

The uncertain climate footprint of wetlands under human pressure

Ana Maria Roxana Petrescu^a, Annalea Lohila^b, Juha-Pekka Tuovinen^b, Dennis D. Baldocchi^c, Ankur R. Desai^d, Nigel T. Roulet^e, Timo Vesala^{f,g}, Albertus Johannes Dolman^h, Walter C. Oechelⁱ, Barbara Marcolla^j, Thomas Friborg^k, Janne Rinne^{b,f,l}, Jaclyn Hatala Matthes^{c,1}, Lutz Merbold^m, Ana Meijide^{a,2}, Gerard Kielyⁿ, Matteo Sottocornola^{n,3}, Torsten Sachs^o, Donatella Zona^{i,p}, Andrej Varlagin^q, Derrick Y. F. Lai^r, Elmar Veenendaal^s, Frans-Jan W. Parmentier^{t,u}, Ute Skiba^v, Magnus Lund^{t,u}, Arjan Hensen^w, Jacobus van Huissteden^h, Lawrence B. Flanagan^x, Narasinha J. Shurpali^y, Thomas Grünwald^z, Elyn R. Humphreys^{aa}, Marcin Jackowicz-Korczyński^t, Mika A. Aurela^b, Tuomas Laurila^b, Carsten Grüning^a, Chiara A. R. Corradi^{bb}, Arina P. Schrier-Uijl^s, Torben R. Christensen^{t,u}, Mikkel P. Tamstorf^u, Mikhail Mastepanov^{t,u}, Pertti J. Martikainen^y, Shashi B. Verma^{cc}, Christian Bernhofer^z, and Alessandro Cescatti^{a,4}

^aEuropean Commission, Joint Research Center, Institute for Environment and Sustainability, Ispra (VA) 21027, Italy; ^bAtmospheric Composition Research, Finnish Meteorological Institute, FI-00101 Helsinki, Finland; ^cDepartment of Environmental Science, Policy, and Management, University of California, Berkeley, CA 94720; ^dAtmospheric & Oceanic Sciences Department, University of Wisconsin–Madison, Madison, WI 53706; ^eDepartment of Geography & the Global Environmental and Climate Change Research Centre, McGill University, Montreal, QC H3A 2K6, Canada; ^fDepartments of ^gPhysics and ^hForest Sciences, University of Helsinki, FIN-00014 Helsinki, Finland; ⁱDepartment of Earth Sciences, Earth and Climate Cluster, VU University Amsterdam, 1081 HV Amsterdam, The Netherlands; ^jGlobal Change Research Group, Department of Biology, San Diego State University, San Diego, CA 92182; ^kSustainable Agro-ecosystems and Bioresources Department, Fondazione Edmund Mach, 1 I-38010 S. Michele all'Adige (TN), Italy; ^lCENTER for PERMAfrost, Department of Geosciences and Natural Resource Management, University of Copenhagen, 1350 K Copenhagen, Denmark; ^mDepartment of Geosciences and Geography, University of Helsinki, FIN-00014 Helsinki, Finland; ⁿDepartment of Environmental Systems Science, Institute of Agricultural Sciences, ETH Zurich, 8092 Zurich, Switzerland; ^oCivil and Environmental Engineering Department and Environmental Research Institute, University College Cork, Cork, Ireland; ^pHelmholtz Centre Potsdam (GFZ) (Geoforschungszentrum) German Research Centre for Geosciences, Department of Inorganic and Isotope Geochemistry, 14473 Potsdam, Germany; ^qDepartment of Animal and Plant Sciences, University of Sheffield, Sheffield S10 2TN, United Kingdom; ^rA. N. Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Moscow 119071, Russia; ^sDepartment of Geography and Resource Management, The Chinese University of Hong Kong, Hong Kong SAR, China; ^tNature Conservation and Plant Ecology Group, Wageningen University, 6700 AA Wageningen, The Netherlands; ^uDepartment of Physical Geography and Ecosystem Science, Lund University, SE-223 62 Lund, Sweden; ^vArctic Research Centre, Department of Bioscience, Aarhus University, DK-4000 Roskilde, Denmark; ^wCentre for Ecology and Hydrology, Bush Estate, Penicuik EH26 0QB, United Kingdom; ^xEnergy Research Centre of the Netherlands (Energieonderzoek Centrum Nederland), Environmental Research, 1755 ZG Petten, The Netherlands; ^yDepartment of Biological Sciences, University of Lethbridge, Lethbridge, AB T1K 3M4, Canada; ^zDepartment of Environmental Science, University of Eastern Finland, FIN-70211 Kuopio, Finland; ^{aa}Institute of Hydrology and Meteorology, Chair of Meteorology, Technische Universität Dresden, D-01062 Dresden, Germany; ^{ab}Department of Geography and Environmental Studies, Carleton University, Ottawa, ON K1S 5B6, Canada; ^{bb}Laboratory of Forest Ecology, Department of Forest, Environment, and Resources, University of Tuscia of Viterbo, 01100 Viterbo, Italy; and ^{cc}School of Natural Resources, University of Nebraska–Lincoln, Lincoln, NE 68583

Edited by William H. Schlesinger, Cary Institute of Ecosystem Studies, Millbrook, NY, and approved February 9, 2015 (received for review August 23, 2014)

Significant climate risks are associated with a positive carbon-temperature feedback in northern latitude carbon-rich ecosystems, making an accurate analysis of human impacts on the net greenhouse gas balance of wetlands a priority. Here, we provide a coherent assessment of the climate footprint of a network of wetland sites based on simultaneous and quasi-continuous ecosystem observations of CO₂ and CH₄ fluxes. Experimental areas are located both in natural and in managed wetlands and cover a wide range of climatic regions, ecosystem types, and management practices. Based on direct observations we predict that sustained CH₄ emissions in natural ecosystems are in the long term (i.e., several centuries) typically offset by CO₂ uptake, although with large spatiotemporal variability. Using a space-for-time analogy across ecological and climatic gradients, we represent the chronosequence from natural to managed conditions to quantify the “cost” of CH₄ emissions for the benefit of net carbon sequestration. With a sustained pulse-response radiative forcing model, we found a significant increase in atmospheric forcing due to land management, in particular for wetland converted to cropland. Our results quantify the role of human activities on the climate footprint of northern wetlands and call for development of active mitigation strategies for managed wetlands and new guidelines of the Intergovernmental Panel on Climate Change (IPCC) accounting for both sustained CH₄ emissions and cumulative CO₂ exchange.

wetland conversion | methane | radiative forcing | carbon dioxide

For their ability to simultaneously sequester CO₂ and emit CH₄, wetlands are unique ecosystems that may potentially generate large negative climate feedbacks over centuries to millennia (1) and positive feedbacks over years to several centuries (2). Wetlands are among the major biogenic sources of

CH₄, contributing to about 30% of the global CH₄ total emissions (3), and are presumed to be a primary driver of interannual variations in the atmospheric CH₄ growth rate (4, 5). Meanwhile, peatlands, the main subclass of wetland ecosystems, cover 3% of the Earth's surface and are known to store large quantities of carbon (about 500 ± 100 Gt C) (6, 7).

The controversial climate footprint of wetlands is due to the difference in atmospheric lifetimes and the generally opposite directions of CO₂ and CH₄ exchanges, which leads to an uncertain sign of the net radiative budget. Wetlands in fact have a great

Author contributions: A.M.R.P. and A.C. designed research and led the discussions; A.M.R.P., A.L., J.-P.T., and A.C. performed research and the RF analysis; A.M.R.P., A.L., J.-P.T., B.M., and A.C. analyzed data; A.M.R.P., A.L., J.-P.T., D.D.B., A.R.D., N.T.R., T.V., A.J.D., W.C.O., B.M., T.F., J.R., J.H.M., L.M., A.M., G.K., M.S., T.S., D.Z., A.V., D.Y.F.L., E.V., F.-J.W.P., U.S., M.L., A.H., J.v.H., L.B.F., N.J.S., T.G., E.R.H., M.J.-K., M.A.A., T.L., C.G., C.A.R.C., A.P.S.-U., T.R.C., M.P.T., M.M., P.J.M., S.B.V., C.B., and A.C. wrote the paper; and A.L., D.D.B., A.R.D., N.T.R., T.V., A.J.D., W.C.O., T.F., J.R., J.H.M., L.M., A.M., G.K., M.S., T.S., D.Z., A.V., D.Y.F.L., E.V., F.-J.W.P., U.S., M.L., A.H., J.v.H., L.B.F., N.J.S., T.G., E.R.H., M.J.-K., M.A.A., T.L., C.G., C.A.R.C., A.P.S.-U., T.R.C., M.P.T., M.M., P.J.M., S.B.V., and C.B. are data providers.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

Freely available online through the PNAS open access option.

¹Present address: Department of Geography, Dartmouth College, 6017 Fairchild Hall, Hanover, NH 03755.

²Present address: Bioclimatology Group, Georg-August-University Göttingen, Büsgenweg 2, 37077 Göttingen, Germany.

³Present address: Department of Chemical and Life Sciences, Waterford Institute of Technology, Waterford, Ireland.

⁴To whom correspondence should be addressed. Email: alessandro.cescatti@irc.ec.europa.eu.

This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1416267112/-DCSupplemental.

Significance

Wetlands are unique ecosystems because they are in general sinks for carbon dioxide and sources of methane. Their climate footprint therefore depends on the relative sign and magnitude of the land–atmosphere exchange of these two major greenhouse gases. This work presents a synthesis of simultaneous measurements of carbon dioxide and methane fluxes to assess the radiative forcing of natural wetlands converted to agricultural or forested land. The net climate impact of wetlands is strongly dependent on whether they are natural or managed. Here we show that the conversion of natural wetlands produces a significant increase of the atmospheric radiative forcing. The findings suggest that management plans for these complex ecosystems should carefully account for the potential biogeochemical effects on climate.

potential to preserve the carbon sequestration capacity because near water-logged conditions reduce or inhibit microbial respiration, promoting meanwhile CH_4 production that may partially or completely counteract carbon uptake. Potential variations of the CO_2/CH_4 stoichiometry in wetlands exposed to climate and land-use change require the development of mitigation-oriented management strategies to avoid large climatic impacts.

The current and future contribution of wetlands to the global greenhouse gas (GHG) budget is still uncertain because of our limited knowledge of the combined and synergistic response of CH_4 and CO_2 land–atmosphere exchange to environmental variability (8, 9) and land-use change (e.g., wetland restoration, drainage for forestry, agriculture, or peat mining) (9, 10). Fluxes of CH_4 and CO_2 from natural wetlands show large spatiotemporal variations (11, 12), arising from environmental interactions controlling the production, transport, consumption, and release of CH_4 (13, 14) as well as the dynamic balance between photosynthetic and respiratory processes that regulate the net accumulation of carbon in biomass and soil. Environmental factors such as variations in air and soil temperature, water table, and substrate availability for methanogenesis lead to a high spatial and temporal variation of CH_4 emissions (15–17). The magnitude of emissions is also controlled by the balance between CH_4 production and oxidation rates and by transport pathways: diffusion (18), ebullition (19), and aerenchyma transport (20).

Climate change influences the GHG balance of wetlands through thawing of the near-surface permafrost (21, 22) and thaw lakes (23), increased nitrogen availability due to accelerated decomposition of organic matter (24), and modification of the water tables with consequent shifts in CH_4 emissions (1, 25). A review of carbon budgets of global peatlands concluded that these ecosystems may remain a small but persistent sink that builds a large C pool, reducing the atmospheric CO_2 burden, whereas the stimulation of CH_4 emissions induced by climate warming may be locally tempered or enhanced by drying or wetting (26). The climate footprint of wetlands can also be affected by anthropogenic activities such as the conversion of natural ecosystems to agricultural or forested land (10, 27). Draining peatlands for forestry may lead to a C loss and reduced CH_4 emissions (10, 26), whereas land use for agriculture typically reduces the CH_4 emissions and increases N_2O emissions (26).

Several studies have analyzed the impact of northern peatlands on the Earth's radiative budget either by computing the radiative forcing (RF) of sustained CH_4 and CO_2 fluxes (2) or by multiplying the annual ecosystem exchange of CO_2 and CH_4 with the global warming potentials of the two gases (28–30). However, although this latter approach is useful for comparison, its appropriateness in computing the actual RF has been questioned (31–33). An alternative approach for assessing the impact of peatland draining/drying on the RF has been applied by driving

an atmospheric composition and RF model with pre- and post-drainage measured fluxes of CO_2 , CH_4 , and N_2O (34).

Here, we ask, what is the climate cost of CH_4 emissions compared with the benefit of net carbon sequestration? We assessed this question, using data from a network of wetland observational sites where direct and quasi-continuous CO_2 and CH_4 chamber and eddy covariance measurements are performed. Using the space for time analogy, flux observations at sites with contrasting land cover are combined with a sustained pulse–response model to predict the potential future RF of natural wetlands converted to agricultural or forested land.

Results and Discussion

As the land–atmosphere fluxes of CH_4 and CO_2 in wetlands can be opposite in sign and very different in magnitude, their net impact on the climate system is difficult to assess and predict. In particular, CH_4 emissions from wetlands are continuous and thus add a positive term to the radiative balance (31) that can be partially or totally offset by a sustained carbon sequestration (35). The availability of consistent and simultaneous measurements of ecosystem CO_2 and CH_4 fluxes provides an opportunity to address these issues, using direct observations collected at 29 both natural and managed wetlands located in the Northern Hemisphere (Fig. 1A). Details on site locations, climate, vegetation type, measurement techniques, and yearly/seasonal GHG budgets are reported in *SI Text, Site Analysis* and *SI Text, Measurement Techniques and Gap-Filling Methods* (Tables S1–S5).

The trade-off between CH_4 net emission and CO_2 net sequestration in wetlands is evident in Fig. 1B, where most sites are sources of CH_4 (positive ecosystem fluxes) and CO_2 sinks (negative values of net ecosystem exchange, NEE). Given that CH_4 has a relatively short lifetime in the atmosphere (~ 10 y) compared to CO_2 , the radiative balance of these two gases depends on the timeframe of the analysis. As an example of this dependence, the two red–blue equilibrium lines in Fig. 1B represent the ratio of sustained CO_2 and CH_4 fluxes that would result in a zero net cumulative radiative balance over 20 y and 100 y. The lines were simulated with a sustained pulse–response model (27) and used in this study also to calculate the RF of management options. The model generates the following flux ratios: -31.3 g and -19.2 g $\text{CO}_2\text{-C}\cdot\text{m}^{-2}\cdot\text{y}^{-1}$ per gram $\text{CH}_4\text{-C}\cdot\text{m}^{-2}\cdot\text{y}^{-1}$ for 20 y and 100 y, respectively. This implies that a continuous emission of 1 g $\text{CH}_4\text{-C}\cdot\text{m}^{-2}\cdot\text{y}^{-1}$ and uptake of 31.3 g $\text{CO}_2\text{-C}\cdot\text{m}^{-2}\cdot\text{y}^{-1}$ would have a positive cumulative RF (warming) for the first 20 y and a negative cumulative RF (cooling) after that. Sites that fall on the right side of the equilibrium lines have a positive radiative budget and those on the left side have a negative radiative budget for the specified 20-y or 100-y timeframe (Fig. 1B). Under the current climate, 59% of arctic and boreal sites' and 60% of temperate sites' observations have a positive radiative balance compared with both 20-y and 100-y equilibrium lines. All but one of the forested wetlands [arctic/boreal (AB)5, AB7, temperate (T)9, and T11] currently have a negative net radiative balance owing to their considerable CO_2 uptake and relatively low CH_4 emissions (Fig. 1B and Fig. S1). Sites located between the two lines have a positive or negative radiative budget, depending on the time span of the analysis (e.g., AB9, AB4, and T8, Fig. 1B).

Changes in the water level in wetlands substantially alter the ratio of CH_4 and CO_2 fluxes. Recent warming and drying in the Arctic has led to increased CO_2 losses from the soil, in some cases switching arctic regions from a long-term carbon sink to a carbon source (36). In other cases, the drying of arctic and boreal wetlands reduces CH_4 emission without generating larger CO_2 emissions, owing to the compensation between accelerated decomposition of organic matter and an increase in net primary productivity (NPP) (37–39). As an example of management impacts, data show that the CO_2 and CH_4 emissions of the site AB3a dropped toward a near zero net radiative budget one year

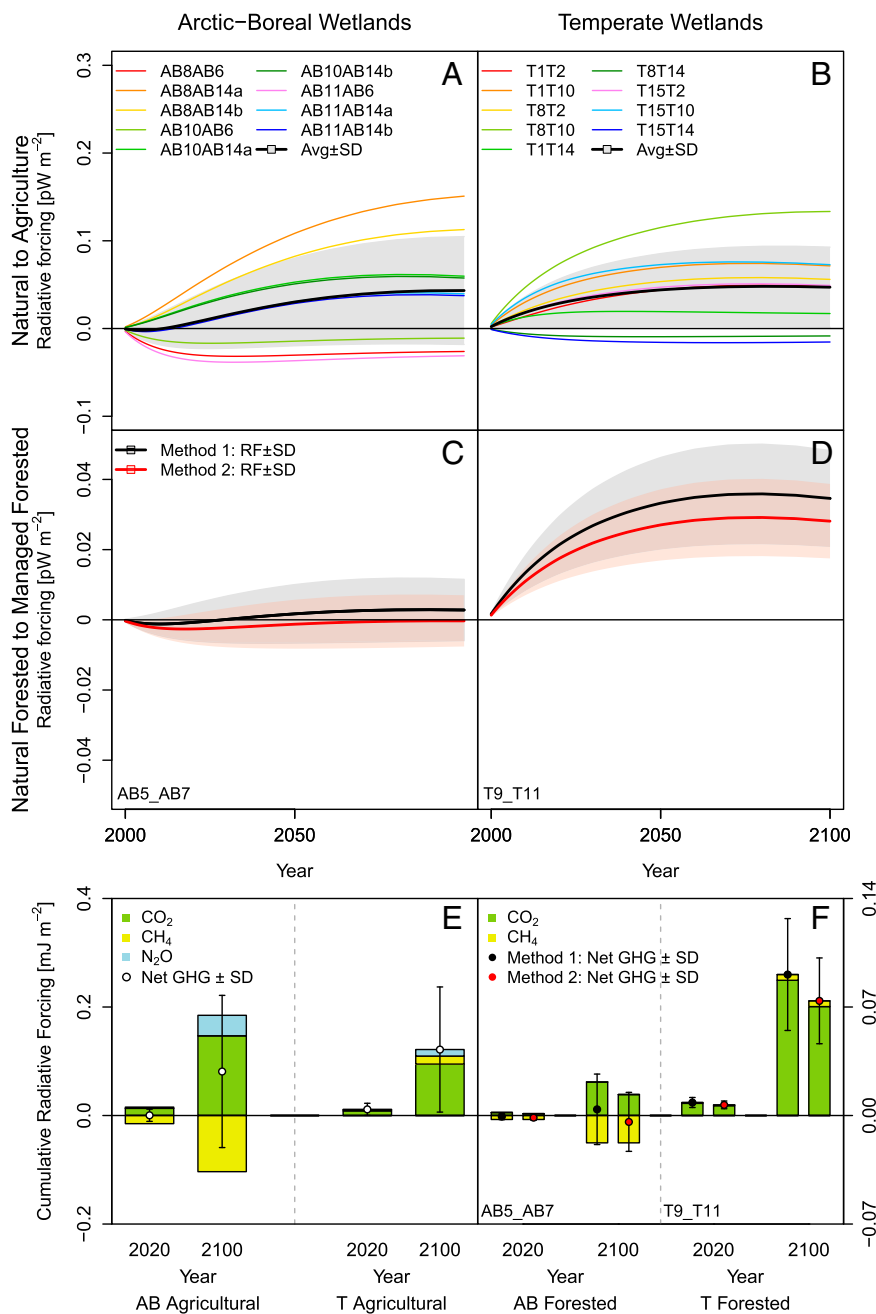


Fig. 2. Trends of radiative forcing (RF, period 2000–2100) for paired sites and ecosystem types. (A and B) Net RF for CO₂, CH₄, and N₂O in natural wetlands converted to agricultural land. (C and D) Net RF for the conversion of natural forested wetland to managed forests (AB5→AB7 and T9→T11). For each of the two pairs an uncertainty analysis on the effect of the harvest rate is presented. (E and F) Cumulative RF of individual gases at 20 y and 100 y for all site pairs, with their net RF (circles ± SD). The forcing units refer to the mean global impact of 1 m² of wetland area (*SI Text, Radiative Forcing Calculations*). Site IDs can be found in *SI Text, Site Analysis* and *Tables S1* and *S2*.

reported in the *IPCC Wetland Supplement* for natural and managed wetlands (48).

Results for the boreal site pair (AB5→AB7) show that the confidence intervals cross the x axis and therefore the ultimate sign of the RF depends on the harvest rate. In addition, with both methods used for the calculation of NPP, at average harvest rates the RF is not statistically different from zero (Fig. 2C). In contrast, for the temperate site pair (T9→T11) RF is positive, independently of the management intensity and of the applied methodology (Fig. 2D). Our analysis demonstrates that, to assess the RF of wetland management, both CH₄ fluxes and the

concomitant changes in CO₂ emissions have to be accounted for. This is especially true at the decadal timescales for boreal wetlands converted to forest or agricultural land (Fig. 2E and F).

Conclusions

The recent availability of simultaneous and continuous ecosystem observations of CH₄ and CO₂ fluxes in wetlands provides fundamental insights into the climate footprint of these ecosystems to support the development of sustainable mitigation strategies based on ecosystem management. Careful accounting of both CO₂ and CH₄ fluxes (and N₂O fluxes where significant) is essential for an

accurate calculation of the climate impact of wetlands. We also stress the importance of direct and quasi-continuous chamber or eddy covariance flux measurements over annual timescales for the observation of ecosystem responses to environmental drivers and management (e.g., flooding, drainage, and land use change) that may be missed with intermittent manual chamber measurements.

The net GHG budget of these ecosystems is spatially and temporally variable in sign and magnitude due to the generally opposite direction of CH₄ (emission) and CO₂ (uptake) exchange and, therefore, can be easily altered by both natural and anthropogenic perturbations (*SI Text, Site Analysis* and *Table S3*). Management and land use conversions in particular play a critical role in determining the future GHG balance of these ecosystems. Our results prove that management intensity strongly influences the net climate footprint of wetlands and in particular the conversion of natural ecosystems to agricultural land ultimately leads to strong positive RF. These considerations suggest that future releases of GHG inventories based on IPCC guidelines for wetlands should indeed address the relationship between the fluxes of CH₄ and CO₂, the management intensity, and the land use/land cover change on the net GHG balance as well as on the RF of these complex ecosystems.

Materials and Methods

This study is based on measurements of net ecosystem exchange of CO₂ and CH₄ trace gas exchange performed with eddy covariance and/or chamber methods (*SI Text, Site Analysis* and *Tables S1* and *S2*). Most of the included study sites are part of FLUXNET, an international network of sites where energy and GHG fluxes are continuously monitored with a standardized methodology (49). The RF due to wetlands management was calculated for CO₂, CH₄, and, where significant (agricultural sites AB6, AB14a,b, T10, and T14), N₂O fluxes, using a sustained pulse–response model (27). Annual concentration pulses were derived from the flux differences between pristine wetlands, taken as reference, and wetlands converted to either cropland or forests.

Natural-managed site pairs were defined for all possible combinations of similar ecosystem types with available annual CO₂ and CH₄ budgets within each climatic or management-related category (arctic/boreal or temperate regions, cropland or forest; *SI Text, Radiative Forcing Calculations* and *Table S6*). These site pairs were selected to represent plausible and representative wetland conversions, and thus part of the sites were excluded from this analysis (e.g., rice fields). In the simple pulse–response RF model used here the perturbations to the tropospheric concentrations of CO₂, CH₄, and N₂O

were derived by integrating the effect of a series of consecutive annual mass pulses that correspond to the mean annual balances of these gases (27) (*SI Text, Radiative Forcing Calculations*). Different radiative efficiencies and atmospheric residence times of CO₂, CH₄, and N₂O were taken into account, as well as the annual variation of their background concentrations. RF was calculated for a 100-y period starting from 2000, assuming that the background concentrations increase as in the A2 scenario of the Special Report on Emissions Scenarios (SRES). The RF methodology is described in detail in *SI Text, Radiative Forcing Calculations*. The data reported in this paper are tabulated in *SI Text* and part is archived in the FLUXNET database and/or published in peer-review articles as shown in *SI Text* references.

ACKNOWLEDGMENTS. The authors gratefully acknowledge support from JRC-IES-H07 ClimEcos project (995) and FP7 ICE-ARC (603887-2). Data collection and analysis were supported by the following grants: National Science Foundation (NSF) Project DEB-0845166 (T11); Natural Sciences and Engineering Research Council of Canada and the Canadian Foundation for Climate and Atmospheric Sciences Grants 313372 (AB9) and 246386-01 (AB5 and T1); Early Career Scheme, Research Grants Council of the Hong Kong Special Administrative Region, China, Project CUHK 458913 (T1); NSF Proposal 1204263 (AB12); Irish Environmental Protection Agency's STRIVE (Science, Research, Technology and Innovation for the Environment) programme (project CELTICFLUX; 2001-CD-C2-M1) and the European Union (EU) 6th Framework Project CarboEurope-IP (505572), NitroEurope-IP (017841) (T7), and 017841/2 (T14); Helmholtz Association [Helmholtz Young Investigator Group, Grant VH-NG-821, and the Helmholtz Climate Initiative "Regional Climate Change" (Regionale Klimaänderungen REKLIM)] (AB4); the Nordic Centre of Excellence, DEFROST (Impact of a changing cryosphere - Depicting ecosystem-climate feedbacks from permafrost, snow and ice), under the Nordic Top-Level Research Initiative, Academy of Finland Centre of Excellence program (Project 1118615) and the Academy of Finland ICOS (Integrated Carbon Observation Systems) Projects (263149, 281255, and 281250) (AB7, AB8, and AB14a,b); Greenland Ecosystem Monitoring Programme; the Danish Energy Agency and the Nordic Center of Excellence DEFROST (AB1b and AB13); the Nordic Center of Excellence DEFROST and EU-GREENCYCLES (512464) (AB11) and the Swedish Research Councils FORMAS (T15); Dutch–Russian Scientific Cooperation Grant 047.017.037 (Nederlandse Organisatie voor Wetenschappelijk Onderzoek NWO); Darwin Center Grant 142.16.3051 and Terrestrial Carbon Observation System TCOS-Siberia (EVK2-CT-2001-00131) (AB2); TCOS-Siberia European Union Project 2002–2004 (EU Project N EVK2-2001-00143) (AB3); NSF Grant ATM-9006327 (T6); The Finnish Funding Agency for Technology and Innovation (Tekes); University of Eastern Finland Grant 70008/08 (AB6); CarboEurope-IP (GOCE-CT-2003-505572); Dutch National Research Programme Climate Changes Spatial Planning (ME2 project) and the province of North Holland (T10); Russian Science Foundation, Grant 14-27-00065 (T12); and Academy of Finland (125238) (AB10).

- Gorham E (1991) Northern peatlands: Role in the carbon cycle and probable responses to climatic warming. *Ecol Appl* 1(2):182–195.
- Frolking S, Roulet NT (2007) Holocene radiative forcing impact of northern peatland carbon accumulation and methane emissions. *Glob Change Biol* 13:1079–1088.
- Ciais P, et al. (2013) Carbon and other biogeochemical cycles. *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 TF, et al. (Cambridge Univ Press, Cambridge, UK), pp 505–510.
- Bousquet P, et al. (2006) Contribution of anthropogenic and natural sources to atmospheric methane variability. *Nature* 443(7110):439–443.
- Nisbet EG, Dlugokencky EJ, Bousquet P (2014) Atmospheric science. Methane on the rise—again. *Science* 343(6170):493–495.
- Limpens J, et al. (2008) Peatlands and the carbon cycle: From local processes to global implications – a synthesis. *Biogeosciences* 5:1475–1491.
- Yu ZC (2012) Northern peatland carbon stocks and dynamics: A review. *Biogeosciences* 9:4071–4085.
- Sturtevant C, Oechel WC (2013) Spatial variation in landscape-level CO₂ and CH₄ fluxes from arctic coastal tundra: Influence from vegetation, wetness, and the thaw lake cycle. *Glob Change Biol* 19(9):2853–2866.
- Zona D, et al. (2009) Methane fluxes during the initiation of a large-scale water table manipulation experiment in the Alaskan arctic tundra. *Global Biogeochem Cycles* 23(2):GB2013.
- Minkinen K, Korhonen R, Savolainen I, Laine J (2002) Carbon balance and radiative forcing of Finnish peatlands 1900–2100 – the impact of forestry drainage. *Glob Change Biol* 8:785–799.
- Drösler M, Freibauer A, Christensen TR, Friborg T (2008) Observation and status of peatland greenhouse gas emission in Europe. *The Continental-Scale Greenhouse Gas Balance of Europe, Ecological Studies*, eds Dolman H, Valentini R, Freibauer A (Springer, New York), Vol 203, pp 237–255.
- Harazono Y, et al. (2006) Temporal and spatial differences of methane flux at arctic tundra in Alaska. *Memoirs of National Institute of Polar Research* 59(Special Issue): 79–95.
- Matthews E (2000) Wetlands. *Atmospheric Methane: Its Role in the Global Environment*, ed Khalil MAK (Springer, Berlin), pp 202–233.
- Vourlitis GL, Oechel WC (1997) The role of northern ecosystems in the global methane budget. *Global Change and Arctic Terrestrial Ecosystem*, Ecological Studies, eds Oechel WC, et al. (Springer, New York), Vol 124, pp 266–289.
- Moore TR, Knowles R (1990) CH₄ emissions from fen, bog and swamp peatlands in Quebec. *Biogeochemistry* 11:45–61.
- Whalen SC, Reeburgh WS (1992) Interannual variations in tundra CH₄ emissions: A four-year time series at fixed sites. *Global Biogeochem Cycles* 6(2):139–159.
- Dise NB (1993) Methane emissions from Minnesota peatlands: Spatial and seasonal variability. *Global Biogeochem Cycles* 7(1):123–142.
- Kip N, et al. (2010) Global prevalence of methane oxidation by symbiotic bacteria in peat-moss ecosystems. *Nat Geosci* 3:617–621.
- Kellner E, Waddington JM, Price JC (2005) Dynamics of biogenic gas bubbles in peat: Potential effects on water storage and peat deformation. *Water Resour Res* 41:W08417.
- Öquist MG, Svensson BH (2001) Vascular plants as regulators of CH₄ emissions from subarctic mire ecosystem. *J Geophys Res* 107(D21):4580.
- Lawrence DM, Slater A, Romanovsky VE, Nicolsky DJ (2008) Sensitivity of a model projection of near-surface permafrost degradation to soil column depth and representation of soil organic matter. *J Geophys Res Earth Surface* 113(F2):000883.
- Lupascu M, et al. (2014) High Arctic wetting reduces permafrost carbon feedbacks to climate warming. *Nature Climate Change* 4:51–55.
- Anthony KM, et al. (2014) A shift of thermokarst lakes from carbon sources to sinks during the Holocene epoch. *Nature* 511(7510):452–456.
- Keuper F, et al. (2012) A frozen feast: Thawing permafrost increases plant-available nitrogen in subarctic peatlands. *Glob Change Biol* 18:1998–2007.
- Nykanen H, Alm J, Silvola J, Tolonen JK, Martikainen PJ (1998) Methane fluxes on boreal peatlands of different fertility and the effect of long term experimental lowering of the water table on flux rates. *Global Biogeochem Cycles* 12(1):53–69.
- Frolking S, et al. (2011) Peatlands in the Earth's 21st century climate system. *Environ Rev* 19:371–396.
- Lohila A, et al. (2010) Forestation of boreal peatlands: Impacts of changing albedo and greenhouse gas fluxes on radiative forcing. *J Geophys Res* 115:G04011.
- Roulet NT (2000) Peatlands, carbon storage, greenhouse gases, and the Kyoto protocol: Prospects and significance for Canada. *Wetlands* 20(4):605–615.

