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Environmental and physical controls on northern terrestrial methane emissions across permafrost zones

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Abstract

Methane (CH_4) emissions from the northern high-latitude region represent potentially significant biogeochemical feedbacks to the climate system. We compiled a database of growing-season CH_4 emissions from terrestrial ecosystems located across permafrost zones, including 303 sites described in 65 studies. Data on environmental and physical variables, including permafrost conditions, were used to assess controls on CH_4 emissions. Water table position, soil temperature, and vegetation composition strongly influenced emissions and had interacting effects. Sites with a dense sedge cover had higher emissions than other sites at comparable water table positions, and this was an effect that was more pronounced at low soil temperatures. Sensitivity analysis suggested that CH_4 emissions from ecosystems where the water table on average is at or above the soil surface (wet tundra, fen underlain by permafrost, and littoral ecosystems) are more sensitive to variability in soil temperature than drier ecosystems (palsa dry tundra, bog, and fen), whereas the latter ecosystems conversely are relatively more sensitive to changes of the water table position. Sites with near-surface permafrost had lower CH_4 fluxes than sites without permafrost at comparable water table positions, a difference that was explained by lower soil temperatures. Neither the active layer depth nor the organic soil layer depth was related to CH_4 emissions. Permafrost thaw in lowland regions is often associated with increased soil moisture, higher soil temperatures, and increased sedge cover. In our database, lowland thermokarst sites generally had higher emissions than adjacent sites with intact permafrost, but emissions from thermokarst sites were not statistically higher than emissions from permafrost-free sites with comparable environmental conditions. Overall, these results suggest that future changes to terrestrial high-latitude CH_4 emissions will be more proximately related to changes in moisture, soil temperature, and vegetation composition than to increased availability of organic matter following permafrost thaw.

Keywords: Methane, permafrost, sedges, static chambers, tundra, wetlands

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Introduction

Methane (CH_4) is again accumulating in the atmosphere at rates similar to those observed before 1990 for reasons that are not clear (Dlugokencky *et al.*, 2011). It is therefore a serious issue to quantitatively understand the source dynamics of CH_4 because of its ability to absorb long-wave radiation in the atmopshere and act as an effective climate forcing agent (Forster *et al.*, 2007). Northern high-latitude biomes have abundant wetland areas (Matthews & Fung, 1987) that are large sources of biogenic CH_4. Emission estimates for the combined boreal and tundra biomes (>50°N) are between 25 and 100 Tg yr^{-1}, with most estimates in the lower half of this range (Cao *et al.*, 1998; Walter *et al.*, 2001; Mikaloff-Fletcher *et al.*, 2004; Zhuang *et al.*, 2006; McGuire *et al.*, 2009; Bousquet *et al.*, 2011; Koven *et al.*, 2011). Of this total, the tundra accounts for 8–30 Tg yr^{-1} (Christensen, 1993; McGuire *et al.*, 2012). The boreal and tundra biomes together are thus responsible for ~3–10% of total CH_4 emissions (550 Tg yr^{-1}), and a significant fraction of global natural wetland emissions (100–200 Tg yr^{-1}) to the atmosphere (Neef *et al.*, 2010; Dlugokencky *et al.*, 2011). With ongoing rapid climate change at high latitudes, including permafrost thaw, there is a need to understand the environmental and physical controls of CH_4 emissions to assess the potential for high-latitude CH_4 emissions to act as biogeochemical feedbacks to the climate system (Arneth *et al.*, 2010; Dlugokencky *et al.*, 2011; Koven *et al.*, 2011; Schneider von Deimling *et al.*, 2012).

Net CH_4 emissions are determined by the balance between CH_4 production and removal through oxidation. Production of CH_4 is an anaerobic microbial process where archaeal methanogens convert acetate, H_2, and CO_2 derived from organic matter into CH_4. Oxidation of CH_4 is a largely aerobic process carried out by

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methanotrophic and methylotrophic bacteria. Residence time of CH_4 in aerobic soils and waters affect the proportion of produced CH_4 that is released to the atmosphere from anaerobic production sites. Complete or near-complete oxidation affects CH_4 that diffuses slowly through aerobic soils and waters. Conversely, advective transport through aerenchymatous roots and stems of certain plant species and the release through episodic ebullition both mediate emissions to the atmosphere that are much less affected by oxidation (King *et al*., 1998; Le Mer & Roger, 2001).

The combination of biological and physical processes that control net CH_4 emissions is responsible for the characteristic high spatial and temporal variability of CH_4 flux measurements. This has resulted in individual studies finding that terrestrial tundra and boreal CH_4 fluxes are related to a broad range of controls. These factors include soil moisture conditions (Moore *et al*., 1994; von Fischer *et al*., 2010), soil temperature (Bubier *et al*., 1995; Christensen *et al*., 1995), vegetation composition – particularly the presence or absence of sedges (Bellisario *et al*., 1999; Ström *et al*., 2005), soil respiration, and plant productivity as indicated by CO_2 fluxes (Öquist & Svensson, 2002; Nykänen *et al*., 2003), quality of soil organic matter (Wagner *et al*., 2005), availability of organic acids in pore water (Christensen *et al*., 2003; Ström *et al*., 2012), structure of the microbial community (Wagner *et al*., 2003; Waldrop *et al*., 2010), atmospheric CO_2 concentration (Hutchin *et al*., 1995; Saarnio *et al*., 2000), and active layer thickness (Christensen *et al*., 1995; van Huissteden *et al*., 2005). While different environmental and physical variables appear to dominate at different temporal and spatial scales, observed relationships also differ among studies and not all variables have been universally found to influence CH_4 fluxes.

The first published studies of CH_4 measurements from high-latitude regions were carried out in northern Sweden in the 1970s (Svensson, 1973), with research continuing in both Eurasia and North America since the mid-1980s. Measurements of CH_4 fluxes are most commonly made using static chambers, whereby a small area of a land surface (0.05–0.5 m^2) is enclosed and CH_4 headspace concentrations are measured repeatedly over a period of time (10–120 min). Static chamber techniques have drawbacks, including high labor intensity, low sampling frequency (unless an automated system is deployed), disturbance to soils during collar installation, alteration of the microenvironment during flux measurement, and the assumption that fluxes are properly characterized by the change in CH_4 concentration in the headspace (Davidson *et al*., 2002; Lai *et al*., 2012). On the other hand, chamber measurements can be implemented in remote locations and allow for a detailed characterization of the spatial variation of CH_4 fluxes and their relationship to environmental variables.

Climate change has been more rapid at high latitudes than the global average over the last few decades – a trend which is very likely to continue during this century. Central estimates for high-latitude temperature and precipitation changes during this century lie between +4 and +6 °C and +10% and +30%, respectively, in IPCC's 'A1B' projections (Christensen *et al*., 2007). Widespread deepening of the active layer and complete near-surface permafrost thaw are projected to accompany climate changes (Delisle, 2007; Lawrence *et al*., 2012). Permafrost thaw can have very different ecological and hydrological consequences depending on the topographical location in the landscape, soil characteristics, and permafrost ice content – examples of thermokarst landforms include collapse fens and bogs along with thermokarst pits, gullies, slumps, drainage basins, and lakes (Jorgenson & Osterkamp, 2005). Loss of permafrost, primarily in peatlands, will make previously frozen organic matter available to microbial activity (Camill, 2005), a store of organic matter that is potentially microbially labile (Schuur *et al*., 2008; Waldrop *et al*., 2010). Studies of CH_4 emissions in thermokarst landforms (primarily collapse bogs and fens) have found higher emissions than in nearby sites where permafrost is still intact (Bubier *et al*., 1995; Liblik *et al*., 1997; Turetsky *et al*., 2002; Wickland *et al*., 2006; Myers-Smith *et al*., 2007; Prater *et al*., 2007; Bäckstrand *et al*., 2008; Desyatkin *et al*., 2009). It is not clear, however, if elevated CH_4 emissions are due to microbial access to recently thawed organic material or due to other changes associated with permafrost thaw, for example altered hydrological setting, thermal regime, and/or vegetation composition.

Both continuous, low winter fluxes (Alm *et al*., 1999; Panikov & Dedysh, 2000; Nykänen *et al*., 2003; Kim *et al*., 2007) and occasional, high fluxes during spring and fall due to thaw and freeze dynamics (Windsor *et al*., 1992; Hargreaves *et al*., 2001; Mastepanov *et al*., 2008) can contribute significantly to the annual CH_4 flux in high-latitude regions. However, in nearly all cases the annual flux is dominated (50–95%) by fluxes during the short (90–150 days) growing season (e.g. Whalen & Reeburgh, 1992). Understanding the controls and sensitivities of growing season emissions is therefore crucial for assessing the impacts of climate change on high-latitude CH_4 emissions.

The objective of this study is to synthesize results from more than three decades of chamber CH_4 chamber measurements from the northern high-latitude regions. We used published literature to compile a database of average growing season CH_4 fluxes along with a range of associated environmental and physical variables. Our database thus contains more ancillary information than previous synthesis efforts of high-latitude CH_4 emissions (McGuire *et al*., 2012). The analysis focuses on terrestrial ecosystems, with a majority of the research carried out in wetlands with varying permafrost conditions. While acknowledging their importance for landscape scale CH_4 emissions, aquatic ecosystems were excluded from this analysis due to assumed differences in controlling variables in comparison to terrestrial ecosystems (e.g. Bastviken *et al*., 2004). Using the database, we evaluated which variables were related to CH_4 fluxes across studies and whether the nature and strengths of these functional relationships led to differences in sensitivities among ecosystems and permafrost conditions. We hypothesized that site CH_4 fluxes would be primarily related to interacting effects of environmental and ecological variables such as soil moisture, soil temperature, plant productivity, and vegetation composition, and that any effect from permafrost conditions could be attributed to its influence on those primary controls. A synthesis of available studies can reveal patterns that are difficult for individual studies to detect and thus provide new knowledge that will improve our understanding of the sensitivity of northern high-latitude CH_4 emissions to continued climate change.

Methods

Database compilation

A database with reported growing season (June to September) CH_4 fluxes was compiled using data from studies published prior to March 2012. All studies were conducted north of 50°N, within permafrost zones as outlined by Brown *et al.* (1998), Fig. 1. All studies used static chambers to measure CH_4 fluxes. The database was compiled to compare CH_4 fluxes among sites and we define a site as a group of static chambers placed on surfaces with similar vegetation composition and physical characteristics (e.g. moisture conditions, permafrost condition, and soil temperature regime) and in proximity to each other (in most cases ~10–100 m apart, although up to a few kilometers was acceptable as done for example by Morrissey & Livingston (1992)). In most cases, chambers were grouped into suitable sites in the primary publications, but for a few studies it was necessary to aggregate or split different chamber locations into appropriate sites. Sites with open water and no emergent vegetation, sites with measurements only outside the growing season, and sites with manipulations of environmental variables (water table, nutrients, soil temperature etc.) were not included. Studies using eddy covariance techniques

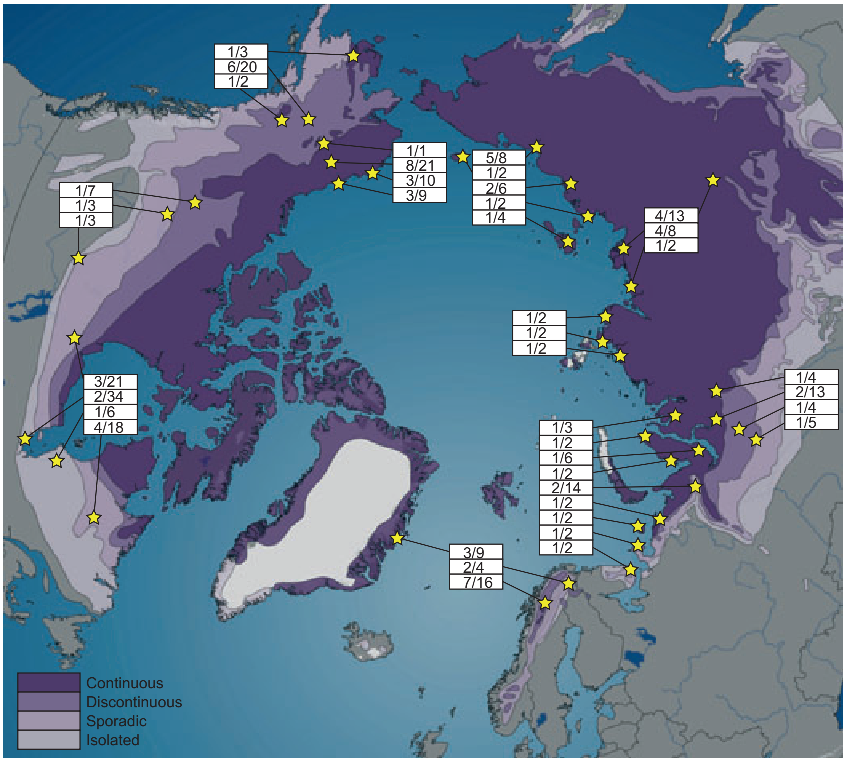

Fig. 1 Map of permafrost zones with study locations indicated by diamonds. First number in boxes indicates how many studies from each location are included in our database, and the second number indicates how many sites these studies contributed. Shadings indicate permafrost zones, using delineations from Brown *et al.* (1998).

were also not considered as they measure CH_4 fluxes over larger spatial scales than chambers, over which environmental and physical variables typically exhibit large heterogeneity.

A total of 303 sites from 65 studies were included in the database, see Supporting Information. The median number of contributed sites per study was four, but eight studies contributed more than 10 sites each for a combined total of 110 sites. Sites had a median of five static chambers (first and third quartiles = 3 and 8) and 10 flux measurement occasions (first and third quartiles = 2 and 15) of each chamber over the measurement period, yielding a median of 30 flux measurements per site (first and third quartiles = 14 and 70). In total, ~14 000 manual chamber flux measurements and ~5000 automatic chamber measurements provide the basis for the database. Analyses showed that the overall results presented in this study were robust with regard to both the influence of individual studies that contributed a large number of sites as well as the influence of sites that were characterized by a low number of flux measurements, see Supporting Information. Only data collected during the growing season were used in the database, as this period is responsible for a majority of the annual flux and because emissions outside the growing season may have other controls than during the growing season. Most studies had measurement periods that included July and August, although data from June and September were also included as long as this did not include a spring or autumn period with substantially lower (higher) CH_4 fluxes (>±50%) than emissions observed during the remainder of the growing season.

Site averaged daily growing season CH_4 flux (F_{CH4}) was estimated from the average CH_4 flux among chambers included in the site over the considered measurement period. Multiyear measurements of individual sites were treated as a single measurement period and are represented by a single F_{CH4} estimate. Several other continuous variables were estimated in a way analogous to F_{CH4}, including average position of the water table (Z_{WT}), average soil temperature measured between 5 and 25 cm below the surface (T_S), average ecosystem respiration (i.e. dark chamber CO_2 fluxes, ER), and average gross primary production (i.e. modelled daily gross primary production based on dark and transparent CO_2 chamber measurements, GPP). Data were also collected on the active layer depth (i.e. the end of season thaw depth, Z_{AL}), the depth of the organic soil layer (Z_{ORG}), soil water pH, and the year of the study (as a proxy for atmospheric CO_2 concentration). Long-term mean annual temperatures and mean summer temperatures for all study locations were obtained from a database compiled by Hijmans *et al.* (2005).

Categorical variables in the database include site location within a permafrost zone (continuous, discontinuous, and sporadic/isolated) (Brown *et al.*, 1998) and surface permafrost conditions (present or absent in the upper 2 m). Our classification of permafrost conditions allowed for a few sites located in the continuous permafrost zone to be classified as being permafrost-free since they were located adjacent to lakes with talik formations. Vegetation composition was assessed by categorizing plant functional types (sedges, trees, woody shrubs, and *Sphagnum* mosses) as dominant, present, or absent within the sites. The sedge category was defined to include species in the *Cyperaceae* family, primarily represented by the genera *Carex* and *Eriophorum*. In the assessment of whether a plant functional type is present or dominant in a site it was impossible to implement a strict objective criterion since studies varied greatly in the level of detail provided on vegetation composition. Dominance was assumed if a species from a plant functional type was mentioned to be the only or one of up to three species present in the site (often the case for tall sedge species such as *Eriophorum aquatilis*, *E. angustifolium*, *E. scheuchzeri*, and *Carex rostrata*), or if vegetation composition found species of a plant functional type to comprise more than 50% of the biomass or have more than 50% areal coverage. Trees were assigned as present if the canopy cover was described as open and dominant if closed. Furthermore, we used Z_{WT} and T_S to split sites into three wetness and temperature categories each (Dry/Wet/Saturated categories with separations at Z_{WT} −15 and −2.5 cm and Cold/Intermediate/Warm categories with separations at T_S 5 and 10 °C), which were further used in combination yielding nine wetness/temperature categories.

Sites were also classified by ecosystem type – including upland forest, dry tundra, palsa, bog, fen, wet tundra, permafrost fen, and littoral ecosystems. Ecosystem classification is based on the general site description in the primary article along with site data on vegetation composition, permafrost conditions, and Z_{ORG}. Permafrost is present in dry tundra, palsa, wet tundra, and permafrost fen, absent in bog and fen and variable in upland forest and littoral ecosystems. Bog, fen, palsa, and permafrost fen are peatland ecosystems, where Z_{ORG} >40 cm. Peatland nutrient status is often qualitatively described in the primary articles, with bog and palsa being nutrient poor ecosystems that are primarily ombrotrophic while fens and permafrost fens are minerotrophic with greatly varying nutrient status. The palsa ecosystem includes sites described both as palsa and peat plateau, which differ in size (peat plateaus > palsas) and vegetation [palsas are treeless while peat plateaus are often treed (Beilman *et al.*, 2001)], but both are nutrient poor, permafrost peatland ecosystems. There is no strict definition of what separates dry and wet tundra, although better drainage of dry tundra causes it to be characterized by dominance of woody shrubs and the presence of *E. vaginatum* whereas wet tundra is commonly dominated by *Sphagnum* spp and tall sedge species. Upland forest includes treed sites with both open and closed canopies and Z_{ORG} < 40 cm. Sites were classified as littoral when described to be located along the edge of lakes or streams. Twelve sites were not classified into any ecosystem, including sites with descriptions such as burned forest, clear felled forest, coastal marsh, taiga swamp, alpine fen, alas grassland, and pingo. In addition, we separated out 24 sites (11 bog, 10 fen, and two littoral sites along with one unclassified site) that were described to have recently (within the last ~100 years) undergone complete near-surface permafrost thaw.

Almost no studies provide information on all variables included in the database. Of the 303 sites, 290 have data on permafrost conditions, 283 on sedge cover, 274 on *Sphagnum* moss, and tree cover, 262 on woody shrub cover, 256 on Z_{WT}, 182 on T_S, 159 on Z_{ORG}, 105 on Z_{AL}, 96 on ER, 82 on pH, and

27 on GPP. Due to the sparse and uneven data matrix, any combination of variables for the purpose of analysis led to further reduced datasets, for example 155 sites have data on Z_{WT}, T_S, permafrost conditions, and sedge cover.

Database analysis

All statistical analyses were carried out in MatLab R2009b. We used Kruskal-Wallis (K-W) analysis to test for differences in median F_{CH4} among categories; a nonparametric analysis was appropriate because F_{CH4} was skewed toward low fluxes. In regression analyses, F_{CH4} was transformed by first adding a constant of 5 mg CH_4 m^{-2} d^{-1} (to enable us to include sites with CH_4 uptake and near zero emissions in our analyses) before log-transforming the data [$\log(F_{CH4+5})$]. Log-transformation was necessary for the dataset to approximate a normal distribution that is an assumption of several statistical analyses. We used analysis of covariance (ANCOVA) to test for differences in the slopes of the relationships between $\log(F_{CH4+5})$ and T_S or Z_{WT} for different categorical variables. Post hoc comparisons of median F_{CH4} (K-W) and slopes (ANCOVA) were performed using Tukey HSD test. We further used regression analysis (stepwise regression, including all permutations of variables) to build empirical models with $\log(F_{CH4+5})$ as the dependent variable. Model selection was performed using the Akaike information criteria with a bias adjustment for small sample sizes (AIC_c) to rank models.

The best model from the regression analysis was used to assess sensitivities of CH_4 fluxes at the ecosystem level to variability in T_S and Z_{WT}, assuming constant vegetation composition and permafrost conditions in the analysis. Ecosystem CH_4 flux was modeled by calculating three fluxes under each set of environmental conditions; one each for the sedge cover categories (using the median Z_{WT} and T_S of sites in each sedge cover categories within each ecosystem type), followed by a weighting of these three fluxes in accordance with the proportion of sites within each sedge cover category within each ecosystem. A bootstrap technique (3000 iterations) based on the 95% confidence intervals of each constant in the empirical model was used to yield uncertainties of ecosystem fluxes.

Results

Of the continuous variables, only Z_{WT}, GPP, and T_S were significantly related to $\log(F_{CH4+5})$ (Z_{WT}: $P < 0.0001$, $r^2 = 0.42$; GPP: $P = 0.001$, $r^2 = 0.37$ and T_S: $P = 0.001$, $r^2 = 0.05$; Fig. 2). Because of the low number of sites that reported comparable GPP estimates, we did not include GPP in any further analyses. In general,

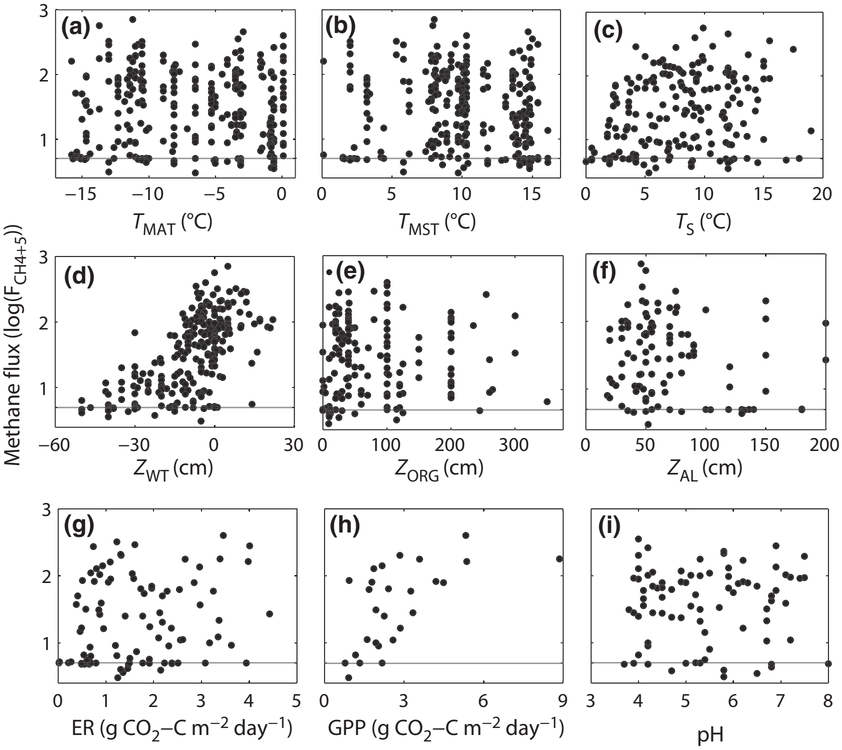

Fig. 2 Relationships between site average growing season CH_4 flux (expressed as $\log(F_{CH4+5})$, where F_{CH4} is in mg CH_4 m^{-2} d^{-1}), environmental variables and CO_2 fluxes; long-term mean annual air temperature (T_{MAT}), long-term mean summer temperature (T_{MST}), mean soil temperature measured between 5 and 25 cm below the surface (T_S), mean water table position (Z_{WT}), depth of the organic soil layer (Z_{ORG}), depth of the active layer (Z_{AL}), mean ecosystem respiration (ER), mean gross primary production (GPP), and soil water pH (pH). The gray line separates sites with net CH_4 uptake and release.

GPP was higher in sites with a dominant sedge cover than sites where sedges were absent (K-W: $P < 0.05$).

There were no differences in median F_{CH4} among permafrost zones or permafrost conditions, but there were significant differences among categories based on wetness and soil temperature and also among vegetation composition categories (Fig. 3). Sites that were wet and saturated had higher median F_{CH4} than dry sites and there were consistent trends of increasing F_{CH4} in warmer temperature categories. Increased sedge cover was related to higher median F_{CH4} (i.e. sedges absent < present < dominant), while the opposite pattern was found for woody shrubs and trees, and no influence was found for *Sphagnum* moss coverage (data not shown).

There were also significant differences in median F_{CH4} among ecosystem types. The highest fluxes were found from littoral, permafrost fen, wet tundra, and fen ecosystems, which were significantly higher than those from upland forest, palsa, and dry tundra ecosystems (Fig. 3 and Table 1). Upland forest was the only ecosystem that had a negative median F_{CH4}, that is net CH_4 uptake. Both median Z_{WT} and the proportion of sites dominated by sedges within an ecosystem increased with ecosystem median F_{CH4} (Table 1 and Fig. 4). Dry ecosystems, for example upland forest and dry tundra, had lower data coverage for Z_{WT} than other ecosystems, possibly due to difficulties in locating the water table – which could mean that median Z_{WT} for these ecosystems are overestimates of representative conditions.

Site CH_4 flux expressed as a percentage of site ER (mg CH_4-C m^{-2} d^{-1} mg^{-1} CO_2-C m^{-2} d^{-1} × 100) was related to site wetness and sedge cover, with highest medians at 4–5% for wet and saturated sites with a dominant sedge cover (Fig. 5). Median percentages also increased among ecosystems with increasing median ecosystem Z_{WT}, excluding the bog and fen ecosystems

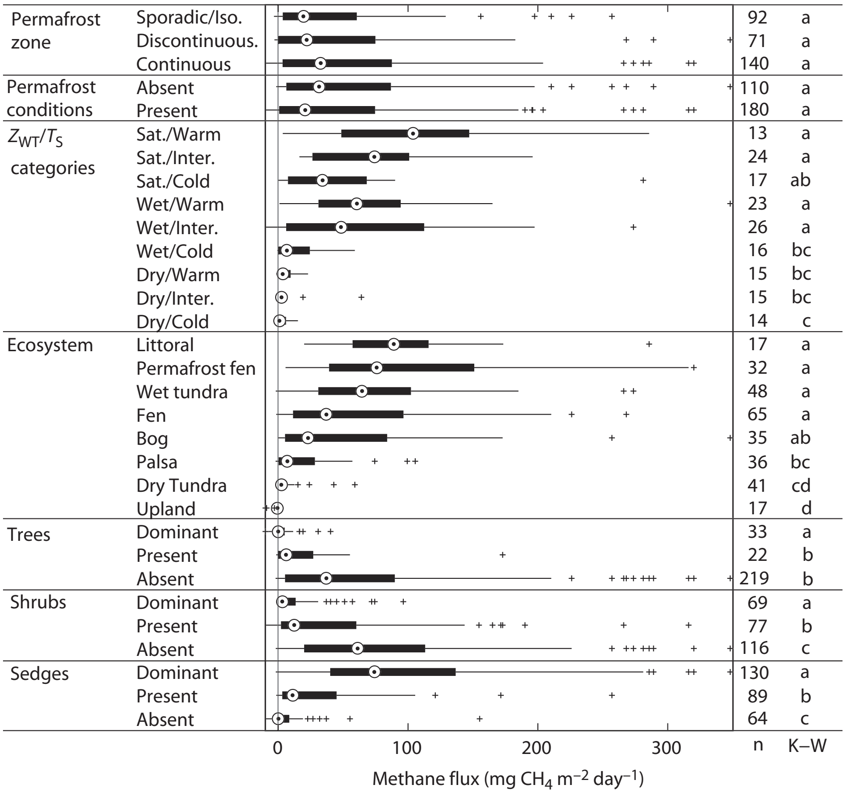

Fig. 3 Site CH_4 fluxes classified by several categorical variables. Circles indicate median flux, boxes show the range between the 25th and 75th percentiles and plus signs represent outliers. Five sites with fluxes >350 mg CH_4 m^{-2} d^{-1} are not shown. The number of sites within each category is indicated on the right (n), and differences among categories within each variable are denoted on the far right (Kruskal-Wallis, K-W, test followed by Tukey HSD, $P < 0.05$). Three permafrost zones are included, continuous, discontinuous, and a combined sporadic/isolated zone. Permafrost conditions refer to the presence or absence of permafrost in the upper 2 m of soils. Classification of water table/soil temperature (Z_{WT}/T_S) categories is based on separations for Z_{WT} at −15 and −2.5 cm (yielding Dry, Wet, and Saturated categories) and for T_S at 5 and 10 °C (yielding Cold, Intermediate, and Warm categories). See text for definitions used to classify ecosystem types and vegetation composition.

Table 1 Characteristics of sites based on ecosystem categorization. Information includes the number of sites for each ecosystem type and the number of contributing studies. Shown are also median (Md.) site average CH_4 flux (F_{CH4}), average water table position (Z_{WT}), long term mean annual temperature (T_{MAT}), long term mean summer temperature (T_{MST}), average soil temperature as measured between 5 and 25 cm below the surface (T_S), depth of the organic layer (Z_{ORG}), soil pH, ecosystem respiration (ER) and CH_4 flux expressed as a per-cent of ER ($F_{CH4\%}$). Characterization of vegetation composition in each ecosystem is represented by tree cover (percent of sites within each ecosystem where trees are absent) and sedge cover (percent of sites classified with a dominant, present or absent sedge cover)

		Upland forest	Dry tundra	Palsa	Bog	Fen	Wet tundra	Permafrost fen	Littoral	*Thawed**
Sites		17	41	36	35	65	48	32	17	24
Studies		12	18	16	11	21	20	14	13	13
F_{CH4}	Md.	−0.7	2.4	7.0	23.0	37.1	64.5	75.8	89.0	56.9
(mg CH_4 m^{-2} d^{-1})	25th	−1.1	0.0	0.4	5.6	11.5	31.9	41.7	58.3	21.5
	75th	−0.4	6.0	27.3	83.0	95.0	100.6	147.3	112.4	99.8
Z_{WT} (cm)	Md.	−25.8	−15	−20	−13	−6	0	0	2.5	−5.5
	Data†	35%	80%	92%	86%	89%	100%	97%	76%	71%
T_{MAT} (°C)	Md.	−6	−11.4	−3.8	−0.8	−3.5	−11.4	−8.5	−8.1	−3.3
T_{MST} (°C)	Md.	14.4	8.1	10.2	14.5	13.6	7.7	9.3	10.2	13.9
T_S (°C)	Md.	8.8	3.9	6.1	12.5	11.8	3.7	6.8	8.8	11.7
	Data†	59%	73%	72%	63%	68%	52%	59%	65%	54%
Z_{ORG} (cm)	Md.	12	18	100	200	100	20	41	40	100
	Data†	59%	37%	44%	69%	57%	52%	56%	29%	38%
Sedges	Dom.	7%	13%	25%	31%	65%	69%	66%	71%	65%
	Pres.	0%	46%	47%	50%	27%	21%	24%	29%	26%
	Abs.	93%	41%	28%	19%	8%	10%	10%	0%	9%
	Data†	83%	95%	100%	91%	92%	100%	91%	100%	96%
Trees	Abs.	0%	100%	74%	72%	74%	100%	89%	100%	92%
	Data†	100%	93%	97%	94%	83%	90%	84%	94%	100%
pH	Md.	5.4	5.4	4.1	4.2	5.8	6.2	5.3	5.7	4.3
	Data†	24%	10%	28%	37%	32%	27%	28%	24%	42%
ER (g C m^{-2} d^{-1})	Md.	3.11	1.70	1.37	0.90	1.99	1.42	1.98	1.91	1.3
$F_{CH4\%}$ (%)	Md.	−0.1%	0.1%	1.6%	1.8%	8.7%	2.7%	6.3%	5.1%	4.9%
	Data†	41%	49%	61%	9%	12%	31%	34%	41%	29%

*The *Thawed* category is not an exclusive group, but contains sites from the other ecosystem types that are described to have recently (within the last 100 years) undergone permafrost thaw (i.e. sites located in thermokarst landforms).

†Data coverage of presented variables is indicated as a percent of reporting sites within each ecosystem. Data coverage for F_{CH4}, T_{MAT} and T_{MST} is 100%.

for which data coverage was low (<12% of sites; Table 1).

Analysis of covariance showed that relationships between log(F_{CH4+5}) and T_S varied with site wetness (Fig. 6a) and sedge cover (Fig. 6c), but were unaffected by permafrost conditions (Fig 6e). Interestingly, sites with a dominant sedge cover were found to have high emissions even at low T_S, yielding a weaker temperature dependency of log(F_{CH4+5}) for sites dominated by sedges than for sites where sedges were merely present. Sedge cover was also found to affect the relationship between log(F_{CH4+5}) and Z_{WT} (Fig. 6d), showing that high CH_4 emissions from sites dominated by sedges were not only due to an association with high water table position but that they also had higher emissions than other sites at comparable water table positions. Emissions were also higher at comparable water table positions from sites with permafrost than from sites where permafrost was absent (Fig. 6f) and higher from sites with warm and intermediate soil temperature categories than from cold sites (Fig. 6b), although the slopes of these relationships remained similar.

In our multivariate regression analysis, we included only sites with complete data sets on Z_{WT}, T_S, sedge cover and permafrost conditions – 155 sites collected from 31 studies. In the analysis we also included the variables Z_{WT}^2, Z_{WT}^3 and interaction variables between Z_{WT} and T_S and between sedge cover and T_S. All possible models were explored and ranked based on AIC_c (Table 2). Dominant sedge cover and Z_{WT} were the two variables with the highest explanatory power in single variable models and, when combined in a two variable model, their explanatory power increased significantly (adj. r^2 = 0.47). Permafrost conditions and T_S could not

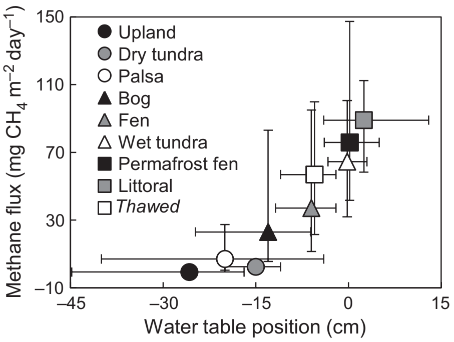

Fig. 4 Relationship between median CH_4 flux and median water table position for sites within each ecosystem. Whiskers represent 25th and 75th percentiles for both methane fluxes and water table position. The *Thawed* category does not represent a unique set of sites, but contains sites from the other ecosystem types that were described as thermokarst landforms that recently experienced complete near-surface permafrost thaw.

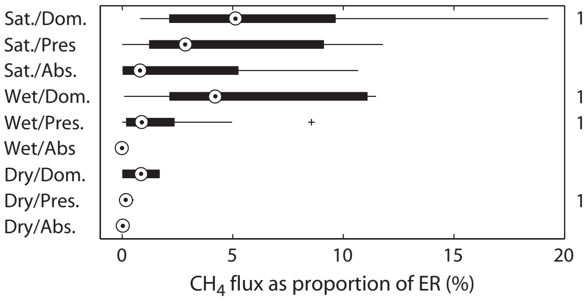

Fig. 5 Site CH_4 flux as a percent of ecosystem respiration (ER) (mg CH_4-C m^{-2} d^{-1}/mg CO_2-C ×100, %) classified by site wetness and sedge cover categories. Category separations were at mean water table positions of −15 and −2.5 cm (yielding Dry, Wet, and Saturated categories), while site sedge cover was classified as either Dominant, Present, or Absent. Circles indicate median proportion, boxes show the range between the 25th and 75th percentiles and plus signs represent outliers. One site with a value of 25% is not shown in the figure, belonging to the Wet/Dom. category. The number of sites within each category is indicated on the right.

both be included in any model that had lower AIC_c than when they were included individually, suggesting that the presence or absence of permafrost is only an indicator of soil temperature and does not in itself influence CH_4 emissions. The results from the model analysis also indicated that the relationship between Z_{WT} and $\log(F_{CH4+5})$ was not properly described by a linear relationship. Including Z_{WT}^2 and Z_{WT}^3 improved the models and caused modeled $\log(F_{CH4+5})$ to increase more rapidly between Z_{WT} of −15 and +5 cm than either above or below this range in several models – indicating that CH_4 emissions peak when the water table is near the soil surface. The best model (adj. $r^2 = 0.59$) included the variables Z_{WT}^2, Z_{WT}^3, T_S, sedges present, sedges dominant, and interaction variables between Z_{WT} and T_S and between sedges dominant and T_S (Fig. 7).

No improvement of the best model was found by further adding year-of-study as a variable – that is no direct detectable influence on CH_4 emissions from increased atmospheric CO_2 concentration was found (see Supporting Information for expanded discussion). Regression analysis was also not able to detect any significant influence from Z_{ORG} on $\log(F_{CH4+5})$, which was tested by adding combinations of Z_{ORG}, $\log(Z_{ORG})$ and interaction variables between $Z_{ORG}/\log(Z_{ORG})$ and Z_{WT} to the best model ($n = 83$) and by building a new model which only included variables based on Z_{WT} and Z_{ORG} ($n = 138$).

The best empirical model was used to assess ecosystem F_{CH4} sensitivities to variable water table levels and soil temperatures. Using measured median water table levels, soil temperatures, and vegetation composition, the model yielded estimated ecosystem F_{CH4} values that were comparable to the median measured ecosystem F_{CH4} ($R^2 = 0.86$, $n = 8$, $P < 0.01$, and the first and third quartile estimates from the boot strap analysis included the median measured F_{CH4}). Sensitivities of ecosystem F_{CH4} were assessed by varying median T_S and/or Z_{WT} in the model. In general, it was found that ecosystems where the median water table was at or above the soil surface, for example littoral and permafrost fen, were more sensitive to changes in T_S while ecosystems with a median water table below the soil surface, for example bog and fen, were more sensitive to changes in Z_{WT} (Fig. 8). A combination of increased T_S and Z_{WT} led to ecosystem F_{CH4} that was enhanced by between 60% and 120%, which is an increase that was greater for all ecosystems than the combined individual effects of raised T_S and Z_{WT}. A combination of drier and warmer conditions yielded both decreased (palsa, bog and fen) and increased (wet tundra, permafrost fen, and littoral) central estimates of ecosystem F_{CH4}.

Of particular interest are the 24 sites that were described as having undergone permafrost thaw during the last ~100 years (see Table 1). This grouping shows that most research in thermokarst landforms has been made in wet sites with moderate to high F_{CH4} (Fig. 4). Any potential effect on site F_{CH4} from microbial access to previously frozen organic matter was smaller than could be detected in our analysis. For example, dominant sedge cover and Z_{WT} between −11 and 0 cm characterized 10 of the 24 thawed sites. This group had an average F_{CH4} of 136.4 ± 22.6 (*SE*) mg CH_4 m^{-2} d^{-1} that was not significantly higher (two tailed *t*-test, $P = 0.23$) than that of a group of sites with similar sedge and Z_{WT} conditions, but one that had not

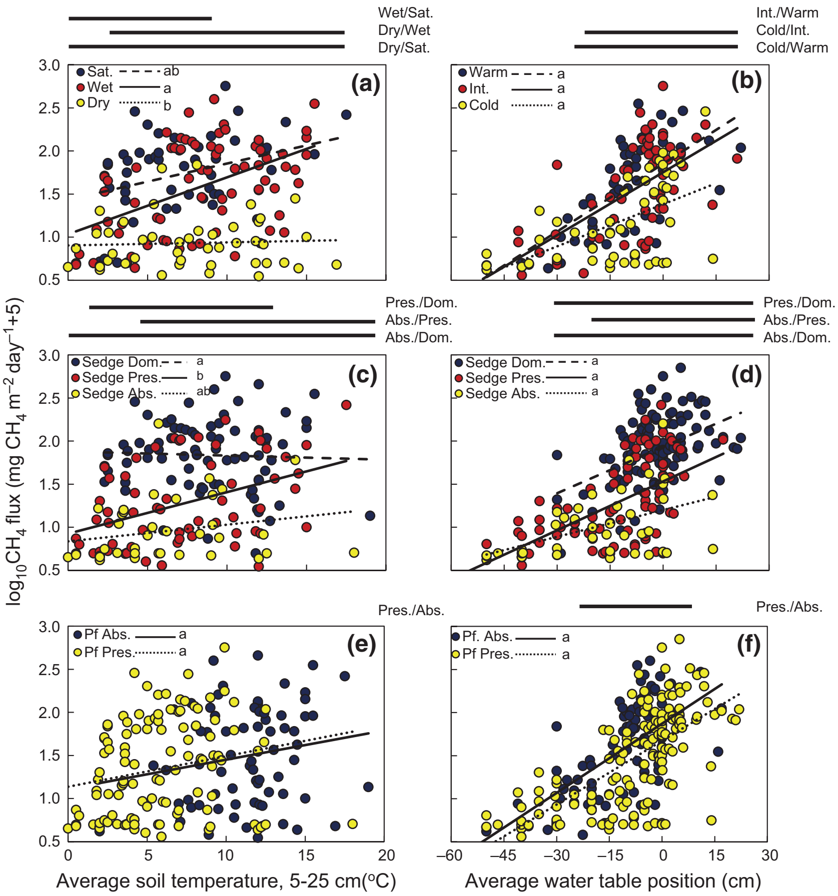

Fig. 6 Visualization of covariance analyses (ANCOVA). Analyses were based on site CH_4 flux being the response variable (represented by $\log(F_{CH4+5})$, where F_{CH4} is in mg CH_4 m^{-2} d^{-1}), while average water table positions or soil temperatures measured between 5 and 25 cm below the surface were covariates (shown on *x*-axes). Factors were either soil temperature categories (Cold, Intermediate, or Warm sites, with category separations at 5 and 10 °C), water table categories (Dry, Wet, or Saturated sites with category separations at −15 and −2.5 cm), sedge cover (Dominant, Present or Absent) or permafrost conditions in the upper 2 m (Present or Absent). Bars above each graph indicate the range over which pairs of factors are significantly different, based on 95% confidence intervals of fits. Lower case letters following the legend indicate differences ($P < 0.05$) for the slopes of the fits, based on Tukey HSD test. See Supplemental information for detailed ANCOVA statistics.

been recently thawed (99.2 ± 21.3 (*SE*) mg CH_4 m^{-2} d^{-1}, $n = 23$). Given the small sample size and large variance in this test, the smallest detectable difference (i.e. $P < 0.05$) would have required the thawed group to have emissions that on average were >65% greater than the non-permafrost group, assuming that the variance among sites remained constant.

Discussion

Controls on site CH_4 emissions

In this study, we evaluated patterns of terrestrial average growing-season CH_4 fluxes across permafrost zones using results from 65 chamber-based studies conducted over the last three decades. We focused on average growing-season fluxes at the site level paired with information on site physical and environmental variables. Although it has long been known that water table, soil temperature, plant productivity, and the presence of sedges influence CH_4 fluxes in high-latitude ecosystems (Svensson, 1980; Sebacher *et al.*, 1986; Moore & Knowles, 1987; Whalen & Reeburgh, 1988; Whiting & Chanton, 1993), our approach corroborates that these variables are the main controls of CH_4 fluxes among sites within the permafrost zones and that their effects are interactive. Our best empirical model, using data on sedge cover along with average water table position and soil temperature, accounted for ~60% of the variation in log-transformed CH_4 fluxes. Remaining variation is likely due to a combination of methodological and functional factors. For example, methodological differences

Table 2 Model selection and results from regression analysis. 155 sites with data on CH_4 flux (F_{CH4}), water table position (Z_{WT}), soil temperature (T_S) and binary (1/0) data for classification of sedge cover (Dominant/Present/Absent – $S_{Dom/Pres/Abs}$) and permafrost conditions (Present/Absent – $P_{Pres/Abs}$). The first four equations had the lowest AIC_c values of all combinations, and the following groups of three or four equations were the equations with the lowest AIC_c for one, two and three variables respectively. The last two equations were the best equations that only used Z_{WT} and T_S

Equation: $\log(F_{CH4+5})$ =	adj. r^2	AIC_c	Δ_i[†]	w_i[‡]
$a+b*Z_{WT}^2+c*Z_{WT}^3+d*T_S+e*Z_{WT}*T_S+f*S_{Dom}+g*S_{Pres}+h*S_{Dom}*T_S$*	0.59	−305.3	0.0	0.66
$a+b*Z_{WT}^2+c*Z_{WT}^3+d*T_S+e*Z_{WT}*T_S+f*S_{Dom}+g*S_{Dom}*T_S$	0.58	−303.7	1.64	0.29
$a+b*Z_{WT}+c*T_S+d*S_{Dom}+e*S_{Pres}*T_S$	0.55	−298.1	7.21	0.02
$a+b*Z_{WT}+c*S_{Dom}+d*S_{Pres}*T_S$	0.54	−296.7	8.59	0.01
$a+b*S_{Dom}$	0.33	−242.3	63.1	0.00
$a+b*Z_{WT}$	0.33	−242.0	63.3	0.00
$a+b*T_S$	0.12	−200.3	105.0	0.00
$a+b*Z_{WT}+c*S_{Dom}$	0.47	−277.6	27.8	0.00
$a+b*Z_{WT}+c*T_s$	0.42	−264.2	41.1	0.00
$a+b*S_{Dom}+c*S_{Pres}$	0.37	−250.1	59.8	0.00
$a+b*Z_{WT}+c*P_{Abs}$	0.36	−248.7	56.6	0.00
$a+b*Z_{WT}+c*T_S+d*S_{Dom}$	0.53	−293.6	11.7	0.00
$a+b*Z_{WT}+c*S_{Dom}+d*P_{Abs}$	0.50	−285.3	20.0	0.00
$a+b*Z_{WT}+c*S_{Dom}+d*S_{Pres}$	0.49	−283.7	21.7	0.00
$a+b*Z_{WT}^2+c*Z_{WT}^3+d*T+e*Z_{WT}*T_S$	0.46	−266.0	39.3	0.00
$a+b*Z_{WT}+c*Z_{WT}^2+d*Z_{WT}^3+e*T_S$	0.43	−264.2	41.1	0.00

*Constants for the best model are: a: 0.859, b: -4.94×10^{-4}, c: -8.96×10^{-6}, d: 7.04×10^{-2}, e: 1.77×10^{-3}, f: 0.926, g: 0.164, h: -5.17×10^{-2}.

[†] Difference in AIC_c between the model and the best model.

[‡] Akaike weights, indicating probability for model to be the best model.

among studies include how vegetation composition is reported, how ebullition events were handled, whether boardwalks were used near the chambers, at what depth soil temperature were measured, as well as variable chamber sizes, closure times, study periods, and sampling frequencies. Furthermore, our model did not include GPP or variables related to atmospheric conditions, which are known to affect CH_4 emissions in the permafrost region. Although GPP had a strong relationship with CH_4 fluxes in our database, too few studies reported comparable estimates for inclusion in the model. Atmospheric stability and turbulence is rarely taken into account in chamber studies, but strongly influence CH_4 fluxes at daily time-scales in eddy-covariance studies (Wille *et al.*, 2008; Parmentier *et al.*, 2011), which is an issue that could affect the quality of CH_4 flux estimates in our database for sites where only few flux measurements were made. In addition, although the relationships between CH_4 fluxes and environmental variables have been shown to strengthen when using seasonal arithmetic averages rather than raw data (Levy *et al.*, 2012), the use of averages is problematic as the functional relationships between CH_4 flux and environmental variables such as water table position and soil temperature are known to be intrinsically nonlinear.

Our analysis stresses dominant sedge cover (in nearly all sites represented by tall sedge species such as *E. aquatilis*, *E. angustifolium*, *E. scheuchzeri*, and *C. rostrata*) as a primary control of site CH_4 fluxes in the permafrost region. At comparable water table positions, sites dominated by sedges had significantly higher CH_4 emissions than those measured at other sites. High CH_4 emissions from sedge dominated areas is attributed to both reduced CH_4 oxidation associated with the presence of aerenchymatous roots and stems (Schimel, 1995; King *et al.*, 1998; von Fischer *et al.*, 2010) and to increased CH_4 production linked to high plant productivity and increased availability of organic acids because of root exudation (Bellisario *et al.*, 1999; Ström *et al.*, 2012). Something that individual studies have been unable to show is that the difference between CH_4 emissions from sedge dominated sites and other sites is more pronounced in colder soils. It is thus possible to encounter high CH_4 emissions even in very cold regions as long as sedges dominate the vegetation, and 9 of the 15 sites in our database with CH_4 emissions >225 mg CH_4 m^{-2} d^{-1}

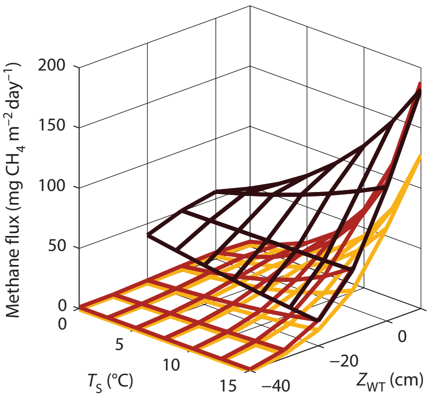

Fig. 7 Visualization of the best model from the regression analysis, after re-transforming to CH_4 flux (mg CH_4 m^{-2} d^{-1}) from log(F_{CH4+5}). Upper dark red grid represents the model when applied to sites with a dominant sedge cover; middle bright red grid represents sites where sedges are present and lower yellow grid represents sites where sedges are absent. The visualization is truncated for $Z_{WT} < -20$ cm for sites with a dominant sedge cover due to few representative sites.

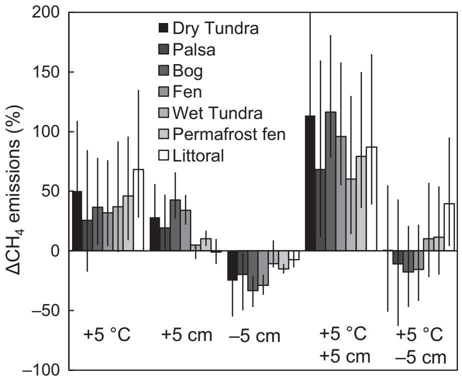

Fig. 8 Sensitivities of ecosystem level CH_4 fluxes to altered water table position and soil temperature – based on implementation of the best model from the regression analysis. See text for how ecosystem level CH_4 fluxes were estimated. Bars represent the difference (%) between estimated CH_4 flux when using median observed and altered water table and soil temperature conditions. Five combinations of water table and soil temperature changes are indicated below the bars. Error bars represent 95% confidence interval of the change based on a bootstrap analysis.

were located in the continuous permafrost zone. Speculation about the cause of this pattern includes geographical distributions of sedges with species-specific patterns of root exudation (Ström *et al.*, 2005, 2012) and interactions between the oxidation potential provided by aerenchymatous roots and mis-matches of temperature sensitivities for CH_4 production and oxidation (Wagner *et al.*, 2003).

Using ecosystem CH_4 emissions to scale emissions and assess sensitivity

At the ecosystem level, median CH_4 fluxes were strongly related to both median water table position and the proportion of sites within each ecosystem type that was dominated by sedges. However, both physical characteristics and CH_4 fluxes varied greatly among sites within each ecosystem. For many wetland ecosystems, this variation can be linked to hummock and hollow patterning. Thus comparisons of median CH_4 fluxes among ecosystems hinge on the assumption that each ecosystem is represented without significant biases related to site selection. We assume robustness of our ecosystem characterization since at least 11 studies contributed sites to each ecosystem type, and each ecosystem was represented by >17 sites and >110 individual chambers.

Characteristic ecosystem CH_4 emissions in combination with databases of wetland distributions have been used to scale to regional or circumpolar emission estimates (e.g. Matthews & Fung, 1987). Scaling emissions is likely to be more sensitive to issues of accurately accounting for the spatial extent of different wetland types rather than to uncertainties of characteristic ecosystem CH_4 emissions (Frey & Smith, 2007; Krankina *et al.*, 2008). For example, littoral sites with the highest median CH_4 emissions in our database will strongly influence landscape level estimates of CH_4 emissions but, at the same time, they are often represented by narrow and elongated landscape features that have spatial extents that are difficult to assess over large geographical regions.

The implementation of the best empirical model at the ecosystem level represents an assessment of CH_4 emission sensitivity to variation in water table position and soil temperature under constant physical conditions, for example unaltered permafrost conditions and vegetation composition. This analysis indicated that wetter ecosystems are relatively more sensitive to soil temperature shifts than drier ecosystems (a 5 °C increase caused estimated ecosystem CH_4 emissions to increase by between 25% and 70%), while drier ecosystems conversely are more sensitive to water table fluctuations (a 5-cm rise was associated with a 0–45% increase in ecosystem CH_4 emissions). The analysis further showed that water table and soil temperature variations had synergistic effects. Although these sensitivities are based on spatial patterns of the relationship between CH_4 emissions and environmental variables, they are of similar magnitude to observed inter-annual variability of seasonal CH_4 emissions at individual sites in response to variation in water table position and temperature (Whalen & Reeburgh, 1992; Moosavi *et al.*, 1996; Bubier *et al.*, 2005; Turetsky *et al.*,

2008) and to the sensitivities observed in studies where environmental variables are manipulated (Turetsky *et al.*, 2008; Merbold *et al.*, 2009). A strong sensitivity of northern high-latitude CH_4 emissions is consistent with inverse modeling studies of inter-annual variability in atmospheric CH_4 concentrations and its relationship with large scale climate patterns (Mikaloff-Fletcher *et al.*, 2004; Dlugokencky *et al.*, 2009; Bloom *et al.*, 2010). Models generally predict a climate with both higher temperatures and increased precipitation at northern high latitudes during this century (Christensen *et al.*, 2007). However, depending on the balance between greater rates of evapotranspiration and precipitation, this could potentially lead to reduced inundated wetland area (Avis *et al.*, 2011), which makes projections of future northern wetland CH_4 emissions uncertain (Bohn *et al.*, 2007; Koven *et al.*, 2011).

Influence of permafrost conditions and permafrost thaw on site CH_4 emissions

Sites underlain by permafrost had lower CH_4 emissions than sites where surface permafrost was absent at comparable water table positions, a difference that was accounted for by the variation among sites in soil temperature. Recently thawed sites did not have higher emissions than comparable sites that had not undergone recent thaw, although it is possible that the low number of recently thawed sites along with the large variation in emissions from these sites could have allowed even a substantial effect (up to +65%) on CH_4 emissions from increased degradation of recently thawed organic matter to remain unnoticed (Wagner *et al.*, 2003; Mackelprang *et al.*, 2011). However, considering that neither depth of the organic layer nor depth of the active layer was found to be related to site CH_4 emissions, our analysis suggests that terrestrial CH_4 emissions are unlikely to be primarily limited by the availability of organic substrate (c.f. Prater *et al.*, 2007).

Thermokarst dynamics are associated with local changes to hydrological setting, thermal regime, and vegetation composition (Hinzman *et al.*, 2005; Jorgenson & Osterkamp, 2005), all of which strongly influenced CH_4 emissions as analysis in this study illustrates. Most research of CH_4 emissions in thermokarst landforms has been undertaken in lowland settings where permafrost often has a substantial ice content, and where thermokarst development leads to subsidence, raised water table and high CH_4 emissions, for example through the conversion of upland or palsa sites into bog or fen sites (Bubier *et al.*, 1995; Liblik *et al.*, 1997; Svensson *et al.*, 1999; Wickland *et al.*, 2006; Myers-Smith *et al.*, 2007; Prater *et al.*, 2007; Bäckstrand *et al.*, 2008). Although not all lowland thermokarst development leads to wet conditions and high CH_4 fluxes (Turetsky *et al.*, 2002; Desyatkin *et al.*, 2009), their development still represents very large relative increases in CH_4 emissions in comparison to pre-thaw conditions. Although lakes were not included in this study, lowland thermokarst development is also responsible for the dynamics between thermokarst lake formation and drainage, both of which can have substantial influences on landscape CH_4 emissions (Walter *et al.*, 2006; Zona *et al.*, 2009). The potential for increased CH_4 emissions through lowland thermokarst development is great, but will be determined by the spatial extents of future thermokarst development, about which current knowledge is relatively low (Humlum & Christiansen, 2008; Grosse *et al.*, 2011; Sannel & Kuhry, 2011).

In contrast to thermokarst dynamics, few studies have documented the influence on CH_4 fluxes due to predicted widespread deepening of the active layer and loss of near surface permafrost without associated subsidence (Hugelius *et al.*, 2011; Lawrence *et al.*, 2012). Absence of permafrost in upland forests has been associated with higher CH_4 uptake than comparable sites with permafrost (Flessa *et al.*, 2008) but this pattern was not confirmed in our analysis. For fen sites, however, we found that permafrost presence was associated with wetter conditions and higher median CH_4 fluxes, suggesting that permafrost loss and improved drainage in some wetland ecosystem types can lead to lower CH_4 emissions. Hence, the effects of permafrost thaw on landscape surface moisture conditions need to be better understood when assessing future CH_4 emissions, particularly as it is likely that CH_4 research in areas of permafrost degradation has been biased toward locations that have become drastically wetter rather than where gradual drainage has occurred.

Model simulations project that permafrost degradation and associated microbial access to thawed organic carbon stores will significantly increase high-latitude CO_2 (Schuur *et al.*, 2009; Schaefer *et al.*, 2011) and CH_4 emissions (Koven *et al.*, 2011; Schneider von Deimling *et al.*, 2012). Between 1% and 4% of mineralized carbon from recently thawed soils is expected to be released as CH_4, which in itself can represent annual CH_4 emissions greater than estimates of total current high-latitude CH_4 emissions (Schuur *et al.*, 2011; Schneider von Deimling *et al.*, 2012). Our study did not characterize lake CH_4 emissions, particularly the potential influence of thermokarst lakes on future CH_4 emissions (Walter *et al.*, 2006), and it did not assess CH_4 emissions from landscape seeps associated with deep CH_4 production (Koven *et al.*, 2011; Walter Anthony *et al.*, 2012). However, our synthesis of terrestrial CH_4 fluxes did not find support for increased CH_4 emissions from areas with greater stores of organic carbon. Furthermore, only wet and saturated sites were found to have CH_4-C emissions that were consistently >1% of ER fluxes. This suggests that CH_4 emissions in terrestrial environments are largely driven by near-surface processes in combination with hydrological conditions. This needs to be taken into account in model simulations to prevent overestimates of future CH_4 emissions. In conclusion, our analysis suggests that future changes in terrestrial CH_4 emissions from the permafrost zones will be more proximately related to changes in soil moisture, thermal conditions, and vegetation shifts than to the direct effects of permafrost thaw on the availability of newly thawed organic matter.

Acknowledgements

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Supporting Information

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

Data S1. The Supporting information includes the database in its entirety along with a full reference list of the studies that contributed sites to the database. The Supplemental information also contains a discussion of the influence of studies that contributed a large number of sites and studies that implemented low frequency sampling regimes on the conclusions in the main manuscript. Detailed statistics on the ANCOVA analysis and an exploration and discussion of the potential influence of increased atmospheric CO_2 concentrations on CH_4 fluxes can also be found.