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Zicheng Yu
Lehigh University

Julie Loisel
Lehigh University

Merritt R. Turetsky
University of Guelph

Shanshan Cai
Lehigh University

Yan Zhao
Chinese Academy of Sciences

See next page for additional authors

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Authors

Zicheng Yu, Julie Loisel, Merritt R. Turetsky, Shanshan Cai, Yan Zhao, Steve Frolking, Glenn M. MacDonald, and Jill L. Bubier

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Evidence for elevated emissions from high-latitude wetlands contributing to high atmospheric CH_4 concentration in the early Holocene

Zicheng Yu,[1] Julie Loisel,[1] Merritt R. Turetsky,[2] Shanshan Cai,[1] Yan Zhao,[3] Steve Frolking,[4] Glen M. MacDonald,[5] and Jill L. Bubier[6]

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[1] The major increase in atmospheric methane (CH_4) concentration during the last glacial-interglacial transition provides a useful example for understanding the interactions and feedbacks among Earth's climate, biosphere carbon cycling, and atmospheric chemistry. However, the causes of CH_4 doubling during the last deglaciation are still uncertain and debated. Although the ice-core data consistently suggest a dominant contribution from northern high-latitude wetlands in the early Holocene, identifying the actual sources from the ground-based data has been elusive. Here we present data syntheses and a case study from Alaska to demonstrate the importance of northern wetlands in contributing to high atmospheric CH_4 concentration in the early Holocene. Our data indicate that new peatland formation as well as peat accumulation in northern high-latitude regions increased more than threefold in the early Holocene in response to climate warming and the availability of new habitat as a result of deglaciation. Furthermore, we show that marshes and wet fens that represent early stages of wetland succession were likely more widespread in the early Holocene. These wetlands are associated with high CH_4 emissions due to high primary productivity and the presence of emergent plant species that facilitate CH_4 transport to the atmosphere. We argue that early wetland succession and rapid peat accumulation and expansion (not simply initiation) contributed to high CH_4 emissions from northern regions, potentially contributing to the sharp rise in atmospheric CH_4 at the onset of the Holocene.

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1. Introduction

[2] Atmospheric methane (CH_4) is a potent greenhouse gas that is linked with climate change and global biogeochemical cycles. Rapid increases in the atmospheric CH_4 during the last glacial termination (18,000 to 9000 yr ago), and especially during the Younger Dryas–Preboreal abrupt climatic transition about 11,600 yr ago, are the most recent examples of global CH_4 cycle–climate change linkage. However, the cause for the deglacial CH_4 rise is still uncertain and debated, despite its importance in understanding the linkage between climate, atmospheric chemistry, and biosphere dynamics. The proposed CH_4 sources during the last termination include permafrost thawing and development of thermokarst lakes [*Walter et al.*, 2007], northern wetlands [*Chappellaz et al.*, 1997; *Brook et al.*, 2000; *Smith et al.*, 2004; *MacDonald et al.*, 2006; *Yu et al.*, 2010], and tropical wetlands [*Chappellaz et al.*, 1997; *Baumgartner et al.*, 2012]. The idea that methane hydrates from continental shelves may have contributed to the deglacial CH_4 rise is inconsistent with isotopic data from ice-core CH_4 that strongly suggests a terrestrial source [*Sowers*, 2006; *Petrenko et al.*, 2009]. Also, model simulations suggest that reduction in CH_4 sinks during the deglacial warming, in particular due to increase in volatile organic compounds that "compete" with CH_4 to react with the hydroxyl radical (OH), may significantly contribute to the deglacial CH_4 increase [*Valdes et al.*, 2005; *Kaplan et al.*, 2006]. However, recent analysis indicates that the effect of volatile organic compounds on CH_4 concentrations is compensated by other factors [*Levine et al.*, 2011].

All supporting information may be found in the online version of this article.

[1]Department of Earth and Environmental Sciences, Lehigh University, Bethlehem, Pennsylvania, USA.
[2]Department of Integrative Biology, University of Guelph, Guelph, Ontario, Canada.
[3]Institute of Geographic Sciences and Natural Resources Research, Chinese Academy of Sciences, Beijing, China.
[4]Institute for the Study of Earth, Oceans, and Space, University of New Hampshire, Durham, New Hampshire, USA.
[5]UCLA Institute of the Environment and Sustainability, Department of Geography and Department of Ecology and Evolutionary Biology, UCLA, Los Angeles, California, USA.
[6]Environmental Studies Department, Mount Holyoke College, South Hadley, Massachusetts, USA.

Corresponding author: Z. Yu, Department of Earth and Environmental Sciences, Lehigh University, 1 West Packer Avenue, Bethlehem, PA 18015-3001, USA. (ziy2@lehigh.edu)

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[3] Some of these proposed ideas on the causes of the deglacial rise in atmospheric CH_4 concentration are based on top-down inferences either from ice-core CH_4 concentration and isotope measurements or from box model calculations [*Chappellaz et al*., 1997; *Dällenbach et al*., 2000; *Brook et al*., 2000; *Fischer et al*., 2008; *Baumgartner et al*., 2012]. For example, the greater north-to-south interpolar gradient in CH_4 concentrations between Greenland and Antarctica during the early Holocene suggests the dominant role of northern wetlands [*Chappellaz et al*., 1997; *Brook et al*., 2000]. Also, decreases in δ`D and $\delta^{13}C$ values of CH_4 from ice cores in the early Holocene suggest increase in northern wetland sources [*Fischer et al*., 2008; *Sowers*, 2010]. A recent high-resolution and high-precision analysis of interpolar differences in atmospheric CH_4 suggests that both boreal and tropical sources increased at about the same rate during the last deglaciation [*Baumgartner et al*., 2012], but this new analysis did not extend much into the Holocene. In contrast, ground-based information from large-scale syntheses of peatlands and thermokarst lakes only cover certain aspects of CH_4 cycle dynamics in terrestrial or aquatic ecosystems [*Smith et al*., 2004; *MacDonald et al*., 2006; *Walter et al*., 2007; *Gorham et al*., 2007; *Korhola et al*., 2010; *Yu et al*., 2009, 2010]. For example, *MacDonald et al*. [2006] presented one of the earliest and most comprehensive datasets of basal peat ages and discussed the dynamics of new peatland formation during the deglacial warming. They concluded that rapid increase in the rate of new peatland formation in the early Holocene likely caused the high atmospheric CH_4 concentration, lending support to previous top-down inferences. Using the same dataset and subtle methodological changes, however, *Reyes and Cooke* [2011] recently challenged these previous findings about northern peatlands' role in CH_4 rise, arguing that peak *peatland* initiation rate lagged the abrupt rise of CH_4 concentration at the onset of the Holocene.

[4] A fundamental shortcoming in the ground-based studies by *MacDonald et al*. [2006], *Jones and Yu* [2010], and *Reyes and Cooke* [2011] is the use of basal peat ages as a proxy for wetland development. Peatlands are the subset of wetlands that have accumulated peat, including ombrotrophic (rain-fed) bogs dominated by *Sphagnum* (peat moss) and minerotrophic fens (groundwater-fed) dominated by sedges and brown mosses. Wetland is a more general term that also includes marshes with little peat accumulation due to highly fluctuating water levels, as well as forested swamps and shallow ponds. The general wetland-to-peatland succession sequence, if peatlands develop eventually, involves early successional marshes, followed by autogenic development of wet fens then drier bogs. Studies that have compared CH_4 emissions among wetland types have found freshwater marshes to be stronger emitters than peatlands, particularly bogs [*Bubier et al*., 1993; *Ding et al*., 2005; *Rouse et al*., 1995]. Therefore, the wetland succession is important for interpreting CH_4 emissions.

[5] While most top-down analyses have been referring to the role of *wetlands* in the abrupt CH_4 rise at the onset of the Holocene, most large-scale empirical syntheses have been based on *peatlands*, owing to the availability of well-stratified peat for dating and analysis. In this paper, we emphasize the distinction between wetlands and peatlands in addressing the roles of northern wetlands in global CH_4 dynamics. To do this, we present a new assessment of northern wetlands' role in global CH_4 changes by synthesizing circum-Arctic datasets on several aspects of wetland-CH_4 dynamics, including (1) net carbon accumulation and peatland productivity, (2) wetland successional sequence, (3) lateral peatland expansion, and (4) new peatland initiation and formation. We also review the current understanding of controls on CH_4 emissions from wetlands, including the relative roles of soil temperature and wetland hydrology as well as vegetation. The analysis presented here is focused on the initiation and successional development of high-latitude wetlands and their impact on atmospheric CH_4 concentrations. Our analysis indicates, in response to climate warming at the onset of the Holocene, that (1) peatlands showed a remarkably steady increase in initiation rates during the first 3000 yr after the onset of the Holocene that would sustain peat expansion and accumulation and CH_4 emissions and also peatlands tend to experience rapid lateral expansion during their early presence, due to more suitable climate, topography, and hydrology; (2) highly productive marshes and wet fen peatlands colonized the landscape during the early Holocene and emitted greater amounts of CH_4 than drier bogs during the late succession stages; and (3) high plant productivity in northern peatlands as inferred from peak net carbon accumulation in the early Holocene provided abundant labile carbon for CH_4 production, and presumably emission, under a warm climate. The rejection of northern wetlands' role in the initial CH_4 rise during the early Holocene [*Reyes and Cooke*, 2011] may represent a lack of consideration of wetland ecology (including the observations that wetlands generally colonize the landscape prior to peatland initiation) and CH_4 emission processes, due to the fact that these diverse aspects of wetland dynamics have not been integrated and evaluated in addressing the global CH_4 dynamics.

2. Data Sources and Methods

[6] Two different types of data were used to evaluate the role of high-latitude wetlands in atmospheric CH_4 increase during the early Holocene: large-scale data syntheses of multiple datasets (Figures 1 and 2) and a new record from a site in the Kenai Lowland in Alaska as a case study (Figure 3).

2.1. Peatland Initiation Ages and Timing

[7] Basal peat ages from the circum-Arctic region that were recently compiled by *MacDonald et al*. [2006], *Gorham et al*. [2007], and *Korhola et al*. [2010] were combined to infer the timing, frequency, and probability of new northern peatland initiation. Overlapping sites among these three datasets were removed, and when more than one basal peat age was available for a site, the oldest one was used as it best represents peatland initiation. In total, our updated database contains 2577 basal peat ages, which were calibrated to calendar years and rounded to decades in the original syntheses (see *MacDonald et al*., 2006; *Gorham et al*., 2007; and *Korhola et al*., 2010 for details). Peat inception ages were summed and presented in 200 yr bins (Figure 2f).

2.2. Peat Carbon Accumulation Calculation and Synthesis

[8] The Holocene peatland carbon accumulation rates for northern peatlands (Figure 2c) were derived on the basis of

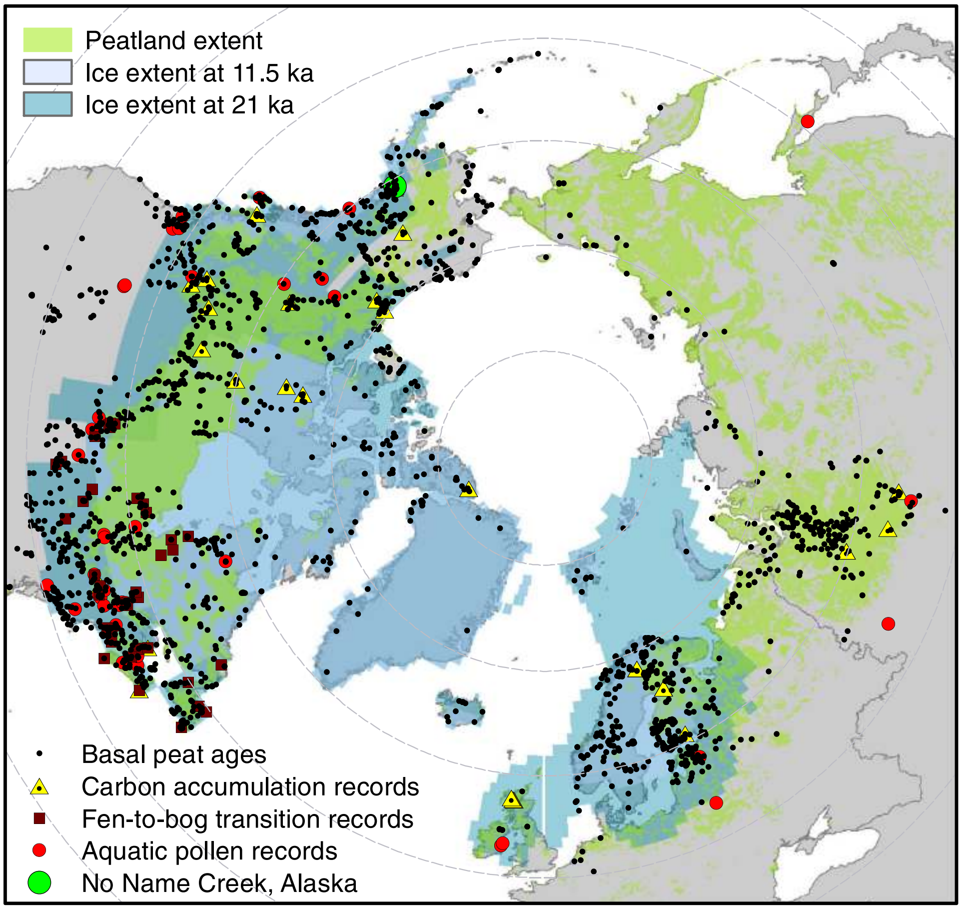

Figure 1. Circum-Arctic peatland distribution and site locations. Peatland-dominant regions (green) were based on *Yu et al*. [2010], and the extent of the northern hemisphere ice sheets at the last glacial maximum at 21 ka (dark blue) and at the onset of the Holocene at 11.5 ka (light blue) was from *Peltier* [2004; ICE-5G]. The extent of ice sheets was shown as two transparent shades to show other geographical features. Sites for paleo records discussed include the following: basal peat ages (black dots; $n = 2577$; combined dataset of non-overlapping sites in *MacDonald et al*., 2006; *Gorham et al*., 2007; and *Korhola et al*., 2010); peatland C accumulation sites (yellow triangles; $n = 33$; *Yu et al*., 2009); sites with fen-to-bog transition ages in eastern North America (brown squares; $n = 39$; see supporting information for site information); wetland sites in Global Pollen Database with aquatic pollen information (red circles; $n = 37$; see supporting information for site information); and No Name Creek peatland site in southern Alaska (big green circle).

1516 basal peat dates [*MacDonald et al*., 2006] and 33 detailed carbon accumulation records [*Yu et al*., 2009, 2010] and long-term decomposition modeling [*Yu*, 2011]. The datasets and modeling process consider peatland area change over time, apparent carbon accumulation rates as observed from peat cores, and continuing decomposition loss of peat after formation and deposition. The results are presented in 1000 yr bins along with error estimates based on the standard errors of mean carbon accumulation rates. Thus, the results represent the true net carbon sequestration rates at millennial scale during the Holocene, not apparent rates as observed from dated peat profiles.

2.3. Fen-to-bog Transition Dataset

[9] Published stratigraphic studies of peat bogs from eastern North America were used as a case study to document the timing of the fen-to-bog transition (FBT) across northern peatlands. We compiled a dataset of 39 sites that are bogs at the present and for which the FBT was dated using the radiocarbon method (for a list of sites and references, see supporting information). Resolution and quality of data varied greatly between sites, from detailed macrofossil diagrams [e.g., *Muller et al*., 2003] to brief descriptions of observed stratigraphic changes in peat properties [e.g., *Glaser*, 1992]. When multiple cores were presented for a single peatland, the longest profile was used to represent the peatland history. When not already calibrated to calendar years in the original publications, radiocarbon dates were calibrated using CALIB 5.10 and INTCAL04 calibration dataset [*Reimer et al*., 2004]. For each site, the fen and bog phases were then coded, pooled into 200 yr bins, and converted to fen and bog percentages relative to the total number of sites (i.e., fen% + bog% = 100%).

2.4. Aquatic Pollen Change From Wetland Sites

[10] Wetland sites (including peatlands) from the Global Pollen Database (GPD) that were located north of 45°N were

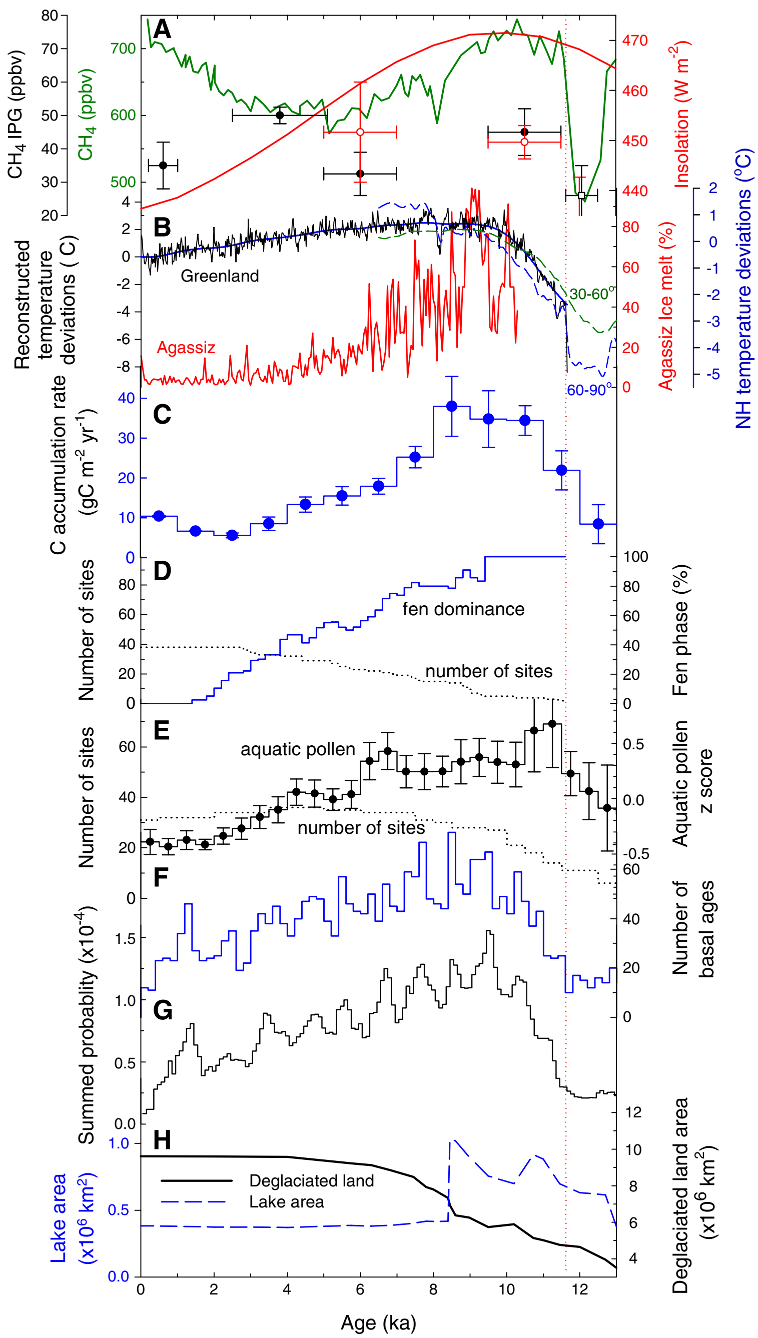

Figure 2. Factors affecting CH_4 emissions from high-latitude wetlands during the Holocene. (a) Atmospheric CH_4 concentrations from Greenland ice core (green line: *Brook et al.*, 2000) and interpolar gradients (black dots: *Chappellaz et al.*, 1997; red open circles: *Brook et al.*, 2000; and black open square: *Dällenbach et al.*, 2000) and mean summer (June, July, and August) insolation curve at 60°N (red line: *Berger and Loutre*, 1991); (b) Paleoclimate records from Greenland ice core (blue line with smoothing curve; *Vinther et al.*, 2009), ice melt record from Agassiz ice core indicating summer warmth [*Fisher et al.*, 1995], and northern hemisphere temperature stacks (blue dashed line for 60–90°N and green dashed line for 30–60°N; *Shakun et al.*, 2012); (c) "True" C accumulation rates and standard errors from northern peatlands [*Yu et al.*, 2011] as calculated from 33 sites with detailed C accumulation records [*Yu et al.*, 2009], basal ages [*MacDonald et al.*, 2006], and decomposition modeling [*Yu*, 2011]; (d) Peatland fen-to-bog succession pattern from 39 sites in eastern North America (see supporting information for detail); (e) Aquatic pollen patterns from wetland sites in North American Pollen Database ($n = 37$; see supporting information for detail); (f) Number of calibrated basal peat ages (median) in 200 yr bins [$n = 2577$; *MacDonald et al.*, 2006; *Gorham et al.*, 2007; *Korhola et al.*, 2010]; (g) Summed probability of basal peat ages (as in *Reyes and Cooke*, 2011 based on data in *MacDonald et al.*, 2006); (h) Changes in land and lake areas from deglaciation of the Laurentide Ice Sheet in North America [from *Dyke et al.*, 2003].

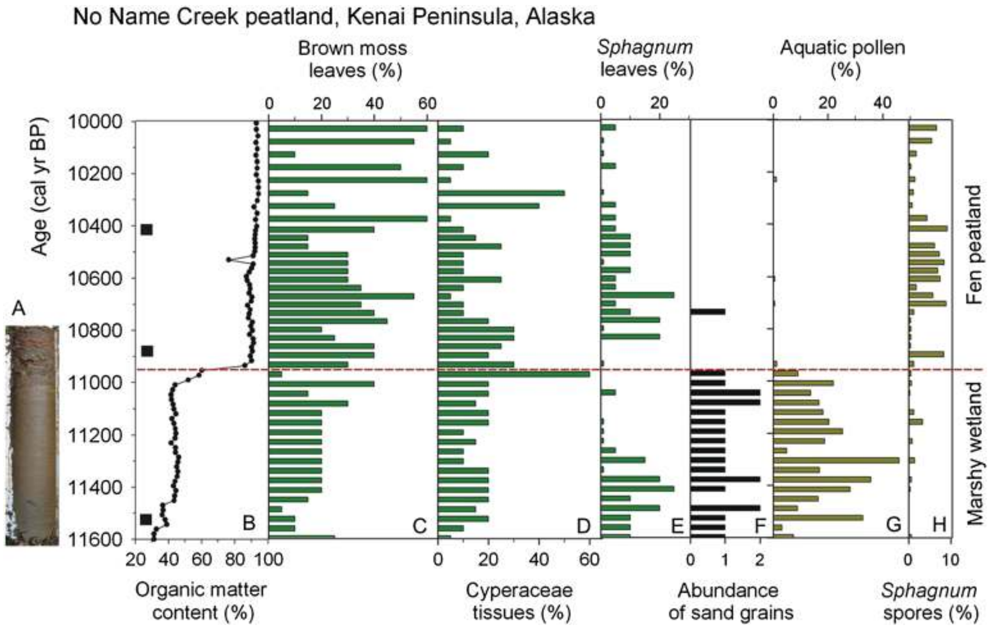

Figure 3. Evidence of pre-peat wetland stage: a case study from Alaska. (a) Core photo of basal peat section from No Name Creek peatland on the Kenai Peninsula, Alaska; (b) Organic matter content showing major transition from a shallow pond/marshy wetland to fen peatland at 10.9 ka; (c) Brown moss macrofossils; (d) Sedge (Cyperaceae) macrofossils; (e) *Sphagnum* macrofossils; (f) Sand-size mineral content (relative abundance); (g) Sum of aquatic plant pollen (including *Typhan*, *Nuphar*, and *Myriophyllum*); (h) *Sphagnum* spores. Black squares indicate AMS ^{14}C dating horizons. Multiple evidence indicates that a marshy wetland existed at 11.6–10.9 ka, immediately before the occurrence of a fen peatland at 10.9 ka, the peatland initiation age at this site.

compiled to document the timing and rate of wetland successional change. Based on published sediment-core data and information available in the GPD, we only selected sites that were wetlands or peatlands at the present, and we avoided sites that experienced major disturbance including flooding events or landslides. We also ensured that each site was only included once, as in a few cases, some peatlands/wetlands have been studied more than once. Among the 37 sites, 31 sites are in North America, and the rest in Eurasia (for a list of sites and references, see supporting information).

[11] We calculated the proportion of wetland pollen taxa relative to the pollen sum for each sample at individual sites. Wetland pollen included all aquatic and lacustrine taxa, as defined by the GPD (for a list of wetland taxa, see supporting information), while the pollen sum included arboreal, herbaceous, aquatic, and lacustrine taxa. Only spores from ferns and mosses were left out of the pollen sum because they were not identified at all sites. These aquatic pollen taxa represent shallow water and marshy environments, rather than peatlands, so their decrease over time indicates the rate and timing of shifts from shallow ponds or wet wetlands to drier wetlands or peatlands, as only contemporary wetland sites are compiled.

[12] As our focus is on relative change in aquatic pollen abundance and site moisture conditions over time, we standardized the raw data to remove site-specific influences on absolute abundance of aquatic pollen at individual sites, including basin depth and morphology, types of substrates, nutrient status, and chemistry. Thus, aquatic pollen percentages were standardized at each site to derive z scores, with positive z scores indicating above-average wetland pollen taxa presence at the site. These scores were then averaged into 500 yr bins to produce a time series describing the evolution of wetland pollen taxa in northern wetlands; this low-temporal resolution binning reflects the dating uncertainty in the pollen database. To assess the possible influence of variable length of each of these records on the temporal pattern shown in our synthesis, we also compiled only the longest 20 records (~10 ka at least) and found a very similar general trend in aquatic pollen abundance during the Holocene (see Figures S1 and S2 in the supporting information). Furthermore, as shown in Figures S1 and S2, the rescaled z scores used for the synthesis curve faithfully reflect the temporal pattern in aquatic pollen abundance at individual sites as well as for the multisite average. We only compiled aquatic pollen data from wetland/peatland sites in the GPD, as lake sites would not allow unequivocal inference about changes in site moisture conditions. For example, increase in aquatic pollen taxa at a lake site could represent either increasing inundation on a peatland or partial infilling of a deep lake.

2.5. Peat Core Analysis From No Name Creek Site in Alaska

[13] A 380 cm long peat core (NNC 07-2) was collected in summer 2007 from the northern Kenai Lowland in south-central Alaska (60°38.436′N; 151°4.788′W; 23 m above sea level). Select macrofossil samples between 11.6 and 10 ka were dated at the University of California-Irvine Keck AMS Carbon Cycle lab, and the radiocarbon dates were calibrated using INTCAL04 dataset [*Reimer et al.*, 2004; see supporting information for dating results]. The organic matter content was estimated using loss-on-ignition analysis

as mass loss at 550°C combustion. Macrofossil analysis was carried out on sieved samples under a stereomicroscope. Pollen analysis followed the modified acetolysis procedure [*Fægri and Iversen*, 1989].

3. Results

[14] Results from the combined basal peat dates indicate that the early Holocene (12–8 ka; 1 ka = 1000 cal yr before present) is characterized by a rapid increase in the number of basal ages (Figure 2f), which is interpreted as a steadily increasing rate of peatland formation. A similar pattern was found when using a summed probability approach for the dataset presented in *MacDonald et al.* [2006] (Figure 2g as calculated in *Reyes and Cooke* [2011]). Along with the new peatland formation, net carbon accumulation rates per unit area from existing peatlands show a sharp increase at the onset of the Holocene and a high value at 11 to 8 ka—more than threefold higher than the late Holocene (Figure 2c).

[15] The pollen records from 37 wetland (including peatland) sites >45°N indicated the highest aquatic pollen abundance in the early Holocene and a decreasing trend in the later half of the Holocene (Figure 2e), suggesting an early succession from marshes or shallow pond environments to progressively drier wetlands and peatlands. This general pattern is robust as shown in synthesis curves of both raw aquatic pollen percentages and *z* scores, which are also not sensitive to the number of sites included and the various lengths of individual records (Figures S1 and S2). Marshes and shallow ponds, which are rich in aquatic species such as *Sparganium* and *Typha*, are characterized by fluctuating water table levels, high CH_4 emissions, and relatively low carbon accumulation [*Moore and Roulet*, 1993; *Moore et al.*, 1994; *von Fischer et al.*, 2010]. This proto-peatland phase typically lasts a few hundred to a thousand years and is followed by the formation of groundwater-fed, wet peat accumulating systems known as fens [*Rydin and Jeglum*, 2006; *Charman*, 2002]. As fen peat accumulates over millennia, peatland surfaces progressively get further away from the mineral groundwater source, and a second successional change, from wet fen to drier bog, often occurs [*Roulet et al.*, 1994; *Leppälä et al.*, 2011; *Strack et al.*, 2006]. This transition to dry and nutrient-poor conditions is accompanied by major shifts in vegetation communities and reductions of CH_4 emissions to the atmosphere [*Rydin and Jeglum*, 2006; *Charman*, 2002]. Newly formed wetlands, including proto- or pre-peatland stages, typically have high water tables. These wetlands are forming throughout the Holocene, but they are forming at substantially lower rates as the Holocene progresses (Figures 2f and 2g). The stratigraphic record of 39 bogs in eastern North America clearly shows this fen-to-bog transition (Figure 2d) during the Holocene, indicating that wet fens dominated the peatland landscape throughout the early Holocene but were progressively replaced by drier and lower CH_4-emitting bogs.

[16] The multiple proxy records from No Name Creek on the Kenai Peninsula in Alaska provide a case study showing the initial ecosystem dynamics before and right after peatland initiation (Figure 3). At this site, sediments started to accumulate at least at 11.6 ka in a shallow pond or marsh, as indicated by lower organic matter content, abundant sand grains, and abundant aquatic plant pollen (including *Typha*, *Nuphar*, and *Myriophyllum*). Peatland initiation through terrestrialization (lake infilling) occurred ca. 10.9 ka, indicated by a sharp increase in organic matter, brown mosses, and peat moss *Sphagnum* macrofossils and *Sphagnum* spores. Some of *Sphagnum* leaves at the base of the record likely came from wet or aquatic species in the marshy pond, while *Sphagnum* spores reflect also surrounding landscape. For this site, basal peat age is 10.9 ka; however, a nonpeat forming wetland existed at this site for at least 500 yr before the initiation of a fen peatland.

4. Discussion

4.1. Accelerated Initiation and Lateral Expansion of New Peatlands

[17] There is a steady, rapid increase in the number of basal peat dates starting at the onset of the Holocene and ending around 8 ka (Figure 2f). This trend is even more remarkable when calculated using the summed probability method (Figure 2g). The rapid increase in new peatland formation, which is attributed to increasing land availability following deglaciation (Figure 2h) as well as to high summer insolation and associated increasing temperatures (Figures 2a and 2b), constitutes the first bottom-up argument suggesting the potentially important contribution of northern peatlands to the early-Holocene CH_4 rise, as first discussed in *MacDonald et al.* [2006].

[18] A pattern of rapid lateral expansion in the early stage of peatland development has been documented in several studies. For example, in northern Québec where deglaciation has occurred around 8–7.5 ka, three peatlands showed the highest rate of lateral expansion shortly after 7.5 ka [*van Bellen et al.*, 2011]. Also, several detailed studies based on dating of multiple cores in peatland basins in Finland show a similar lateral expansion pattern [*Korhola*, 1994; *Mäkilä*, 1997; *Mäkilä and Moisanen*, 2007]. Our data from a peatland in south-central Alaska also show that the peatland had almost reached its modern extent by 8 ka [*Loisel et al.*, 2013]. Although only about 10% of northern peatlands existed before the Holocene [*MacDonald et al.*, 2006; *Yu*, 2011], these existing peatlands also likely expanded rapidly following Holocene warming [*Loisel et al.*, 2013]. The possible rapid increase in wetland and peatland area in the early Holocene under a warmer and wet climate likely contributed to the increase in atmospheric CH_4 concentration.

[19] In a synthesis of multiple dates from individual peatlands, *Korhola et al.* [2010] showed that more basal dates in their dataset occurred during the late Holocene, and they concluded greater lateral expansion of these peatlands after 5 ka. This result seems to be contradictory with detailed studies at individual sites [e.g., *Korhola*, 1994; *van Bellen et al.*, 2011]. We believe that a simple tally of basal dates presented by *Korhola et al.* [2010] would not provide a robust record of peatland expansion history, as the histogram pattern from the limited number of basal dates at an individual peatland (more than three or seven dates per site) is highly sensitive to any addition or deletion of dates at a site. A more realistic interpretation of peatland expansion using limited number of basal dates from individual sites would be to use these dates to estimate peatland area changes at individual sites first and then to combine individual records to generate a synthesis curve for peatland expansion pattern in northern peatlands.

Otherwise, a much larger number of randomly selected dates than currently available from individual sites would be required to infer a robust pattern of peatland expansion using the histogram method.

4.2. Pre-peatland Wetlands and Wet Fens as High CH_4 Emitters

[20] The existence of a lag between peatland initiation and the CH_4 rise (Figures 2a, 2f, and 2g), which was first identified by *MacDonald et al*. [2006], was recently used to question the importance of northern peatlands or wetlands in explaining the early Holocene CH_4 rise [*Reyes and Cooke*, 2011]. Ecologically speaking, however, we should not expect that new peatlands would be formed immediately after the warming at the onset of the Holocene. Peatland formation depends on site-specific topography and hydrology as well as regional climate [*Gorham*, 1957; *Yu et al*., 2009], and there might have been repeated failed attempts of initiation at individual sites. As shown from our synthesis and new record from Alaska, the successional pathway that leads to the formation of peat deposits oftentimes starts with a wetland environment (shallow pond or marsh) dominated by emergent and submerged aquatic plants and is followed by the inception of peatlands at least a few hundred years later [Figures 2e and 3; *Frolking et al*., 2001; *Jones et al*., 2009]. A similar successional pattern during terrestrialization has been documented at multiple sites, including a detailed macrofossil analysis from south-central Alaska [*Jones et al*., 2009] and in south-eastern Canada [*Frolking et al*., 2001]. Even for peatlands that initiated via paludification process of mineral soils, which is the most important process for peatland initiation in some regions [e.g., *Vitt et al*., 2000], initial phases before the establishment of a mature peatland are likely wetter than late stages. These marshy and wet, pre-peatland ecosystems were likely widely distributed on the northern landscape after ice retreat at the end of the Pleistocene, often transitioning to wetter (fen) and then drier (bog) peatlands through the Holocene.

Table 1. Synthesis of Experiments Demonstrating the Influence of Emergent Plants on CH_4 Emissions From Wetlands

Wetland Type	Location	Species Removed	% Reduction in CH_4 Emissions	Reference	Notes
Marsh	China	*Carex lasiocarpa*	78	*Ding et al*. [2005]	Species removal by cutting stems below water table
		Carex meyeriana	64		Species removal by cutting stems below water table
		Deyeuxia angustifolia	28		Species removal by cutting stems below water table
Fen	Switzerland	*Eriophorum latifolium*	64	*Koelbener et al*. [2010]	Compared emissions between cores from same area with and without vegetation; estimated from Figure 2
		Potentilla palustris	80		Compared emissions between cores from same area with and without vegetation; estimated from Figure 2
		Carex rostrata	81		Compared emissions between cores from same area with and without vegetation; estimated from Figure 2
		Anthoxanthum odoratum	77		Compared emissions between cores from same area with and without vegetation; estimated from Figure 2
		Carex elata	77		Compared emissions between cores from same area with and without vegetation; estimated from Figure 2
		Carex acutiformis	57		Compared emissions between cores from same area with and without vegetation; estimated from Figure 2
		Phragmites australis	16		Compared emissions between cores from same area with and without vegetation; estimated from Figure 2
		Phalaris arundinacea	34		Compared emissions between cores from same area with and without vegetation; estimated from Figure 2
Poor fen	Quebec, Canada	*Carex oligosperma*, *Carex limosa*, *Rhyncospora alba*	66	*Strack et al*. [2006]	Species clipped at peat surface and sealed with petroleum jelly
Poor fen	New Hampshire, United States	*Carex rostrata*	39	*Noyce* [2011]	Species clipped at peat surface and sealed with petroleum jelly
Thermokarst bog	Alaska, United States	*Carex aquatilis*	71	*M. Turetsky* [unpublished]	Species removal by cutting stems below water table
Peatland	UK	*Eriophorum vaginatum*	56	*Greenup et al*. [2000]	Species removal by cutting stems below water table
Wet meadow tundra	Alaska, United States	*Carex aquatilis*, *Eriophorum angustifolium*	88	*King et al*. [1998]	Species removal
Wet meadow tundra	Alaska, Unites States	*Carex aquatilis*, *Eriophorum angustifolium*	up to 60	*Verville et al*. [1998]	Species removal

[21] Marshes and shallow ponds tend to release 2–20 times more CH_4 than fens and bogs [e.g., *Matthews and Fung*, 1987; *Aselmann and Crutzen*, 1989; *Bartlett and Harriss*, 1993; *Christensen et al*., 2003]. Also, early-stage peatlands are dominated by groundwater-fed wet fens, as shown in our synthesis for peatlands in eastern North America (Figure 2d). These ecosystems tend to release much larger quantities of CH_4 to the atmosphere than drier peat bogs. Since the transition from fen to bog likely occurred during the middle- and late-Holocene for most peatlands (Figure 2d), high CH_4 emissions can be expected from early-Holocene peatlands. In addition to high water table that has been shown to be a dominant control on CH_4 emissions (e.g., *Moore and Roulet*, 1993), emissions from marshes and wet fens are high in part because of the presence of emergent vascular plants with aerenchymous tissue that facilitate CH_4 release through vascular transport [*Whiting and Chanton*, 1992; *Waddington et al*., 1996; *Joabsson et al*., 1999; *Chanton*, 2005; *Ström et al*., 2005; *Laanbroek*, 2010], though the loss of oxygen to the rhizosphere from these waterlogged-adapted species can reduce emissions [*Sutton-Grier and Megonigal*, 2011]. Overall, however, much of the CH_4 released from northern wetlands is thought to be from plant-mediated transport [*Garnet et al*., 2005], and several experiments have found that the presence of emergent plants have large effects on wetland CH_4 emissions, showing that the removal of emergent plants reduces CH_4 emissions by 61% on average (±21%, SD) (Table 1).

4.3. Holocene Warming, High Wetland Productivity, and Elevated CH_4 Emissions

[22] Holocene warming has been documented in many high-latitude regions. The elevation-corrected temperature reconstruction from Greenland ice cores show an abrupt warming at the onset of the Holocene [Figure 2b; *Vinther et al*., 2009]. Also, a recent synthesis of global proxy temperature records shows that a rapid warming occurred at the onset of the Holocene across the northern hemisphere, especially at high latitudes above 60° [Figure 2b; *Shakun et al*., 2012], where many peatlands are distributed. Many peatland-dominated regions experienced the Holocene thermal maximum in the early Holocene, including Arctic Canada (e.g., Agassiz ice melt record; Figure 2b; *Fisher et al*., 1995), Alaska [*Kaufman et al*., 2004], and other high-latitude regions [*IPCC*, 2007]. Summer temperatures during the Holocene thermal maximum were up to about 2°C warmer than recent pre-industrial period [*Kaufman et al*., 2004]. High peat carbon accumulation has been documented during the early Holocene from recent large-scale data synthesis [Figure 2c; *Yu et al*., 2009] as well as at individual sites in Alaska [*Jones and Yu*, 2010] and elsewhere. The high accumulation rates were most likely caused by high primary productivity under warmer summer conditions during the Holocene thermal maximum under maximum summer insolation (Figure 2a). This high productivity overcompensated the increased decomposition expected under warmer summer conditions—which likely contributed to the high CH_4 emission rates, as discussed earlier.

[23] Summer warmth can stimulate CH_4 production and emission in wetlands directly and indirectly. A positive correlation between CH_4 emission rates from peatlands and peat soil temperature has been documented on seasonal scale at several sites in Alaska and northern Canada [e.g., *Bubier et al*., 1995, 2005; *Turetsky et al*., 2008]. *Christensen et al*. [2003] showed that mean seasonal soil temperature was a major factor controlling mean seasonal CH_4 emission from a range of high latitude wetlands. Also, higher plant productivity under warmer climates provides more labile carbon, and this increase in substrate availability will induce higher heterotrophic respiration and greater CH_4 production in wetlands. The large-scale robust temperature-CH_4 relationships have been observed in ice cores during the last glacial-interglacial transition at 15–10 ka [*Blunier and Brook*, 2001] and during the warm Dansgaard-Oeschger events in the last glacial period [*Bock et al*., 2010]. Thus, warmer climate in the early Holocene in these peatland-dominated regions would have significantly increased the plant production, labile carbon availability, and CH_4 emissions from existing peatlands and other wetlands.

5. Concluding Remarks

[24] In summary, the initiation and formation of new peatlands are only one aspect of peatland dynamics and perhaps are less important in affecting CH_4 emissions than other processes. Other peatland processes that could be more important in causing CH_4 increases in the Holocene include pre-peatland conditions, the temperature dependence of primary productivity and its controls on CH_4 emissions, and peatland lateral expansion. Large seasonal water-table fluctuations in initial shallow organic layers during the pre-peatland phases and warm conditions in the early Holocene promote fast decomposition and high CH_4 production. These proto-peatlands might have been partly responsible for the CH_4 rise at the onset of the early Holocene, which explains the identified "lags" between increasing CH_4 concentration and peatland initiation. The new synthesis and site-specific data presented in this study are highly suggestive that northern peatlands and their precursor wetlands were the major sources of CH_4 for the rapid rise and high CH_4 concentration in the early Holocene.

[25] In order to better constrain the global CH_4 cycle and dynamics during the Holocene, more comprehensive syntheses of relevant datasets are needed. In particular, an expanded database on pan-Arctic wetland-to-peatland as well as fen-to-bog transitions will provide a pan-Arctic assessment of the role of vegetation and wetland community changes in CH_4 dynamics. Also, further synthesis and expanded datasets focused on permafrost degradation and the CH_4 emissions from resultant thermokarst lakes from North America and Siberia will provide a large-scale database for assessing the importance of permafrost dynamics in driving CH_4 changes. Furthermore, an expanded synthesis of relevant paleo records from more southern (temperate) locations may help evaluate if a similar wetland succession process coincided with the rapid rise in CH_4 concentration following the initial deglacial warming (Termination 1A) at 14.7 ka. Also, a similar wetland database from the tropical region would provide a ground-based evaluation of the role of tropical CH_4 sources during Termination 1A, as suggested by the new interpolar gradient analysis from ice cores [*Baumgartner et al*., 2012].

[26] Better process understanding of controls of CH_4 emissions from different types of wetlands over various time scales is needed. In particular, it is critical to build the ability

to infer the dominant controlling factors over decades and centuries on the basis of field and lab-based studies that are oftentimes conducted over shorter seasonal or interannual time scales. Some modeling effort, based on ecological dynamics and empirical data, would be required to bridge the gaps in time scales. Eventually, the integration of data and models would allow us to generate a quantitative assessment of controls of Holocene CH_4 dynamics.

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