum incubation length and longer time periods if low incubation temperatures are used. Second, a sampling bias toward hot spots of CH_4 production across the landscape (McClain *et al.*, 2003), that is, wetlands, could affect our estimates of lag time and maximum CH_4 production rates among some classifications we used, especially for permafrost presence/absence. Increased sampling of additional mineral or upland soils might reduce bias in our estimates of maximum rates of CH_4 production and lag times in the permafrost zone. New methodologies need to be used to identify pathways of anaerobic CO_2 and CH_4 production, including use of stable isotopes and chemical characterization of organic matter (Corbett *et al.*, 2013; Tfaily *et al.*, 2013; Hodgkins *et al.*, 2014). Furthermore, measurements of methanogen communities, redox status and pH in mineral or upland soils and both dry and saturated wetland soils may help clarify whether long lag times prior to maximum CH_4 production rates are due to redox conditions or methanogen community abundances. Furthermore, we did not consider CH_4

oxidation in this synthesis; additional research on rates of oxic and anoxic CH_4 oxidation (Whalen & Reeburgh, 2000; Blazewicz *et al*., 2012; Haroon *et al*., 2013) will better constrain CH_4 budgets from the permafrost zone.

Results from this synthesis highlight the importance of understanding the complex interactions among geochemistry, methanogen communities, and organic matter quality for determining ecosystem scale patterns of CH_4 and CO_2 production as the thaw regime and vegetation dynamics continue to change in northern latitude systems. Our results suggest that the largest source of anaerobic CO_2 and CH_4 produced will be from seasonally saturated surface soils rather than from the decomposition of newly thawed substrate found in permafrost soils. Therefore, increased wetland area associated with permafrost thaw will result in larger CH_4 emissions than deeper seasonally thawed soils and underscores a need for capturing hydrologic changes associated with ecosystem transitions.

Acknowledgements

We thank the Permafrost Carbon Vulnerability Research Coordination Network (NSF Grant to EAGS) for helping us to organize this study. CT acknowledges funding from the U.S. DOE-SCGF and the University of New Hampshire Graduate School Dissertation Year Fellowship. Additional funding was provided by NSF OPP (ARC-1203777) to SMN; the Next-Generation Ecosystem Experiments (NGEE Arctic) project, supported by the Office of Biological and Environmental Research in the U.S. DOE Office of Science, to CMI, RJN, TRC, VLS; European Research Network CryoCARB (FWF – I370-B17) to AR; and USGS Global Change R&D program and the USGS Climate Science Center to MW. Craig Connolly and Adam Marquis provided assistance with GIS and data extraction. We thank Steve Frolking, Evan Kane, and four anonymous reviewers for comments that improved the manuscript. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

References

Agren GI, Bosatta E (1996) Quality: a bridge between theory and experiment in soil organic matter studies. *Oikos*, **76**, 522–528.

Bates D, Maechler M, Bolker BM, Walker S (2014). lme4: Linear mixed-effects models using Eigen and S4. ArXiv e-print; submitted to Journal of Statistical Software, http://arxiv.org/abs/1406.5823

Bellisario LM, Bubier JL, Moore TR, Chanton JP (1999) Controls on CH_4 emissions from a northern peatland. *Global Biogeochemical Cycles*, **13**, 81–91.

Bergman I, Svensson BH, Nilsson M (1998) Regulation of methane production in a Swedish acid mire by pH, temperature and substrate. *Soil Biology & Biochemistry*, **30**, 729–741.

Blazewicz SJ, Petersen DG, Waldrop MP, Firestone MK (2012) Anaerobic oxidation of methane in tropical and boreal soils: ecological significance in terrestrial methane cycling. *Journal of Geophysical Research-Biogeosciences*, **117**, G02033.

Bohn TJ, Podest E, Schroeder R *et al*. (2013) Modeling the large-scale effects of surface moisture heterogeneity on wetland carbon fluxes in the West Siberian Lowland. *Biogeosciences*, **10**, 6559–6576.

Brown J, Ferrians OJ Jr., Heginbottom JA, Melnikov ES (1998, revised 2001). *Circum-Arctic map of permafrost and ground-ice conditions*. National Snow and Ice Data Center/World Data Center for Glaciology: Digital Media, Boulder, CO.

Chanton JP, Bauer JE, Glaser PA *et al*. (1995) Radiocarbon evidence for the substrates supporting methane formation within northern minnesota peatlands. *Geochimica Et Cosmochimica Acta*, **59**, 3663–3668.

Christensen TR, Johansson TR, Akerman HJ *et al*. (2004) Thawing sub-arctic permafrost: effects on vegetation and methane emissions. *Geophysical Research Letters*, **31**, L04501.

Conrad R (1999) Contribution of hydrogen to methane production and control of hydrogen concentrations in methanogenic soils and sediments. *FEMS Microbiology Ecology*, **28**, 193–202.

Corbett JE, Tfaily M, Burdige D, Cooper W, Glaser P, Chanton J (2013) Partitioning pathways of CO_2 production in peatlands with stable carbon isotopes. *Biogeochemistry*, **114**, 327–340.

Dise NB, Verry ES (2001) Suppression of peatland methane emission by cumulative sulfate deposition in simulated acid rain. *Biogeochemistry*, **53**, 143–160.

Duddleston KN, Kinney MA, Kiene RP, Hines ME (2002) Anaerobic microbial biogeochemistry in a northern bog: acetate as a dominant metabolic end product. *Global Biogeochemical Cycles*, **16**, 1063.

Dunfield P, Knowles R, Dumont R, Moore TR (1993) Methane production and consumption in temperate and sub-arctic peat soils – response to temperature and pH. *Soil Biology & Biochemistry*, **25**, 321–326.

Dutta K, Schuur EAG, Neff JC, Zimov SA (2006) Potential carbon release from permafrost soils of Northeastern Siberia. *Global Change Biology*, **12**, 2336–2351.

Elberling B, Michelsen A, Schadel C *et al*. (2013) Long-term CO_2 production following permafrost thaw. *Nature Climate Change*, **3**, 890–894.

Ernakovich J, Schimel J, Wallenstein M (2014, updated 2014-07-14). Soil chemistry and characteristics measured for incubation of microbial communities in permafrost. UCAR/NCAR – CISL – ACADIS. Dataset. http://dx.doi.org/10.5065/D66M34S3

Ganzert L, Jurgens G, Münster U, Wagner D (2007) Methanogenic communities in permafrost-affected soils of the Laptev Sea coast, Siberian Arctic, characterized by 16S rRNA gene fingerprints. *Fems Microbiology Ecology*, **59**, 476–488.

Grömping U (2006) Relative importance for linear regression in R: the package relaimpo. *Journal of Statistical Software*, **17**, 1–27.

Halsey LA, Vitt DH, Zoltai SC (1995) Disequilibrium response of permafrost in boreal continental western Canada to climate-change. *Climatic Change*, **30**, 57–73.

Hamdi S, Moyano F, Sall S, Bernoux M, Chevallier T (2013) Synthesis analysis of the temperature sensitivity of soil respiration from laboratory studies in relation to incubation methods and soil conditions. *Soil Biology and Biochemistry*, **58**, 115–126.

Harden JW, Koven CD, Ping C-L *et al*. (2012) Field information links permafrost carbon to physical vulnerabilities of thawing. *Geophysical Research Letters*, **39**, L15704.

Haroon MF, Hu S, Shi Y *et al*. (2013) Anaerobic oxidation of methane coupled to nitrate reduction in a novel archaeal lineage. *Nature*, **500**, 567–570.

Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, **25**, 1965–1978.

Hines ME, Duddleston KN, Rooney-Varga JN, Fields D, Chanton JP (2008) Uncoupling of acetate degradation from methane formation in Alaskan wetlands: connections to vegetation distribution. *Global Biogeochemical Cycles*, **22**, Gb2017.

Hinzman LD, Bettez ND, Bolton WR *et al*. (2005) Evidence and implications of recent climate change in northern Alaska and other arctic regions. *Climatic Change*, **72**, 251–298.

Hobbie SE (1996) Temperature and plant species control over litter decomposition in Alaskan tundra. *Ecological Monographs*, **66**, 503–522.

Hodgkins SB, Tfaily MM, McCalley CK *et al*. (2014) Changes in peat chemistry associated with permafrost thaw increase greenhouse gas production. *Proceedings of the National Academy of Sciences*, **111**, 5819–5824.

Holland S (1992). *Methane emission in the northern subarctic wetland environment of Churchill, Manitoba*. Department of Geography. McMaster University, Hamilton, Ontario. Master of Science: 108 pp.

Hugelius G, Strauss J, Zubrzycki S *et al*. (2014) Improved estimates show large circumpolar stocks of permafrost carbon while quantifying substantial uncertainty ranges and identifying remaining data gaps. *Biogeosciences Discussions*, **11**, 4771–4822.

Johansson T, Malmer N, Crill PM, Friborg T, Akerman JH, Mastepanov M, Christensen TR (2006) Decadal vegetation changes in a northern peatland, greenhouse gas fluxes and net radiative forcing. *Global Change Biology*, **12**, 2352–2369.

Jorgenson MT, Osterkamp TE (2005) Response of boreal ecosystems to varying modes of permafrost degradation. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere*, **35**, 2100–2111.

Jorgenson MT, Racine CH, Walters JC, Osterkamp TE (2001) Permafrost degradation and ecological changes associated with a warming climate in central Alaska. *Climatic Change*, **48**, 551–579.

Kane ES, Chivers MR, Turetsky MR *et al.* (2013) Response of anaerobic carbon cycling to water table manipulation in an Alaskan rich fen. *Soil Biology and Biochemistry*, **58**, 50–60.

King JY, Reeburgh WS, Regli SK (1998) Methane emission and transport by arctic sedges in Alaska: results of a vegetation removal experiment. *Journal of Geophysical Research-Atmospheres*, **103**, 29083–29092.

King JY, Reeburgh WS, Thieler KK, Kling GW, Loya WM, Johnson LC, Nadelhoffer KJ (2002) Pulse-labeling studies of carbon cycling in Arctic tundra ecosystems: the contribution of photosynthates to methane emission. *Global Biogeochemical Cycles*, **16**, 1062.

Knoblauch C, Beer C, Sosnin A, Wagner D, Pfeiffer E-M (2013) Predicting long-term carbon mineralization and trace gas production from thawing permafrost of Northeast Siberia. *Global Change Biology*, **19**, 1160–1172.

Knorr KH, Blodau C (2009) Impact of experimental drought and rewetting on redox transformations and methanogenesis in mesocosms of a northern fen soil. *Soil Biology & Biochemistry*, **41**, 1187–1198.

Kotsyurbenko OR, Friedrich MW, Simankova MV, Nozhevnikova AN, Golyshin PN, Timmis KN, Conrad R (2007) Shift from acetoclastic to H-2-dependent methanogenes is in a West Siberian peat bog at low pH values and isolation of an acidophilic Methanobacterium strain. *Applied and Environmental Microbiology*, **73**, 2344–2348.

Koven CD, Riley WJ, Stern A (2012) Analysis of permafrost thermal dynamics and response to climate change in the CMIP5 earth system models. *Journal of Climate*, **26**, 1877–1900.

Kuder T, Kruge MA (2001) Carbon dynamics in peat bogs: insights from substrate macromolecular chemistry. *Global Biogeochemical Cycles*, **15**, 721–727.

Lawrence DM, Slater AG, Swenson SC (2012) Simulation of present-day and future permafrost and seasonally frozen ground conditions in CCSM4. *Journal of Climate*, **25**, 2207–2225.

Lee H, Schuur EAG, Inglett KS, Lavoie M, Chanton JP (2012) The rate of permafrost carbon release under aerobic and anaerobic conditions and its potential effects on climate. *Global Change Biology*, **18**, 515–527.

Lipson DA, Zona D, Raab TK, Bozzolo F, Mauritz M, Oechel WC (2012) Water-table height and microtopography control biogeochemical cycling in an Arctic coastal tundra ecosystem. *Biogeosciences*, **9**, 577–591.

Lupascu M, Wadham JL, Hornibrook ERC, Pancost RD (2012) Temperature sensitivity of methane production in the permafrost active layer at Stordalen, Sweden: a comparison with non-permafrost northern wetlands. *Arctic Antarctic and Alpine Research*, **44**, 469–482.

McCalley CK, Woodcroft BJ, Hodgkins SB *et al.* (2014) Methane dynamics regulated by microbial community response to permafrost thaw. *Nature*, **514** (7523), 478–481.

McClain ME, Boyer EW, Dent CL *et al.* (2003) Biogeochemical hot spots and hot moments at the interface of terrestrial and aquatic ecosystems. *Ecosystems*, **6**, 301–312.

McGuire AD, Anderson LG, Christensen TR *et al.* (2009) Sensitivity of the carbon cycle in the Arctic to climate change. *Ecological Monographs*, **79**, 523–555.

McGuire AD, Christensen TR, Hayes D *et al.* (2012) An assessment of the carbon balance of Arctic tundra: comparisons among observations, process models, and atmospheric inversions. *Biogeosciences*, **9**, 3185–3204.

Moore TR, Heyes A, Roulet NT (1994) Methane emissions from wetlands, southern hudson-bay lowland. *Journal of Geophysical Research-Atmospheres*, **99**, 1455–1467.

Myers-Smith IH, McGuire AD, Harden JW, Chapin FS (2007) Influence of disturbance on carbon exchange in a permafrost collapse and adjacent burned forest. *Journal of Geophysical Research-Biogeosciences*, **112**, G04017.

Myers-Smith I, Forbes BC, Wilmking M *et al.* (2011) Shrub expansion in tundra ecosystems: dynamics, impacts and research priorities. *Environmental Research Letters*, **6**, 045509.

Myhre G, Shindell D, Bréon FM *et al.* (2013). Anthropogenic and Natural Radiative Forcing. In: *Climate Change 2013: The Physical Science Basis. Contributions of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* (eds Stocker TF, Qin D, Plattner G-K *et al.*), pp. 659–740. Cambridge University, Cambridge, UK and New York, NY, USA.

Natali SM, Schuur EAG, Webb EE, Hicks Pries CE, Crummer KG (2014) Permafrost degradation stimulates carbon loss from experimentally warmed tundra. *Ecology*, **95**, 602–608.

Nilsson M, Oquist M (2009). Partitioning litter mass loss into carbon dioxide and methane in peatland ecosystems. In: *Carbon Cycling in Northern Peatlands* (eds Baird AJ, Belyea LR, Comas X, Reeve AS, Slater L), pp. 131–144. American Geophysical Union, Washington, DC.

O'Donnell JA, Jorgenson MT, Harden JW, McGuire AD, Kanevskiy M, Wickland KP (2012) The effects of permafrost thaw on soil hydrologic, thermal, and carbon dynamics in an Alaskan Peatland. *Ecosystems*, **15**, 213–229.

Olefeldt D, Turetsky MR, Crill PM, McGuire AD (2013) Environmental and physical controls on northern terrestrial methane emissions across permafrost zones. *Global Change Biology*, **19**, 589–603.

Overland J, Hanna E, Hanssen-Bauer I *et al.* (2013). Air Temperature. Arctic Report Card: Update for 2013. M. O. Jeffries, J. Richter-Menge and J. Overland. http://www.arctic.noaa.gov/reportcard/National Oceanic and Atmomospheric Administration.

Payette S, Delwaide A, Caccianiga M, Beauchemin M (2004) Accelerated thawing of subarctic peatland permafrost over the last 50 years. *Geophysical Research Letters*, **31**, L18208.

Prater JL, Chanton JP, Whiting GJ (2007) Variation in methane production pathways associated with permafrost decomposition in collapse scar bogs of Alberta, Canada. *Global Biogeochemical Cycles*, **21**, GB4004.

R Development Core Team (2008) *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.

Repo ME, Susiluoto S, Lind SE *et al.* (2009) Large N_2O emissions from cryoturbated peat soil in tundra. *Nature Geoscience*, **2**, 189–192.

Riley WJ, Subin ZM, Lawrence DM *et al.* (2011) Barriers to predicting changes in global terrestrial methane fluxes: analyses using CLM4Me, a methane biogeochemistry model integrated in CESM. *Biogeosciences*, **8**, 1925–1953.

Schädel C, Schuur EAG, Bracho R *et al.* (2014) Circumpolar assessment of permafrost C quality and its vulnerability over time using long-term incubation data. *Global Change Biology*, **20**, 641–652.

Schlesinger WH (1997) *Biogeochemistry: An analysis of Global Change*. Academic Press, San Diego, CA.

Schuur EAG, Bockheim J, Candell JG *et al.* (2008) Vulnerability of permafrost carbon to climate change: implications for the global carbon cycle. *BioScience*, **58**, 701–714.

Schuur EAG, Vogel JG, Crummer KG, Lee H, Sickman JO, Osterkamp TE (2009) The effect of permafrost thaw on old carbon release and net carbon exchange from tundra. *Nature*, **459**, 556–559.

Schuur EAG, Abbott BW, Bowden WB *et al.* (2013) Expert assessment of vulnerability of permafrost carbon to climate change. *Climatic Change*, **119**, 359–374.

Serreze MC, Walsh JE, Chapin FS *et al.* (2000) Observational evidence of recent change in the northern high-latitude environment. *Climatic Change*, **46**, 159–207.

Strom L, Mastepanov M, Christensen TR (2005) Species-specific effects of vascular plants on carbon turnover and methane emissions from wetlands. *Biogeochemistry*, **75**, 65–82.

Svensson BH (1984) Different temperature optima for methane formation when enrichments from acid peat are supplemented with acetate or hydrogen. *Applied and Environmental Microbiology*, **48**, 389–394.

Tarnocai C, Canadell JG, Schuur EAG, Kuhry P, Mazhitova G, Zimov S (2009) Soil organic carbon pools in the northern circumpolar permafrost region. *Global Biogeochemical Cycles*, **23**, GB2023.

Tfaily MM, Hamdan R, Corbett JE, Chanton JP, Glaser PH, Cooper WT (2013) Investigating dissolved organic matter decomposition in northern peatlands using complimentary analytical techniques. *Geochimica et Cosmochimica Acta*, **112**, 116–129.

Treat CC, Wollheim WM, Varner RK, Grandy AS, Talbot J, Frolking S (2014) Temperature and peat type control CO_2 and CH_4 production in Alaskan permafrost peats. *Global Change Biology*, **20**, 2674–2686.

Turetsky MR, Wieder RK, Vitt DH, Evans RJ, Scott KD (2007) The disappearance of relict permafrost in boreal north America: effects on peatland carbon storage and fluxes. *Global Change Biology*, **13**, 1922–1934.

Tveit A, Schwacke R, Svenning MM, Urich T (2013) Organic carbon transformations in high-Arctic peat soils: key functions and microorganisms. *ISME Journal*, **7**, 299–311.

Valentine DW, Holland EA, Schimel DS (1994) Ecosystem and physiological controls over methane production in northern wetlands. *Journal of Geophysical Research-Atmospheres*, **99**, 1563–1571.

Venables WN, Ripley BD (2002) *Modern Applied Statistics with S*. Springer, New York.

Waldrop MP, Wickland KP, White R, Berhe AA, Harden JW, Romanovsky VE (2010) Molecular investigations into a globally important carbon pool: permafrost-protected carbon in Alaskan soils. *Global Change Biology*, **16**, 2543–2554.

Walter KM, Zimov SA, Chanton JP, Verbyla D, Chapin FS (2006) Methane bubbling from Siberian thaw lakes as a positive feedback to climate warming. *Nature*, **443**, 71–75.

Wania R, Ross I, Prentice IC (2010) Implementation and evaluation of a new methane model within a dynamic global vegetation model: LPJ-WHyMe v1.3.1. *Geoscientific Model Development*, **3**, 565–584.

Whalen SC, Reeburgh WS (2000) Methane oxidation, production, and emission at contrasting sites in a boreal bog. *Geomicrobiology Journal*, **17**, 237–251.

Wickland KP, Striegl RG, Neff JC, Sachs T (2006) Effects of permafrost melting on CO_2 and CH_4 exchange of a poorly drained black spruce lowland. *Journal of Geophysical Research-Biogeosciences*, **111**, G02011.

Williams RT, Crawford RL (1985) Methanogenic bacteria, including an acid-tolerant strain, from peatlands. *Applied and Environment Microbiology*, **50**, 1542–1544.

Yavitt JB, Basiliko N, Turetsky MR, Hay AG (2006) Methanogenesis and methanogen diversity in three peatland types of the discontinuous permafrost zone, boreal western continental Canada. *Geomicrobiology Journal*, **23**, 641–651.

Zhang Y, Chen WJ, Riseborough DW (2008) Transient projections of permafrost distribution in Canada during the 21st century under scenarios of climate change. *Global and Planetary Change*, **60**, 443–456.

Zhuang Q, Melillo JM, Kicklighter DW *et al.* (2004) Methane fluxes between terrestrial ecosystems and the atmosphere at northern high latitudes during the past century: a retrospective analysis with a process-based biogeochemistry model. *Global Biogeochemical Cycles*, **18**, GB3010.

Zona D, Lipson DA, Paw U *et al.* (2012) Increased CO_2 loss from vegetated drained lake tundra ecosystems due to flooding. *Global Biogeochemical Cycles*, **26**, Gb2004.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Median CO_2:CH_4 production on the day of maximum CH_4 production, excluding samples in which maximum CH_4 production occurred after day 150 (n = 193).
Table S2. Number of measurements in the aggregated dataset for each category, and number of studies that reported ancillary data (e.g., pH, %C, %N).
Table S3. Linear models used to estimate missing % C and bulk density values.
Figure S1. Rates of CH_4 production for all incubations measurements included in the full dataset by sample day. The aggregated dataset included maximum CH_4 production for each sample.
Figure S2. Rates of CO_2 production for all incubations measurements included in the full dataset over time.
Figure S3. Using the daily CH_4 production to maximum CH_4 production ratio, we calculated the lag time before maximum CH_4 production, which occurs on Day 0 in this figure, during each incubation experiment.
Figure S4. For all depths included in study (a) Maximum CH_4 production rates, (b) mean CO_2 production, and (c) and CO_2:CH_4 production for organic (dark circles) and mineral (gray triangles) soil types.
Figure S5. Relationship between %C and depth for top 250 cm of soils. Also plotted are the regression lines for the empirical relationship developed between % C, depth, and soil type. Regression coefficients are found in Table S3.
Figure S6. Relationships between % C in soils and CH_4 production (top) and CO_2 production (bottom) in anaerobic incubations.
Figure S7. The relationship between pH and maximum CH_4 production was dependent on incubation temperature (χ^2 = 35, df = 4, $P < 0.001$).
Figure S8. Non-metric Multidimensional Scaling of CH_4:CO_2 production, mean CH_4 production (μg CH_4-C gC^{-1} h^{-1}), maximum CH_4 production (μg CH_4-C gC^{-1} h^{-1}), and CO_2 production (μg CO_2-C gC^{-1} h^{-1}) from combined dataset of measurements and imputation.
Figure S9. Fit showing vectors of continuous predictor variables: pH and %C loss; and centroids of levels of the class variable, depth (Active Layer, AL and Permafrost, PF).