Variable effects of climate change on carbon balance in northern ecosystems

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Abstract. Accumulation of carbon dioxide (CO\textsubscript{2}) and methane (CH\textsubscript{4}) in the atmosphere of the planet accelerates climate change, and northern high-latitude regions are warming faster than the planetary average. This accelerated warming of northern regions is associated with multiple climate feedbacks, including those linked to the mobilization of old organic carbon previously sequestered in the frozen ground. This critical climate-feedback mechanism has major uncertainties, and may respond nonlinearly to ongoing warming at high latitudes. This study examines the role of freshwater ecosystems in the subarctic carbon balance, and addresses some sources of nonlinearity in the effect of climate warming on these ecosystems. Specifically, I examine the CO\textsubscript{2} and CH\textsubscript{4} dynamics in permafrost thaw-related ecosystems, and the associated biogeochemical processes. Our results show that major sources of variation in the dynamics of these two gases are associated with the geomorphological properties of the landscape, the degree of ground warming and seasonal biogeochemical dynamics. Accelerated climate change in northern regions may also intensify the CO\textsubscript{2} and CH\textsubscript{4} cycles in these regions, and may substantially increase the current CH\textsubscript{4} flux from these ecosystems.

1. Introduction

The ecosystems, landscapes and, ultimately, climate of the planet have been extensively altered by human activity over the past 250 years [1]. The primary cause of the observed rapid climate change is the accelerated accumulation of greenhouse gases in the atmosphere [2]. Two of several greenhouse gases, namely carbon dioxide (CO\textsubscript{2}) and methane (CH\textsubscript{4}), are the most prominent contributors to the atmospheric heat accumulation [2]. Both gases have risen to unusually high values in the troposphere, to levels that are far in excess of the known interglacial maxima (ca. 45\% higher CO\textsubscript{2} and ca. 240\% higher CH\textsubscript{4} [3, 4]).

The atmospheric balance of these two gases on sub-geologic timescale is largely controlled by the biosphere [5]. Yet, many of the major biospheric sources and sinks of both CH\textsubscript{4} and CO\textsubscript{2} have eluded scientific understanding to date [6]. One of the major current knowledge gaps is the carbon balance in the arctic and subarctic regions [7], and the problem has been exacerbated by rapid climatological changes in these areas [8]. Northern high-latitude regions are warming two- to four-times faster than the planetary average, resulting in an excessive regional accumulation of heat energy in the lower troposphere, increasing humidity and landscape changes, including expansion of vegetation cover [9, 10]. Further complicating a predictive understanding of these effects is that most of these changes result from, or amplified by, the multiple biophysical feedbacks originated in the arctic and subarctic...
regions [11]. Among them, the feedback mechanisms linking the arctic carbon balance with the observed climatic changes are probably the most critical, yet also the most uncertain [6].

This work addresses some of the nonlinear changes in northern ecosystems arising from their accelerated warming. The aim of this article is to: (1) briefly summarize some of the current gaps in understanding of carbon balance in the northern terrestrial environment, and (2) describe the biogeochemical importance, ubiquity, and ecologic dynamics of freshwater systems in northern regions. Specifically, I focus on the thermokarst processes that give rise to numerous lakes and ponds within ice-rich permafrost (perennially frozen) landscapes and then (3) examine the role of these specific freshwater ecosystems, associated with thawing ground, in the current subarctic carbon balance, (4) identify the major sources of variability in estimates of the greenhouse gas emissions from these small arctic lakes, and, finally, (5) evaluate the potentially nonlinear effect of climate change on the CO₂ and CH₄ dynamics in these freshwater ecosystems and associated processes.

2. Carbon balance in arctic and subarctic regions
One of the major sources of carbon in the cold regions is the sedimentary layer of ground, up to several hundred meters thick, that has remained frozen for thousands of years, but that is now thawing at an accelerated rate [12]. Some regions of this perennially frozen ground (permafrost; Figure 1) contain rich carbon deposits, typically associated with the ancient organic sediments and wetlands [13, 14]. Hence, these landscapes hold the potential to play a key role in ongoing climate change, and are sites of increasing global attention and research.

Figure 1. Permafrost is defined as ground that remains frozen for at least two consecutive years. Permafrost environment is a system composed of the layer of frozen ground (light blue) surrounded by seasonally frozen and non-frozen ground (grey). The surface layer (light grey - designated as active layer) is influenced by seasonal cycle of air temperature (black line is the annual ground isotherm, with seasonal isotherms in blue and red). In addition, the ice-rich permafrost may contain agglomerates of the segregation ice (ground ice - white). This ice is sensitive to warming, and its thaw may lead to the ground erosion and subsidence. (Modified form [15]).
Increasing annual air temperature has caused prominent changes to northern ecosystems over the last few decades [8], and more substantial change is projected for the future [16, 17]. On the other hand, the biogeochemical responses to this change and the associated shifts in greenhouse gas (GHG) emissions remain uncertain [18, 19]. Several modeling studies have aimed to quantify the thermal response of northern regions based on soil physical and biological processes within the constraints of available data (e.g. [20-22]). Hilbert et al. [23] created a general model of peatland dynamics that simulated the relations between water table depth and peat production, and Raymond et al. [24] found that a large portion of atmospheric carbon emissions is associated with inland waters. Holgerson and Raymond [25] subsequently identified a particularly large contribution to carbon emissions from inland waters in northern regions, with possible global implications. Yet, insights from paleoclimatological research suggest that global GHG contribution from northern water bodies might at present still be largely underestimated. For example, ice core records from the polar regions show that more than 30% of the global increase in CH₄ concentrations from 14,000 calendar years before present (14 ka BP) and during the Younger Dryas (13 to 11.5 ka BP) originated from northern high latitudes [26, 27]. A ‘northern source’ was also credited for more than 30% (30 to 40 Tg CH₄) of 83 to 99 Tg total CH₄ emissions per year during the early Holocene, ca. 11.5 to 9.5 Ka B.P. [28], and although the exact origins of that CH₄ is still debated, the observed rates of GHG emissions from recent to Pleistocene-aged organic sediments underlying the current northern inland waters and the geomorphological history of their basins, both suggest these water bodies as a possible origin of the emissions [29, 30].

3. Freshwater bodies in northern regions
Freshwater lakes and ponds presently cover more than 1,400,000 km² of landscapes underlain by permafrost [31]. These water bodies include lakes carved by glaciers, lakes accumulated in depressions left by the retreated ice sheets (kettle lakes and bedrock-basin lakes), some boreal lakes, and lakes and ponds associated with thaw and subsidence of ice-rich permafrost [32, 33]. The latter category of lakes is of particular climatological interest, because these waters are directly linked to both the cause and effects of climate change (i.e., GHG emissions, climate warming and permafrost thaw), and are transitional features. The life cycle of these lakes is associated with permafrost ground containing a large volumetric fraction of frozen water, which is a precursor to formation of thermokarst landscapes.

3.1. Thermokarst landscapes
Thermal erosion of permafrost with high ice content leads to melting of ground ice and ejection of excess pore water, which results in loss of substrate volume and subsidence of the land surface. This vertical mass displacement is often coupled with positive hydrological feedbacks, when flowing water further degrades ice-rich permafrost by heat transfer and hydraulic action. This, in turn, causes further vertical and also lateral erosion, thus increasing the spatial extent of irregular terrain. By conceptual association with karst landscapes (geological formations resulting from chemical weathering of carbonate rocks), this type of thermal erosion was named thermokarst.

Thermokarst terrains are associated with permafrost thaw, and thus are pervasive in most periglacial environments of Arctic and Subarctic regions. About 3,600,000 km², or ca. 20 % of the total northern permafrost is affected by thermokarst [34]. Northern permafrost regions contain close to 1000 Pg of carbon in the upper soil layers [35], most of which is old, Pleistocene-aged carbon [30, 36]. Thermokarst processes allow this carbon to be exposed to bacterial decomposition, resulting in ecosystem respiration [37, 38], and thus adding to the atmosphere the carbon previously sequestered in permafrost for thousands of years. In addition, the natural progression of thermokarst to deeper soil layers, adds progressively more carbon to the climate system [39].

Most of the current extent of thermokarst landscape was formed during the Holocene [40]. However, accelerated warming of northern regions during the last decades also accelerated
thermokarst processes [41], especially in the regions of discontinuous permafrost where the spatial extent of thermokarst terrain increased by up to 30% over the last decades [42].

Since thermokarst processes are naturally associated with ice-rich permafrost and ground ice, one of the prominent features of thermokarst landscape is accumulation of flowing water in thaw depressions. These water bodies were first described by Wallace [43] as cave-in lakes, and by Hopkins [44] as thaw lakes and thaw sinks. Based on the current understanding of their origin and development, these are now termed thermokarst lakes.

3.2. Thermokarst lakes

The formation and morphological dynamics of thermokarst lakes is associated with thermal erosion and progressive degradation of surrounding and underlying permafrost. Several lake development pathways were described in the current literature. Payette et al. [45] and Van Huissteden et al. [46] have shown that rapid degradation of the adjacent permafrost may be associated with decreasing volume and eventual disappearance of thermokarst lakes, while Bouchard et al. [47] found that lakes underlain by bedrock, or compacted layers of fine-grained materials (e.g., clay and silt), may persist even after the complete disappearance of surrounding permafrost. The accelerated warming of northern regions has increased geomorphological dynamics of thermokarst lakes [31, 41]. At present, thermokarst lakes cover ca. 300,000 km² of landscape affected by permafrost [33]. Though the changes in their spatial extent and distribution vary by region and are still debated [48, 49], vast permafrost areas exposed by glacial retreat during the early Holocene contain large volumes of ground ice (Figure 2), and, thus, hold the potential for rapid thermokarst erosion, landscape collapse and filling with water. The increased geomorphological dynamics of known thermokarst lakes is likely also to accelerate their biogeochemical processes, specifically organic carbon breakdown to GHG [50, 51].

3.3. Biogeochemical dynamics of thermokarst lakes

Palaeolimnological records from over a 100 thermokarst lakes have shown biological species shifts in response to habitat expansion and nutrient regime changes, including in both aquatic plant and microbial communities [52-54]. Progressive microbial mobilization of permafrost carbon within thermokarst lakes is accelerating carbon turnover in northern regions by adding the new biologically available carbon [55], by augmenting bacterial respiration [56], and by altering the balance between biogenic CH₄ production (methanogenesis) and consumption (methanotrophy) [29, 56].

The balance between methanogenesis and methanotrophy controls the amount of CH₄ emissions from thermokarst lakes. In addition, this balance is important in regulating the amount of CO₂
emissions, since CO\textsubscript{2} is both a main product of methanotrophy and a possible substrate for methanogenesis.

Methanogenesis is typically associated with anoxic environments, particularly lake sediments [58], and may also directly deliver a part of the old (previously sequestered in permafrost) carbon to lake hypolimnia as a microbial substrate (Figure 3). Under anoxic conditions, methanogenic archaea use various metabolic pathways for CH\textsubscript{4} synthesis from products of anaerobic degradation of organic matter, specifically acetate (CH\textsubscript{3}COO\textsuperscript{-}), methyl groups (R-CH\textsubscript{3}), hydrogen (H\textsubscript{2}) and CO\textsubscript{2} [59]. The produced CH\textsubscript{4} either enters the hypolimnion by in situ production in the water column (e.g., [60]), by molecular diffusion at the sediment-water interface, or as small bubbles of biogas released from sediment. These bubbles, however, may be large enough to achieve sufficient flotation velocities to float up, bypassing both lake hypolimnion and epilimnion, and enter the atmosphere directly, or else via the aerenchyma in aquatic plants, which act as conduits with similar effect. The gas entering the hypolimnion may further be delivered to the lakes epilimnion by a physical transport (diffusion or bubble nucleation), or recycled by bacteria and certain methanogens [61, 62], that have been shown to be also active in oxygenated waters [63-65]. Eventually, in addition to the bubbles of biogas, accumulation of CH\textsubscript{4} and CO\textsubscript{2} in the lake surface waters may also generate a sustained diffusive flux of the two GHGs to the atmosphere.

![Figure 3. Synthesis and pathways of CH\textsubscript{4} and CO\textsubscript{2} in a thermokarst lake. Methanogenic archaea use substrates derived from the degradation of organic matter to synthesize CH\textsubscript{4} in anoxic environments, including sediments, hypolimnion, and anoxic microenvironments within the lake epilimnion. Methanotrophic bacteria oxidize some of the methane streams entering the oxic layer of the water column. Lake gas emissions include two types of gas exchange with the atmosphere: (1) by ebullition, directly from the sediment through the water column; and (2) by diffusion of dissolved gases at the lake surface. In addition, (3) accumulation of dissolved gases in the water column indicate the lake’s storage capacity that may be available for future emissions (modified from [66, 73]).](image)

About 30 to 90 % of CH\textsubscript{4} entering lakes may be oxidized by methanotrophs before it has a chance to escape to the atmosphere [66-68]. Methanotrophic communities, however, have also been shown to react very rapidly to changes in abiotic conditions, entraining the associated change in the rates of methanotrophy [69, 70]. Shifts in methanotrophic community structure have been documented in thermokarst lakes, from methane oxidation dominated by psychrotolerant Gammaproteobacteria (Type I) in cold waters to Type II methanotrophy, which is usually dominated by Alphaproteobacteria with high affinity to temperatures above 20 °C [71, 72].
4. Conclusions

About 500 Gt of Pleistocene-aged carbon are estimated to remain preserved in high latitudes, a substantial part of which is in the Canadian Arctic [74-77]. The current CH₄ flux from thermokarst lakes in the Arctic represents ca. 20% of global methane emissions [73]. However, large uncertainty exists in this estimate, and even a greater uncertainty is associated with potential emission patterns under changing climate conditions [78-81]. Despite the increased volume of literature on thermokarst lakes in recent years, much of this research has been restricted to yedoma-type permafrost regions and to sites in close proximity to well-established research facilities, such as in southern Alaska, northern Sweden, and parts of northern Russia. Lakes in other permafrost regions, including peatland thermokarst (Figure S1) with a much higher carbon content relative to yedoma-type permafrost, have received less attention, partly because of the difficulty of access. For similar reasons, winter CH₄ and CO₂ dynamics remain largely enigmatic for most thermokarst lake types (Figure S2). Previous research on thermokarst lakes drew attention to their role in greenhouse gas production in the global carbon cycle, and indicated that these emissions of CH₄ and CO₂ are potentially large [25, 82] but variable [80, 83] and poorly constrained [81].

Our studies build upon and extend this earlier research, and show that major sources of variation are associated with the type of permafrost landscape and the seasonal changes in ice cover, stratification and mixing. Moreover, the observed CH₄ and CO₂ emissions from geomorphologically distinct thermokarst lakes appear to be related to the degree of permafrost degradation, indicating the likely response of these subarctic freshwater systems to ongoing climate change. In addition, the thermokarst landscapes are subject to rapid change, particularly in response to accelerated rates of climate warming of the northern hemisphere. Of particular significance for understanding the current and ongoing changes in the global carbon balance are the permafrost regions storing large amounts of carbon in their surface soil layers, especially those at the southern limits of permafrost that are vulnerable to rapid degradation in the current warming climate.

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References

[1] Ripple W J, et al. 2017 World scientists’ warning to humanity: A second notice. BioSci. 67 1026
[2] Drake T W, Holmes R M, Zhulidov A V, Gurtovaya T, Raymond P A, McClelland J W and Spencer R G 2018 Multidecadal climate-induced changes in Arctic tundra lake geochemistry and geomorphology. Limnology and Oceanography S (First published online 19 September 2018)
[3] Delmotte M 2004 Atmospheric methane during the last four glacial-interglacial cycles: Rapid changes and their link with Antarctic temperature J. Geophys. Res. 109 D12104
[4] Past Interglacials Working Group (P. I. W. G.) of PAGES. 2016. Interglacials of the last 800,000 years Rev. Geophys. 54 162
[5] Lovelock J E and Margulis L 1974 Atmospheric homeostasis by and for the biosphere: the Gaia hypothesis Tellus A 26 2
[6] Tian H, et al. 2016 The terrestrial biosphere as a net source of greenhouse gases to the atmosphere Nature 531(7593) 225
[7] Parmentier F-J W, et al. 2017 A synthesis of the arctic terrestrial and marine carbon cycles under pressure from a dwindling cryosphere Ambio 46(S1) 53
[8] Vincent W F, Lemay M and Allard M 2017 Arctic permafrost landscapes in transition: towards an integrated earth system approach. Arctic Sci. 3(2) 39
[9] ACIA 2005 Arctic Climate Impact Assessment Scientific Report. Cambridge University Press,
IPCC 2013 Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change eds. Stocker, T.F., D. Qin, G.-K. Plattner, M. Tignor, S.K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex and P.M. Midgley (Cambridge: Cambridge University Press) p. 1535

Grosse G, Goetz S, McGuire A D, Romanovsky V E and Schuur E A G 2016 Changing permafrost in a warming world and feedbacks to the Earth system Env. Res. Lett. 11 040201

Arp C D, Jones B M, Grosse G, Bondurant A G, Romanovsky V E, Hinkel K M and Parsekian A D 2016 Threshold sensitivity of shallow Arctic lakes and sublake permafrost to changing winter climate Geophys. Res. Lett. 43 6358

Bhiry N, et al. 2011 Environmental change in the Great Whale River Region, Hudson Bay: Five decades of multidisciplinary research by Centre d’études nordiques (CEN) Ecoscience 18 182

Hugelius G, et al. 2014 Estimated stocks of circumpolar permafrost carbon with quantified uncertainty ranges and identified data gaps Biogeosciences 11 6573

Nötzig J and Gruber S 2005 Alpiner Permafrost - ein Überblick Jahrbuch des Vereins zum Schutz der Bergwelt 70 111

MacDougall A H, Avis C A and Weaver A J 2012 Significant contribution to climate warming from the permafrost carbon feedback Nat. Geosci. 5 719

Anderson N J, et al. 2017 The Arctic in the twenty-first century: Changing biogeochemical linkages across a paraglacial landscape of Greenland. Bioscience 67(2) 118

Abbott B W, et al. 2016 Biomass offsets little or none of permafrost carbon release from soils, streams, and wildfire: an expert assessment Env. Res. Lett. 11 034014

Chaudhary N, Miller P A and Smith B 2017 Modelling past, present and future peatland carbon accumulation across the pan-Arctic region Biogeosciences 14 4023

Biesinger Z, Rastetter E B, and Kwiatkowski B L 2007 Hourly and daily models of active layer evolution in Arctic soils. Ecological Modelling 206 131-46

Douglas 2016, et al. Diverse origins of Arctic and Subarctic methane point source emissions identified with multiply-substituted isotopologues Geochimica et Cosmochimica Acta 188 163

Kaplan J O, et al. 2003 Climate change and Arctic ecosystems: II. Modeling, paleodata-model comparisons, and future projections J. Geophys. Res. 108 D18 8171

Tranvik L, et al. 2009 Lakes and reservoirs as regulators of carbon cycling and climate, Limnol. Oceanogr. 54 2298

Yu Z, Loisel J, Turetsky M R, Cai S, Zhao Y, Frolking S, MacDonald G M and Bubier J L 2013 Evidence for elevated emissions from high-latitude wetlands contributing to high atmospheric CH₄ concentration in the early Holocene Glob. Biogeoch. Cy. 27 131

Muster S, Heim B, Abnizova A and Boike J 2013 Water body distributions across scales: a remote sensing based comparison of three arctic tundra wetlands Remote Sensing 5 1498

Lehner B and Doll P 2004 Development and validation of a global database of lakes, reservoirs, and wetlands J. Hydrol. 296 1-22

Grosse G, Jones B and Arp C 2013 Thermokarst lakes, drainage, and drained basins, Treatise on
Geomorphology ed. Shroder J F (San Diego: Academic Press) pp. 325-353.

[34] Olefeldt D, Goswami S, Grosse G, Hayes D, Hugelius G, Kuhry P and Turetsky M R 2016 Circumpolar distribution and carbon storage of thermokarst landscapes Nat. Commun. 7 13043

[35] Tarnocai C, Canadell J, Schuur E A G, Kuhry P, Mazhitova G and Zimov S 2009 Soil organic carbon pools in the northern circumpolar permafrost region Glob. Biogeochem. Cy. 23 3327

[36] Zimov S A, Davydov S P, Zimova G M, Davydova A I, Schuur E A G, Dutta K and Chapin F S 2006 Permafrost carbon: Stock and decomposability of a globally significant carbon pool Geophys. Res. Lett. 33 L20502

[37] Oechel W C, Hastings S J, Vourlitis G, Jenkins M, Riechers G and Grulke N 1993 Recent change of arctic tundra ecosystems from a net carbon dioxide sink to a source Nature 361 520

[38] Heimann M and Reichstein M 2008 Terrestrial ecosystem carbon dynamics and climate feedbacks Nature 451 289

[39] Schuur E A G, Vogel J G, Crummer K G, Lee H, Sickman J O and Osterkamp T E 2009 The effect of permafrost thaw on old carbon release and net carbon exchange from tundra Nature 459 556

[40] Grosse G, Schirrmeister L, and Malthus T J 2006 Application of Landsat-7 satellite data and a DEM for the quantification of thermokarst-affected terrain types in the periglacial Lena-Anabar coastal lowland. Polar Research 25 51-67

[41] Hinzman L D, Deal C J, McGuire A D, Mernild S H, Polyakov I V, and Walsh 2013 Trajectory of the Arctic as an integrated system. Ecological Applications 23 1837-68

[42] Osterkamp T E, Jorgenson M, Schuur E A G, Shur Y L, Kanevskiy M, Vogel J and Tumskoy V E 2009 Physical and ecological changes associated with warming permafrost and thermokarst in interior Alaska Permafrost Periglac. 20 235

[43] Wallace R E 1948 Cave-in lakes in the Nabesna, Chisana, and Tanana river valleys, Eastern Alaska J. Geol. 56 171

[44] Hopkins D M 1949 Thaw lakes and thaw sinks in the Imuruk Lake area, Seward Peninsula, Alaska J. Geol. 57 119

[45] Payette S, Delwaide A, Caccianiga M and Beauchemin M 2004 Accelerated thawing of subarctic peatland permafrost over the last 50 years Geophys. Res. Lett. 31 L18208

[46] van Huistened, J, Bertrittella C, Parmentier F J W, Mi Y, Maximov T C and Dolman A J 2011 Methane emissions from permafrost thaw lakes limited by lake drainage Nature Climate Change 1 119

[47] Bouchard F, Francus P, Pienitz R and Laurion I 2011 Sedimentology and geochemistry of thermokarst ponds in discontinuous permafrost, subarctic Quebec, Canada J. Geophys. Res. 116 G00M04

[48] Smith L C, Sheng Y and MacDonald G M 2007 A first pan-arctic assessment of the influence of glaciation, permafrost, topography and peatlands on northern hemisphere lake distribution. Permafrost Periglac. 18 20108

[49] Boike J, Grau T, Heim B, Günther F, Langer M, Muster S, Gouttevin S and Lange S 2016 Satellite-derived changes in the permafrost landscape of central Yakutia, 2000-2011: wetting, drying, and fires Global Planet Change 139 116

[50] Vogel J, Schuur E A G, Trucco C and Lee H 2009 Response of CO2 exchange in a tussock tundra ecosystem to permafrost thaw and thermokarst development J. Geophys. Res. 114 G04018

[51] Vincent W F 2010 Microbial ecosystem responses to rapid climate change in the Arctic ISME Journal 4 1087

[52] Smol J P, et al. 2005 Climate-driven regime shifts in the biological communities of arctic lakes Proceedings of the National Academy of Sciences USA 102 4397

[53] Kessler M A, Plug L J and Walter Anthony K M 2012 Simulating the decadal- to millennial-scale dynamics of morphology and sequestered carbon mobilization of two thermokarst lakes in NW Alaska J. Geophys. Res. 117 G00M06

[54] Lee H, Schuur E A G, Inglett K S, Lavoie M and Chanton J P 2012 The rate of permafrost carbon release under aerobic and anaerobic conditions and its potential effects on climate Glob. Change Biol. 18 51527
[55] Fenchel T 2008 The microbial loop - 25 years later J. Exp. Mar. Biol. Ecol. 366 99
[56] Deshpande B N, S Crevecoeur, A Matveev and Vincent W F 2016. Bacterial production in subarctic peatland lakes enriched by thawing permafrost Biogeosci. 13 4411
[57] Brown J, Ferrians O, Heginbottom J A and Melnikov E 2002 Circumpolar Map of Permafrost and Ground-Ice Conditions, Version 2. [Subset: Ground Ice] Boulder, Colorado USA. NSIDC: National Snow and Ice Data Center [Date Accessed: 2017-11-27]
[58] Negandhi K, Laurion I, Whiticar M J, Galand P E, Xu X and Lovejoy C 2013 Small thaw ponds: An unaccounted source of methane in the Canadian High Arctic PLoS ONE 8 e78204
[59] Baptiste E, Brochier C and Boucher Y 2005 Higher-level classification of the Archaea: evolution of methanogenesis and methanogens Archaea 1 353
[60] Crevecoeur S, Vincent W F and Lovejoy C 2016 Environmental selection of planktonic methanogens in permafrost thaw ponds Scientific Reports 6 31312
[61] Azam F, Fenchel T, Field J G, Gray J S, Meyer-Reil L A and Thingstad F 1983 The ecological role of water-column microbes in the sea Mar. Ecol. Progr. Ser. 10 257
[62] Brankovits D, Pohlman J W, Niemann H, Leigh M B, Leewis M C, Becker K W, Iliffe T, Alvarez F, Lehmann M F and Phillips B 2017 Methane- and dissolved organic carbon-fueled microbial loop supports a tropical subterranean estuary ecosystem Nat. Commun. 8 1835
[63] Schulz A, et al. 2001 Arctic ozone loss in threshold conditions: Match observations in 1997/1998 and 1998/1999 J. Geophys. Res. Atm. 106(D7) 7495
[64] Grossart H-P, Frindte K, Dziallas C, Eckert W and Tang K W 2011 Microbial methane production in oxygenated water column of an oligotrophic lake Proceedings of the National Academy of Sciences USA 108 19657
[65] Bogard M J, Del Giorgio P A, Boutet L, Chaves M C G, Prairie Y T, Merante A and Derry A M 2014 Oxic water column methanogenesis as a major component of aquatic CH4 fluxes Nat. Commun. 5 5350
[66] Kankaala P, Huotari J, Peltomaa E, Saloranta T and Ojala A 2006 Methanotrophic activity in relation to methane efflux and total heterotrophic bacterial production in a stratified, humic, boreal lake Limno. Oceanogr. 51 1195
[67] Bastviken D, Cole J J, Pace M L and Van der Bogert M C 2008 Fates of methane from different lake habitats: Connecting whole-lake budgets and CH4 emissions J. Geophys. Res. 113 G02024
[68] Oswald K, Milucka J, Brand A, Hach P, Littmann S, Wehrli B, Kuypers M M and Schubert C J 2016 Aerobic gammaproteobacterial methanotrophs mitigate methane emissions from oxic and anoxic lake waters Limnol. Oceanogr. 61(S1) S101
[69] Gebert J, Singh B K, Pan Y and Bodrossy L 2009 Activity and structure of methanotrophic communities in landfill cover soils Env. Microbiol. Rep. 1 414
[70] Kumaresan D, Abell G C J, Bodrossy L, Stralis-Pavese N and Murrell J C 2009 Spatial and temporal diversity of methanotrophs in a landfill cover soil are differentially related to soil abiotic factors Env. Microbiol. Rep. 1(5) 398
[71] Abell G C, Revill A T, Smith C, Bissett A P, Volkman J K and Robert S S 2010 Archaeal ammonia oxidizers and nirS-type denitrifiers dominate sediment nitrifying and denitrifying populations in a subtropical macrotidal estuary ISME J. 4 286
[72] He R, Wooller M J, Pohlman J W, Quensen J, Tiedje J M and Leigh M B 2012 Shifts in identity and activity of methanotrophs in Arctic lake sediments in response to temperature changes Appl. Env.Microbiol. 78 4715
[73] Bastviken D, Persson L, Odham G, and Tranvik L 2004 Degradation of dissolved organic matter in oxic and anoxic lake water Limnol. Oceanogr. 49 109
[74] Bigelow N H, et al. 2003 Climatic change and Arctic ecosystems I. Vegetation changes north of 55°N between the last glacial maximum, mid-Holocene, and present J. Geophys. Res. Atm. 108 2169
[75] Cohen S J 1997 What if and so what in northern Canada: Could climate change make a difference to the future of the Mackenzie Basin Arctic 50 293
[76] Dällenbach A T, Blunier J, Flückiger B, Stauffer J, Chappellaz D and Raynaud D 2000 Changes
in the atmospheric CH$_4$ gradient between Greenland and Antarctica during the last Glacial and the transition to the Holocene Geophys. Res. Lett. 27 1005

[77] Schuur E A G, et al. 2015 Climate change and the permafrost carbon feedback Nature 520 171

[78] Turetsky M R, Wieder K, Vitt D H, Evans R J and Scott K D 2007 The disappearance of relict permafrost in boreal North America: effects on peatland carbon storage and fluxes Glob. Change Biol. 13 1922

[79] Breton J, Vallieres C, and Laurion I 2009 Limnological properties of permafrost thaw ponds in northeastern Canada. Canadian Journal of Fisheries and Aquatic Science 66 1635

[80] Laurion I, Vincent W F, MacIntyre S, Retamal L, Dupont C, Francus P, and Pienitz R 2010 Variability in greenhouse gas emissions from permafrost thaw ponds Limnol. Oceanogr. 55 115

[81] Vonk, et al. 2015 Effects of permafrost thaw on Arctic aquatic ecosystems Biogeosci. 12 7129

[82] Matveev A, Laurion I, Deshpande B N, Bhiry N, and Vincent W F 2016 High methane emissions from thermokarst lakes in subarctic peatlands Limnol Oceanogr. 61(S1) S150

[83] Matveev A, Laurion I and Vincent W F 2018 Methane and carbon dioxide emissions from thermokarst lakes on mineral soils Arctic Science 4 584
Supplement

Figure S1. Peatland thermokarst lakes in Nunavik region (Quebec, Canada), August 2015. (Photo credit: Author, CEN 2016).

Figure S2. Peatland thermokarst lakes in Nunavik region (Quebec, Canada), March 2016. (Photo credit: Author, CEN 2016).