The Arctic Carbon Cycle and Its Response to Changing Climate

Lori Bruhwiler 1 · Frans-Jan W. Parmentier 2,3 · Patrick Crill 4 · Mark Leonard 1,5 · Paul I. Palmer 6

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Abstract
Purpose of Review The Arctic has experienced the most rapid change in climate of anywhere on Earth, and these changes are certain to drive changes in the carbon budget of the Arctic as vegetation changes, soils warm, fires become more frequent, and wetlands evolve as permafrost thaws. In this study, we review the extensive evidence for Arctic climate change and effects on the carbon cycle. In addition, we re-evaluate some of the observational evidence for changing Arctic carbon budgets.
Recent Findings Observations suggest a more active CO2 cycle in high northern latitude ecosystems. Evidence points to increased uptake by boreal forests and Arctic ecosystems, as well as increasing respiration, especially in autumn. However, there is currently no strong evidence of increased CH4 emissions.
Summary Long-term observations using both bottom-up (e.g., flux) and top-down (atmospheric abundance) approaches are essential for understanding changing carbon cycle budgets. Consideration of atmospheric transport is critical for interpretation of top-down observations of atmospheric carbon.

Keywords Arctic · Climate change · Carbon cycle · Permafrost · Methane

Introduction—a Review of Arctic Change and the Carbon Cycle

Arctic Climate Change

In recent decades, the Arctic mean annual surface temperature has increased at over twice the rate of the global average [1, 2]. This polar amplification of surface air temperature is due to a combination of surface albedo feedbacks...

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Lori Bruhwiler
lori.bruhwiler@noaa.gov

1 NOAA Global Monitoring Laboratory, Boulder, CO, USA
2 Department of Geosciences, University of Oslo, Oslo, Norway
3 Department of Physical Geography and Ecosystem Science, Lund University, Lund, Sweden
4 Department of Geological Sciences and Bolin Centre for Climate Research, Stockholm University, Stockholm, Sweden
5 Cooperative Institute for Research in Environmental Sciences, University of Colorado, Boulder, CO, USA
6 School of GeoSciences, University of Edinburgh, Edinburgh, UK
reductions are unprecedented since the fourteenth century [16]; Notz and Stroeve [17] directly linked these changes to anthropogenic carbon emissions. The Arctic Ocean may become ice-free during summer months by the middle of the twenty-first century unless anthropogenic emissions are significantly decreased [18]. Lack of sea ice results in increased absorption of solar radiation by surface ocean waters and, combined with transport of heat from lower latitudes, Arctic Ocean heat content is increasing and summer mixed layer temperatures are increasing by 0.5 °C/decade [1, 19, 20].

Ocean heat content is increasing and summer mixed layer significantly decreased [18]. Lack of sea ice results in increased twenty-first century unless anthropogenic emissions are significant.
satellite observations of surface reflectance of near-infrared light, which is reflected by vegetation, and red light, which is absorbed by vegetation. This difference is known as the normalized difference vegetation index (NDVI). Maximum summer values of NDVI have been increasing across the Arctic (“greening”, [51]), especially for 1982–1998, likely due to longer growing seasons, warmer temperatures, and a more intense hydrological cycle. From 1999 to 2015, some regions exhibit negative (“browning”) trends, which also shows up in NDVI integrated over the growing season. Although peak summertime productivity has been increasing, during other periods of the growing season, increases are not as prominent and in recent years do not occur for the entire Arctic. NDVI changes could be interpreted as an expansion of woody vegetation, such as shrubs, and disturbance in the case of browning. However, Myers-Smith [52] highlighted some of the complexities in interpretation of vegetation index data. Standing water, snow cover, and soil moisture can influence surface reflectance of vegetated land. Vegetation indices can also be nonlinear with vegetation biomass so that they become more or less sensitive to changes over time with vegetation changes. Myers-Smith et al. [52] also highlighted the fact that spatial heterogeneity of Arctic vegetation and lack of coverage of in situ data make it difficult to compare changes in satellite vegetation indices directly with ground observations.

Biomass burning is an important disturbance in boreal ecosystems, and more frequently in tundra regions. Large amounts of carbon can be quickly released into the atmosphere from both above-ground biomass and soil organic matter. Over 1997–2016, van der Werf et al. [53] found emissions of CO$_2$ from fires to average 185 TgC/year with minimum and maximum yearly emissions of 57 and 408 TgC/year. Emissions of CH$_4$ are a small fraction of this amount since the CO$_2$ emission factor is 250 times larger than that of CH$_4$ for boreal forests and 81 times larger for peat fires which tend to be more intense hydrological cycle. From 1999 to 2015; however, a trend towards an increasing area burned since 2006 was noted. Ponomarev et al. [62] found an increasing number of fires and burned area over recent decades for a transect in Siberia. However, there is large interannual variability in burned area, so longer records are needed to obtain clarity on trends. Satellite burned area products have been available since the late 1990s, and small but not statistically significant increases in area burned were found by Andela et al. [63]. Lightning is the most common ignition source for high-latitude fires, and Veraverbeke et al. [64] showed evidence for increasing lightning ignition between 1975 and 2015 for the Northwest Territories and Interior Alaska.

The Future of Arctic Climate

Past emissions and long lag times in ocean response mean that changes in Arctic climate will continue at least into the mid-twenty-first century [23], longer if no climate mitigation occurs. Surface temperatures will continue to increase at about twice the rate as lower latitudes, and depending on future emissions, they could rise at another 4–5 °C above late 1990s’ temperatures by the mid-twenty-first century. For high-emission scenarios, climate models (CMIP6) predict ice-free summers in the Arctic Ocean after the mid-twenty-first century [65]. By the middle of the century, snow cover duration is expected to decrease by 10–20% from present-day [23]. Earlier snowmelt will have implications for summer soil moisture and fire ignition. Glaciers will continue to melt leading to increases in sea level rise, and more coastal erosion exacerbated by permafrost thaw and the loss of protective landfast sea ice [66]. The hydrologic cycle is expected to continue to intensify with 30–50% increases in winter precipitation over the ocean and increasing runoff from land. The CMIP5 climate model ensemble also suggests that extreme precipitation events will become more common as variability of precipitation increases due to changes in moisture transport from mid-latitudes, possibly linked to changes in modes of variability such as the Arctic Oscillation, and the Pacific Decadal Oscillation [67]. At the same time, more precipitation may fall as rain rather than snow with further implications for hydrology [68]. Evapotranspiration is expected to increase. For the worst-case high-emission scenario (e.g., Representative Concentration Pathway leading to a radiative
forcing of 8.5 W m\(^{-2}\) (RCP8.5) [69]), CMIP5 models show that Arctic temperatures could soar above late-twentieth-century levels by 13 °C in winter and 5 °C in summer [70].

In response to projected increases in Arctic air temperature, the CMIP5 models show significant changes to the Arctic permafrost distribution [23]. For RCP4.5, areas where discontinuous permafrost currently exists will disappear. For the highest emission scenario (RCP8.5), permafrost may only remain in the top 3 m of soils in the northernmost regions and at highest elevations. McGuire et al. [71] analyzed an ensemble of models with relatively detailed representations of permafrost and found that the model average suggests that 90% of near-surface (<3 m) permafrost will be lost by 2300 for RCP8.5. For RCP4.5, the models predict an average loss of 29%. Models suggest that much of the permafrost area loss will occur by 2100, but they do not include the effects of abrupt thaw and fires on permafrost, both processes that could lead to more widespread and rapid permafrost loss. Recent model simulations that include abrupt thaw suggest a three to twofold increase in the amount of carbon that may be affected, depending on emission scenario [72].

Fire and other disturbances are expected to increase in boreal regions and Arctic tundra [73, 74]. For RCP6.0, Young et al. [74] found that the area of tundra burned in Alaska could double. Walter Anthony et al. [75] project an increase in thaw lake area, an indicator of abrupt thaw, of over 50% for the high-emission RCP8.5 scenario. Decreases in snow cover and changes in drainage due to permafrost thaw can further dry Arctic ecosystems, leading to increased burning and changes in vegetation.

Vegetation in the Arctic is expected to change significantly in the future. A statistical approach associating climate and vegetation types and considering two distinct emission trajectories found that trees and shrubs are projected to cover 24–52% of present-day tundra area by 2050, replacing current vegetation communities [76]. Expansion of woody vegetation into tundra regions may have additional effects that will feed back on climate through more evaportranspiration, albedo changes, and impacts on soil temperature [77]. Pearson et al. [76] argue that these effects could serve as positive feedbacks on regional Arctic climate.

**Effects of Changing Climate on the Carbon Cycle**

Arctic climate change will have important effects on the carbon cycle. Figure 1 summarizes schematically climate change and its effects on the carbon cycle. Currently, the Arctic Ocean is thought to be a small net carbon sink of 0.1–0.2 PgC/year [23]. Increased open water should result in increased CO\(_2\) uptake by the Arctic Ocean both due to physical gas exchange and increased marine productivity [78]. Freshwater input from rivers and melting ice could, however, change this picture. Increased freshwater could increase thermohaline stability inhibiting transfer of carbon from surface to deep waters, and nutrient loss from stratified surface waters could decrease productivity, thereby limiting the biological sink. Increased inputs of freshwater can reduce the buffering capacity of the Arctic Ocean and limit increased uptake of CO\(_2\) by delivering carbon to surface ocean waters. Export of carbon and nutrients from land to the Arctic Ocean can also increase productivity, especially in coastal regions [79].

Warming of ocean waters could lead to enhanced CH\(_4\) emissions from subsurface permafrost and possibly destabilized hydrates. Shakhova et al. [80] estimated that ~ 8 TgCH\(_4\)/year is being emitted to the atmosphere from submerged hydrates in the subsea permafrost of the Laptev sea. However, emissions this large are not supported by atmospheric observations of CH\(_4\) abundance. Berchet et al. [81] found that emissions were likely to be less than half of that proposed by Shakhova et al. [80] and that atmospheric observations were more consistent with terrestrial or marine biosphere emissions rather than methane hydrates. Shipborne eddy covariance observations suggest ~ 3 TgCH\(_4\)/year for the Eastern Siberian Arctic Shelf [82], in agreement with Berchet et al. [81].

On land, longer growing seasons and higher temperatures are expected to drive increased productivity, and greening trends seen in NDVI data are consistent with this. However, many factors add to the complexity of how the terrestrial Arctic carbon cycle will change. Warming soils could drive an increase in respiration that partially offsets increases in productivity [83]. Long-term eddy covariance studies show that opposing fluxes of photosynthesis and respiration mostly cancel each other out, and changes in the net carbon balance are small [84, 85]. Increases in precipitation and earlier snowmelt could affect soil moisture over the growing season, benefitting some plant communities while disadvantaging others. Expansion of woody plants into tundra regions will

**Fig. 1** Schematic illustrating Arctic climate change and its effects on the carbon cycle. Purple labels indicate carbon cycle responses. (Figure produced by S. Masais, NOAA Global Monitoring Laboratory)
increase evapotranspiration [76], while thawing of permafrost could initially increase inundated areas due to subsidence leading to expanded methane-producing environments. In areas of discontinuous permafrost, drainage, encroachment of vegetation, and filling of shallower lakes will all have implications for carbon exchange [35, 86]. With drier conditions and possibly increased ignition by lightning, fires could increase in the Arctic releasing built up carbon from organic-rich soils [57].

The amounts of CO2 and CH4 emitted to atmosphere as permafrost thaws depend on the decomposability of organic matter stored in the soil and whether the decomposition occurs aerobically or anaerobically. Aerobic and anaerobic conditions are dependent on soil hydrology, which is susceptible to change as permafrost thaws [87]. As permafrost thaws, carbon release will initially increase rapidly as easily decomposed material is broken down leaving less labile carbon with slower release rates. Rates of carbon release are dependent on hydrological status, and field studies have shown considerable spatial variability in this over relatively small scales as shown by Chang et al. [38] who also pointed out that uncertainty in temperature and precipitation driving data could cause biases in CO2 and CH4 fluxes that are comparable to variability due to landscape heterogeneity. Methane is consumed in dry soil and oxic water columns [88, 89], and this must also be accounted for. In organic-rich, inundated environments, anaerobic respiration dominates, a slow process in comparison to aerobic respiration that leads to higher CH4 emissions. This is important because of the larger radiative impact of CH4 with a 100-year global warming potential that is about 25 times greater than CO2 on a per mass basis [90]. Incubation studies show that aerobic respiration releases about 6 times the amount of carbon per year as anaerobic respiration ([42], see Fig. 2b). Abrupt permafrost thaw can lead to both formation and drainage of wetlands and small lakes, and the balance between lake/wetland formation and drainage determines whether aerobic or anaerobic decomposition dominates. The largest carbon emissions from permafrost regions could occur after present-day continuous permafrost has transitioned to discontinuous permafrost. Schuur et al. [42] estimated that 5–15% of permafrost could thaw by 2100. Assuming that 10% thaws over the next century, then 130–160 PgC could be vulnerable to thaw, although Turetsky et al. [91] project that 200 PgC could be vulnerable by 2300 with another 60–100 PgC vulnerable due to abrupt thaw. Models that include permafrost predict lower amounts of vulnerable carbon, ~30–115 PgC thawing by 2100 (e.g., [92]) likely because they do not include landscape changes such as those due to abrupt thaw and thermokarst formation. Schuur et al. [42] estimate that, assuming a constant release rate, 0.9 ± 0.5 PgC/year could be emitted into the atmosphere over the next century. If 2.3% of this is emitted as CH4 (e.g., [93]) then 28 TgCH4/year could be emitted as CH4. However, release of permafrost carbon will not be evenly distributed over the next century; rather, it will slowly increase with time into the twenty-second century unless CO2 emissions are significantly mitigated.

We have thus far documented the changing Arctic climate and its effect on the ecosystem and carbon emissions. Consideration of permafrost emissions aside, the current climate changes should have profound effects on carbon emissions in the Arctic. We therefore turn to the question of what changes in Arctic carbon emissions have been observed and whether they are attributable to specific processes.

### Observational Evidence for Carbon Cycle Changes at High Northern Latitudes

#### Current Understanding of Arctic Carbon Cycle Changes

Some analyses of atmospheric observations have found changes in high-latitude CO2 fluxes. Graven et al. [94] used surface monitoring observations at Barrow, Alaska, and Mauna Loa, Hawaii, along with aircraft campaign observations to conclude that significant changes in the annual cycle of atmospheric CO2 (~50% amplitude increase) occurred between 1958 and 1961 (campaigns associated with the International Geophysical Year) and 2009–2011 for latitudes north of 45°N. They attributed these changes to an increase in CO2 uptake of 30–60% mainly by boreal forests. Graven et al. [94] also found that the CMIP 5 models were unable to produce this large of an increase in terrestrial productivity. These findings were later confirmed by the annual cycle analysis of Barlow et al. [95] and similar conclusions were also reached by Forkel et al. [96]. Barlow et al. [95] showed that changes in the seasonal amplitude of atmospheric CO2 at Barrow from 1973 to 2015 were strongly correlated with trends in net carbon uptake during spring and summer months but had only a weak relationship with the net release of CO2 in autumn and winter months. They also showed that the start and end of the carbon uptake period have been getting earlier each year, but the length of the uptake period has remained comparatively constant, likely due to increased respiration. Collectively, these observations are consistent with northern latitude ecosystems progressively taking up more carbon during spring and summer months.

Atmospheric observations have shown that respiration from Arctic soils may also be increasing, at least for the North Slope region of Alaska. Commane et al. [98] used high-frequency observations from the Barrow Observatory to show that regional tundra emissions during the early cold season rose by 73% over 41 years, a response not captured by CMIP5 models. Further, they estimated that during 2012–2014, net emissions from tundra in Alaska dominated a small
net uptake by boreal forest ecosystems, making Alaska a net carbon source during these years. Consistent with these results, Jeong et al. [99] used the long-term Barrow record of atmospheric CO2 and a carbon balance model to show that the carbon residence time in tundra ecosystems on the North Slope of Alaska has decreased by ~13%. They also proposed that increasing cold season soil carbon emissions could exceed warm season uptake making these ecosystems a net source of carbon to the atmosphere. Although long-term atmospheric records of CO2 seem to support changing CO2 fluxes, it is interesting that they do not yet indicate that CH4 emissions are increasing at least for the region near the Barrow Observatory on the North Slope of Alaska [100]. This can be explained if lake drainage and drying of wetlands reduced the area of methane emitting landforms.

Insights from Global Atmospheric Observations

Globally distributed, long-term monitoring observations of CO2 and CH4 in the atmosphere can provide information about the spatial and temporal distribution of fluxes. Figure 2 shows observed zonal average growth rate anomaly for both gases. Growth rates vary interannually with latitude and time, providing clues about the mechanisms of changing fluxes. However, atmospheric transport of lower latitude emissions must be taken into account to correctly interpret this information. Dlugokencky et al. [101] proposed that spatial gradient information like that shown in Fig. 2 could be used as a sensitive indicator of changing Arctic CH4 emissions, specifically by calculating the difference in measured mole fraction between zonally and annually averaged sites at northern (53–90° N) and southern (53–90° S) latitudes. This interpretation of the CH4 observations could be possible in part because the high latitudes of the Southern Hemisphere have no known significant sources or sinks of CH4 except for photochemical loss in the atmosphere which is relatively small at polar latitudes. Dlugokencky et al. [101] referred to this difference as the “interpolar difference” (IPD). They noted a decrease between the IPD prior to 1991 and afterwards (Fig. 3) and attributed this difference to the collapse of the Soviet Union and subsequent reduction in oil and gas leaks due to infrastructure investments by the Russian gas industry. Dlugokencky et al. [102] concluded that the existing long-term measurement network could detect changes in Arctic emissions of at least 10 TgCH4/year.

Implicit in the IPD is the assumption that signals from changes in emissions and sinks outside of the Arctic are transported equally to the polar latitudes of both hemispheres within the same calendar year (the IPD is an annually averaged quantity). Tropospheric interhemispheric transit times

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Fig. 2 Zonal average growth rate anomalies of CO2 (top, ppm/year) and CH4 (bottom, ppb/year) from the NOAA Global Greenhouse Gas Reference network. Warm colors represent higher than average atmospheric growth and cooler colors show slower than average atmospheric growth. Growth rate anomalies were calculated using observations from the NOAA Global Monitoring Laboratory’s Greenhouse Gas Reference Network (https://www.esrl.noaa.gov/gmd/ccgg/)

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are about 1 year \[103\] so that the IPD cannot capture transport of low-latitude emissions to both polar regions within a year. Dimdore-Miles et al. \[104\] showed that relaxing the assumption of symmetric hemispheric transport results in significant interannual variability in the IPD that is not exclusively attributable to Arctic emissions.

We further explore the sensitivity of the IPD to changes in Arctic emissions using atmospheric transport modeling. It is important to force simulations with emissions that result in a realistic north-south gradient. For this reason, we use estimates of CH\(_4\) emissions from an atmospheric inversion (see the “Bottom-up Approaches” section) because the magnitude and spatiotemporal distribution of CH\(_4\) emissions are uncertain. In essence, emission estimates from inverse models have been adjusted in order to agree optimally with atmospheric observations. This is shown in the top panel of Fig. 4, where there is reasonable agreement between the observed and the IPD simulated using emissions estimated by the inversion. The bottom panel of Fig. 4 shows a comparison simulated annual average differences from the South Pole observations for each Arctic network site. Two sets of simulations are shown, one using estimated emissions that have been adjusted to agree with observations by using an atmospheric inversion model and another using a constant repeating seasonal cycle of emissions north of 60° N constructed by averaging the estimated emissions. This figure shows that interannual variability in the IPD is dominated by atmospheric transport, not emissions. Furthermore, the long-term trend towards increasing IPD after 2005 is also dominated by atmospheric transport and likely is a reflection of increasing CH\(_4\) emissions from lower latitudes. In addition, some sites have a lot more variability than others, and there is a gradient between sites at lower and higher latitudes. Sites such as Iceland and those on the Aleutian Islands often see air from the North Pacific or Atlantic during the warm season and therefore do not always capture Arctic signals. Clearly, atmospheric transport complicates any attempt to directly link atmospheric concentration with emissions and must be accurately taken into account.

**Bottom-up Versus Top-down Estimates of Arctic Carbon Budgets**

Techniques for estimating carbon budgets can be classified as either “bottom-up” or “top-down” approaches. Bottom-up approaches (the “Bottom-up Approaches” section) make use of measurements or process-based models that are upscaled regionally. Examples include upscaling of the chamber and eddy flux observations to pan-Arctic scales (e.g., Ueyama et al. \[106, 107\]) or global scales \[108\]. Process models of emissions are also a bottom-up approach since they model specific processes, are evaluated against flux observations, and used to predict regional fluxes (e.g., \[109\]). In contrast, top-down approaches use atmospheric observations to infer fluxes. Atmospheric observations reflect integrated contributions from fluxes encountered by air parcels as they are transported to measurement sites, including contributions from lower latitudes. These signals must be decomposed spatially and temporally to estimate fluxes at desired scales, generally by using an atmospheric transport model with realistic meteorology (“Atmospheric Inversions” section).

A perennial problem is disagreement between bottom-up and top-down estimates of Arctic carbon budgets. The AMAP Assessment of Arctic Methane (\[110\], Chapter 6) found that published estimates of emissions for various natural sources totaled over 70 TgCH\(_4\)/year, almost three times top-down estimates that included both natural and anthropogenic Arctic emissions. At the global scale, Saunois et al. \[111\] highlighted
large discrepancies between estimates from bottom-up and top-down approaches. For example, for the category of “other natural emissions” (inland waters, geological emissions, oceans, termites, wild animals, and permafrost) bottom-up global estimates are 222 TgCH₄/year (range 143–306 TgCH₄/year), while top-down estimates based on atmospheric observations are almost an order of magnitude smaller, 37 TgCH₄/year (21–50 TgCH₄/year)—an astounding difference! Saunois et al. [111] discussed a number of possible approaches that could lead to better agreement between top-down and bottom-up CH₄ emission estimates, including increased spatial and temporal coverage of flux observations and their use for evaluation of models of natural CH₄ fluxes, improving understanding of uncertainties due to atmospheric chemical destruction of CH₄, more frequent updates of anthropogenic emission inventories and further development of wetland and lake datasets. They also point out that top-down estimates could be improved by incorporating stable isotope observations, for example, ¹³CH₄ which can help constrain the relative contributions from microbial and thermogenic emissions. Space-based column retrievals could also provide better spatial and temporal coverage although good quality retrievals can be relatively sparse at high latitudes due to solar geometry and long atmospheric path lengths. Uncertainty in atmospheric transport is an additional source of disagreement between bottom-up and top-down approaches, and Saunois et al. [111] advocate for the expanded use of vertical profile measurements to evaluate transport uncertainty.

**Bottom-up Approaches**

Bottom-up estimates of the Arctic carbon budget are typically achieved by upscaling observations or by simulating the carbon cycle with process models. These approaches have
advantages and limitations. Process models can provide a large-scale view across decades but are limited by the accuracy of the climatic forcing and their representation of biogeochemical processes. Models need detailed spatial information about soil and vegetation that often is not available. Observations with flux chambers and eddy covariance towers are detailed snapshots of the carbon exchange of Arctic landscapes but severely restricted in time due to data outages or the short duration of field campaigns. Spatial coverage is also limited, and biases in pan-Arctic budget estimates can result from historic decisions to focus resources on establishing the importance and magnitude of the most significant carbon fluxes. Infrastructure limitations range from access or power availability, to meeting theoretical assumptions critical to the measurement; for example, the need to place flux towers in uniform terrain due to the complexities of atmospheric boundary layer dynamics. For CH₄, flux observations may be made near-broad, uniform wetlands with fewer nearby ecologically diverse or drier upland environments, leading to a bias towards larger overall emissions in upscaled flux products [112].

CH₄ emissions from lakes are an interesting example of the difficulties in extrapolating field observations. Based on studies of Siberian thermokarst lakes underlain by organic-rich yedoma soils, Walter et al. [113] estimated that ebullition could lead to significant local CH₄ emissions (3.8 TgCH₄/year for their study area). They also proposed that permafrost thaw over 25 years led to a nearly 60% increase in emissions from their study area. Having established the existence, local magnitude, persistence, and potential significance of a source that previously had not been considered in Arctic CH₄ budgets, they estimated the pan-Arctic significance of their source: 24.2 ± 10.5 TgCH₄/year [114]. This amount would account for most of the emissions estimated from atmospheric observation using inversions [110], leaving no room in the Arctic budget for wetland emissions, anthropogenic emissions, and emissions from shallow continental shelves (assuming atmospheric inversions are correct and assuming sinks are not underestimated).

Wik et al. [115] pointed out the difficulties in scaling up emissions using techniques exploited by Walter et al. [113] to estimate emissions, namely using bubbles frozen in ice over winter. They pointed out that bubbles collected over winter cannot be used to scale up to continuous emissions; more transects are needed covering larger sections of lakes. Another complication is the possible oxidation of CH₄ over time in trapped bubble air. A comprehensive study by Sepulvedo-Jauregui et al. [116] that looked at emissions of both CH₄ and CO₂ from high-latitude lakes found that CH₄ in fresh bubbles was 33% higher than bubbles trapped in ice. Wik et al. [117] synthesized CH₄ flux measurements from over 700 lakes located north of 50° N and used the satellite databased lake inventory of Verpoorter et al. [118] to estimate high northern latitude lake emissions. They found total emissions of 16.5 ± 9.2 TgCH₄/year, closer to top-down estimates. Wik et al. [117] also found that those post-glacial lakes, rather than thermokarst lakes, were likely to account for the largest share of emissions due to their larger surface areas, a conclusion that could vary depending on latitude range considered due to the distribution of permafrost and yedoma soils.

Wik et al. [117] upscaled site-specific flux observations by using spatial information about lake distributions from remote sensing data. A significant challenge for estimating CH₄ emissions from lakes and wetlands is accurate information about where the CH₄-producing environments are and how their distribution changes over time. Not all CH₄-producing lakes and ponds are visible from space, and there is a continuum between small ponds and wetlands as pointed out by Holgerson and Raymond [119] who estimated that small ponds could contribute about 600 TgC/year (both CO₂ and CH₄) to the global carbon budget. Furthermore, shallow water bodies, especially with vegetation growing in them, are among the highest CH₄ emitters, and getting information about water depth from remote sensing observations is difficult. Thornton et al. [120] showed that the problems with definition of small water bodies and wetlands complicate the understanding of the relative contributions of lakes and wetlands and can lead to double-counting of emissions and bottom-up estimates that are biased high.

Even with the difficulties highlighted above, significant advances have been made over recent decades to estimate the carbon balance of the Arctic through simultaneous increase in observations and advancement of models, together with the assimilation of remote sensing data. By combining both observations and process models over the time period 1990–2006, McGuire et al. [121] estimated that Arctic tundra may be a sink of carbon of −110 TgC year⁻¹, with an uncertainty ranging from a modest sink of −291 TgC year⁻¹ to a small source of 80 TgC year⁻¹. They also estimated that the tundra biome is a CH₄ source of 19 TgC year⁻¹, with a lower and upper boundary of 8 and 29 TgC year⁻¹. In this study, flux measurements were grouped into dry/mesic and wet vegetation classes. This distinction of water availability is important, since anoxic wet soils are a source of CH₄ and exhibit lower respiration rates than drained oxygenated soils. Differences in water availability can, given the high heterogeneity of Arctic landscapes, lead to large contrasts in CO₂ and CH₄ fluxes across short distances [122, 123]. Accurate knowledge of the distribution of wetlands and drained uplands, and their relative extents, is critical for accurate Arctic carbon budget estimates. The full climatic and ecological range present in the Arctic remains severely under-sampled, and this complicates constraining changes in the regional budget without the use of models or statistical methods.

Process models have, since the turn of the century, been instrumental in showing how carbon cycle feedbacks can...
accelerate climate change [124, 125]. The global models in use at the time had a basic representation of the terrestrial biosphere and early model development focused on the demography of tropical and mid-latitude forests, rather than the tundra biome and the permafrost region. Since then, significant advances have been made to make transient simulations of the Arctic carbon cycle, either forced by observations of past climate or under future climate scenarios. For example, terrestrial biosphere models have started to represent dwarf shrubs, sedges, and mosses (e.g., [126–129]) as well as the simulation of carbon stocks in permafrost and peatland soils (see e.g. [109, 130–132]). These advances have made it possible to explore changes in the Arctic carbon budget over time, and the potential for carbon cycle feedbacks.

A comparison of 10 terrestrial biosphere models showed a uniform increase in net primary production (NPP) over the period 1960–2009 across the permafrost region [133]. This increase was interpreted to be in response to higher temperatures and a fertilization effect of elevated CO₂ concentrations. Individual models, however, showed large differences in gross primary production (GPP)—up to a factor of two—highlighting the large uncertainty in quantifying actual changes in the regional carbon budget. Moreover, it is unclear whether there will be a net uptake of CO₂ with more climate warming since the release of carbon from permafrost soils may offset the increased uptake by vegetation. A comparison of 5 biogeochemical land models up to 2300 [71] showed a continued net uptake of carbon under the moderate warming scenario of RCP4.5, where litter input into the soil offset some of the permafrost carbon loss. However, model responses of vegetation and soil carbon strongly diverged under the high warming scenario RCP8.5—showing both a net release and net uptake of carbon by 2300.

Besides diverging model results, it is important to note that there are a number of important processes missing from the models, or poorly implemented, which make future projections highly uncertain. Rapid thaw due to thermokarst has the potential to double permafrost carbon loss [134], but these processes play out at small scales and few implementations in land surface schemes exist [135]. Models strongly underestimate winter emissions, even though these may be large enough to offset the carbon uptake during the summer [107]. Extreme winter events have also been pinpointed as the cause of recent reductions in the growth of and carbon uptake by arctic vegetation [52, 136], which models fail to represent. Although a large uncertainty exists on the current and future importance of these factors, they have the capacity to reduce the uptake of CO₂ by the Arctic and need to be a focus of model development.

Despite the uncertainty on the current and future sign of Arctic CO₂ exchange, it is clear that the Arctic is a source of CH₄, and there is a valid concern that these emissions may increase in the future. Much of this work has focused on wetlands, the largest natural CH₄ source globally and in the Arctic. Early bottom-up studies of wetland CH₄ emissions north of 50⁰N estimated that these emitted 15 ± 10 TgC year⁻¹ [137, 138]. The representation of CH₄ production and consumption in these early model implementations was rudimentary and used fixed relationships with NPP, which is why they were mostly useful to estimate steady-state budgets rather than a response of wetland emissions to global warming. Improving upon these pioneering studies, Walter and Heimann [139] designed a methane model that was both process-based and climate-sensitive, and therefore useful for studies of global change. Production and consumption of CH₄ were modeled as temperature-sensitive processes, and diffusion, plant transport, and ebullition were explicitly represented. Most methane schemes that are used in land surface models today incorporate some or all of the concepts introduced by the studies above (e.g., [140–144]). Moreover, new processes continue to be added, such as the inclusion of microbial mechanisms [145], sensitivity to pH [144], or improved oxidation of atmospheric CH₄ in upland soils [146]. This progressive improvement of process representation has made methane models skillful when compared to field observations at the site level (e.g., [147]), but it remains challenging to derive accurate pan-Arctic budgets.

Since CH₄ production is a temperature-sensitive process, global methane models typically simulate an increase in emissions with global warming [148]. The Arctic is the fastest-warming region in the world, partly due to the sea ice-albedo effect, and models predict that this has led to a pan-Arctic rise in CH₄ emissions of a few TgC per year over the period 2005–2010 compared to the 1980s [141]. Regional drying, however, can compensate for such increases [149], which would explain why this signal has not been detected in the atmosphere [148]. Precipitation is expected to increase following sea ice retreat [150], but the moisture status of the surface will also depend on how evapotranspiration and drainage will change with temperature increase, snow cover loss, and permafrost thaw [30]. Whether the Arctic will become a larger source of CH₄ depends not only on temperature but also at least as much on whether the region will become drier or wetter.

Knowledge of the location and extent of wetlands is paramount for estimating the pan-Arctic methane budget. To illustrate, modeled estimates of CH₄ emissions can easily vary by a factor of 4 depending on the prescribed wetland product [151]. Besides, even if static wetland maps are perfect representations of the location of wetlands today, it cannot be expected that this extent will remain constant for decades, especially with changing climate. Accurate representations of the transient response of the wetland distribution to changing climate are needed to answer important questions about how carbon...
fluxes will evolve in the future. In recent years, this problem has been tackled by combining the knowledge of static wetland maps with the dynamics of surface inundation products derived from microwave remote sensing data [152]. Static maps provide useful information about the locations of wetlands and lakes at a particular point in time, while the surface inundation products vary over time but are typically not sensitive enough to capture saturated soil environments typical of wetlands. In combining these two types of information, a hopefully more comprehensive distribution of potential methane-producing environments can be produced that is useful for models. In practice, this is a movement away from an ecological definition of wetlands, such as vegetation composition, to a hybrid definition that relies on a physical property—water table—that varies throughout the year. This approach assumes that the land surface does not emit CH\textsubscript{4} unless the water table is at or above the surface, even though CH\textsubscript{4} emissions can continue when the water table is 10 to 15 cm below the surface [153]. It also ignores frozen soils while up to half of annual emissions from permafrost wetlands may originate from deeper unfrozen layers during the winter [154–156]. Wetland products that rely on surface inundation may therefore have limited value for the high latitudes, even though it is clear that such products could be a valuable advancement from a global modeling perspective.

Saunois et al. [111] determined global wetland emissions with thirteen biogeochemical models that used the latest remote sensing–based wetland area and dynamics dataset (WAD2M; Wetland Area Dynamics for Methane Modeling). For the region north of 60° N, the models estimated that wetland CH\textsubscript{4} emissions were 7 [2–14] TgC year\textsuperscript{-1} in the time period 2008–2017. This is only about a quarter of the 26 [16–35] TgC year\textsuperscript{-1} previously estimated with many of the same models for the significantly smaller area of Arctic tundra [121]. The lower estimate is due to the subtraction of surface area covered by ponds and small lakes to avoid double-counting [120] as well as the above-mentioned high-latitude issues with surface inundation and frozen soils. Then again, even biogeochemical models that include microbial oxidation of CH\textsubscript{4} in soils, especially drained upland soils, may underestimate the Arctic soil sink by as much as ~4 TgC year\textsuperscript{-1} [88]. This illustrates the importance of including all landscape types in assessing net emissions of methane.

While many advances have been made to simulate the biogeochemistry of wetlands and their extent, fewer studies have attempted to model CH\textsubscript{4} emissions from other CH\textsubscript{4} sources in the Arctic, such as lakes, geological sources, and the ocean. One of the few modeling studies that have estimated lake emissions with explicit representation of biogeochemical processes derived a pan-Arctic budget of 9 [5–13] TgC year\textsuperscript{-1} [157]. This compares reasonably well to bottom-up estimates based on extrapolations of flux measurements [111, 117, 158], but the continuous formation and drainage of thermokarst lakes in permafrost landscapes make it challenging to model emissions prognostically [159]. For the Arctic Ocean, detailed models exist that can simulate the evolution of gas hydrates and their emission to the atmosphere (e.g., [160]) but due to the slow thaw of subsea permafrost, which has been ongoing since these environments were submerged at the end of the last glacial, gas hydrates are not expected to destabilize until the next millennium [161]. Bottom-up estimates of geological emissions from the terrestrial Arctic are relatively small, ~2 TgC year\textsuperscript{-1} [162], but these emissions may respond to changes in permafrost thickness and disappearance of glaciers and ice caps.

Current bottom-up estimates of the Arctic carbon budget show that the region is a sink of CO\textsubscript{2} but a source of CH\textsubscript{4}. Model simulations suggest that the strong rise in arctic temperatures and the thaw of permafrost may turn the region into a net source of carbon, although current projections for the twenty-first century do not indicate a release of greenhouse gases that is larger than anthropogenic emissions [42, 163]. However, these projections are highly uncertain due to missing representation of thermokarst and key winter processes that may enhance arctic carbon loss. The risk of a large, uncontrolled, carbon cycle feedback from the Arctic remains a distinct possibility as long as anthropogenic emissions continue to rise and the amplified warming of the Arctic worsens.

**Atmospheric Inversions**

Atmospheric flux inversions use statistical optimization procedures and atmospheric transport models to estimate carbon fluxes that are in optimal agreement with both prior (first-guess) flux estimates and observations that are distributed in time and space (e.g., [164, 165]). Prior flux estimates come from scaled-up field observations, process emission models, and economic inventories of anthropogenic emissions (livestock populations, fossil fuel production, etc.). Sparseness of observations, especially in the Arctic (and other regions such as the tropics), limits the spatial and temporal information that can be retrieved about fluxes, and therefore, prior flux estimates are used to stabilize an under-determined estimation problem. In regions where data are sparse or nonexistent, the estimated flux remains close to the prior estimate, producing posterior estimates that may be biased or not vary in time realistically.

A potential source of error for atmospheric inversions comes from uncertainty in transport of emissions by atmospheric circulation at both regional/global and local scales. Atmospheric transport models often have large
grid boxes that range in size from 10 to 100 s of km, such that coarse-resolution simulations are compared with point observations introducing representation errors. Although the original measurement network sites were chosen to sample air located far from strong local sources that are relatively easy for models to simulate (background atmospheric sites), representation errors become much more significant for air samples collected near sources, yet these samples offer potentially useful constraints of source variability in space and time. This problem is especially difficult for regions that have large spatial heterogeneity of sources. Increasing horizontal and vertical resolution of a transport model may improve the representation of transport in models and this has led to use of higher resolution (10 km) regional models for atmospheric inversions (e.g., [166]). Use of regional transport models requires specification of boundary conditions to capture the inflow of carbon from other latitudes or regions, however, and these are difficult to constrain with sparse observations.

Carbon fluxes estimated using an inverse model combine information coming from prior flux estimates, and information from observations. The relative weighting of these two types of observational constraints is dependent on uncertainties associated with the prior flux estimates and the observations. For observations, the uncertainties come from both the measurement uncertainty, which is generally very small for atmospheric in situ network observations, and the transport model error, which is difficult to quantify and much larger than the measurement uncertainty. This type of error is referred to as “model-data mismatch error.” For the prior fluxes, uncertainties are often difficult to quantify, although emission inventories sometimes include uncertainty estimates. A small prior uncertainty will lead to a solution that stays close to the prior fluxes and therefore may fail to capture actual flux variability. A small model-data mismatch error will result in a solution that tracks observations closely, possibly with unrealistic variability in flux estimates. A sparse network sampling the background atmosphere can still be useful for constraining some large-scale aspects of source distributions.

Figure 5 shows CO$_2$ fluxes from 4 atmospheric inversions for the Boreal (50°–60° N) and the Arctic (60°–90° N) zones. The top figures show the model average monthly CO$_2$ fluxes and the range of the models (light blue area). For this study, we used inversions that were constrained only by in situ data. Retrievals from satellite-based instruments do exist that include some coverage of the Arctic in the summer; however, it is not currently possible to capture year-round carbon fluxes due to the viewing and solar geometry [171]. For the Boreal zone, there appears to be a jump in summertime uptake in the early 1990s; however, estimates prior to 1993 exist only for one of the 4 inversions, and differences between inversion systems could produce such a discontinuity. Note also that the inter-model range of the monthly estimates is quite large, a reflection of differences among the inversions; priors, transport models, prior errors, and data selection. For both zones, it appears that the maximum summer uptake has been increasing since 1980, especially for the Boreal zone. This agrees with the observational analysis of Graven et al. [94], discussed further by Leonard et al. [172]. The bottom panels of Fig. 5 show annual average net CO$_2$ fluxes from the inversion ensemble. The Boreal zone net CO$_2$ flux is about $-0.3$ PgC/year, while the Arctic zone takes up only about 1/3 this amount ($-0.13$ PgC/year). There is a slight trend of increasing net uptake that is statistically significant for the Boreal zone ($p = 0.0003$), but the small trend for the Arctic is not statistically significant. These results agree with the study of Welp et al. [173], who did not find significant trends north of 60° N from flux inversions, but small trends in the Boreal zone. Statistically significant trends in CO$_2$ respiration were not found by the inversions used here, implying that the results of Commare et al. [98] are possibly localized to the vicinity of Barrow, Alaska, or that the inversions do not have the sensitivity to recover an increase in cold season respiration, or that increases in respiration are compensated for by another process, perhaps increased ocean uptake with lower sea ice cover.

Global inversions have been collected by the Global Carbon Project CH$_4$ Project [111]. Figure 6 shows estimated natural emissions for 11 inversions that are constrained by in situ observations. The model spread is quite large due to differing transport models, priors, uncertainties, and observations. Interannual variability is seen in the flux estimates, and 2016 and 2017 appear to have significantly higher emissions. Emissions from the Boreal zone, which includes some large wetland complexes such as the Hudson Bay Lowlands in Canada and the southern part of the West Siberian lowlands, are about twice as large as for the Arctic zone. There is no statistically significant trend in emissions from the Boreal zone in contrast to Thompson et al. [97] who used a regional inverse model to find that CH$_4$ emissions have been increasing north of 50° N. For the Arctic zone, there does appear to be a small, but statistically significant trend towards increasing emissions of $-0.2$ TgCH$_4$/year.

Trends in fluxes estimated from inverse models should be considered with caution because the data used to constrain inversions is still very sparse and records do not yet cover the very long periods necessary to robustly detect trends. Biases in transport and prior fluxes are also possible sources of error in inversions. However, at present, inverse models are not suggesting large changes in the net carbon flux north of 50° N are occurring.
Cold Season Emissions

Cold season CO₂ emissions from Arctic soils are expected to increase due to increasing winter temperatures (the “Arctic Climate Change” section). Winter snowpack increases could further affect cold season emissions by insulating soils, keeping them warmer, and allowing more respiration. Using in situ atmospheric CO₂ observations from Barrow, Alaska, Commane et al. [98] inferred increased emissions of CO₂ early in the cold season. Natali et al. [107] synthesized both chamber and eddy covariance flux measurements for the cold season (October-April) from over 100 sites throughout the Arctic and Boreal high latitudes using machine learning techniques with a variety of environmental drivers (vegetation type, soil moisture, soil temperature). Their approach is similar to that used by Jung et al. [108] to produce the FLUXCOM product based on global eddy covariance flux tower observations. Natali et al. [107] found that 1.7 PgC/year is emitted as CO₂ from permafrost region soils during the cold season, an amount exceeding their modeled estimate of uptake during the warm season giving a net CO₂ source. They also noted that they did not find any trends in cold season emissions for 2003–2017, which they attribute to a lack of circumpolar trends in the reanalysis data used in their algorithm. They did, however, find increases in winter respiration for site-level data from Alaska.

Figure 7 shows annual net CO₂ exchange and cold/warm season fluxes for latitudes north of 60°N estimated using top-down and bottom-up approaches. Results from two atmospheric inversion systems (CarbonTracker and CarbonTracker-Europe) suggest that the Arctic is taking up more CO₂ than is respired over a year. The prior flux estimates used in these inversions are the CASA-GFED model for CarbonTracker [174, 175] and SiB-CASA for CarbonTracker-Europe [176], both dependent on remotely sensed NDVI for estimating GPP. In the annual mean, both priors are nearly annually balanced with uptake about equal to respiration. The SiB4 terrestrial ecosystem model [177, 178], which has prognostic phenology and does not use NDVI, produces annual net CO₂ fluxes that are similar to the prior estimates. FLUXCOM’s annual net flux lies between the inversions and bottom-up models. During the warm season, FLUXCOM shows significantly less uptake than the other estimates and also less respiration during the cold season. Likewise, the inversions estimate less cold season respiration than their prior estimates or SiB4. During the cold season,
emissions range from ~0.8 PgC/year for FLUXCOM to over 2.5 PgC/year for SiB4. The estimate of Natali et al. [107], 1.6 PgC/year, falls between the inversions and the priors; however, their calculated warm season uptake (~−1.0 PgC/year) is significantly smaller than the inverse estimates by at least a factor of 3. These results show the difficulty in interpretation of annual net CO2 fluxes since they are a balance of respiration and photosynthesis for which estimates from different methods can significantly diverge.

Conclusions and Recommendations

Multiple lines of observational evidence show that presently the remote Arctic is undergoing rapid environmental change. These changes have been directly linked to anthropogenic emissions [12].

Our understanding of Arctic climate tells us that there are important feedbacks in operation, such as between the cryosphere and the atmosphere, and between vegetation and atmospheric energy/moisture budgets. It is certain that changes in Arctic climate will drive changes in the carbon budget of the Arctic as vegetation changes, soils warm, fires increase, and wetlands evolve with permafrost thaw. Massive amounts of carbon are stored in Arctic soils, and some fraction of this carbon is likely to be mobilized to the atmosphere and oceans with consequences that will feedback to affect global climate. This permafrost carbon feedback needs to be understood, quantified, and taken into account when considering climate mitigation (e.g., [179]), and formulating policy designed to ensure temperatures remain below particular thresholds. This will require a commitment to long-term pan-Arctic observations, as well as improvements in models used to help better understand the Arctic climate system.

Observations currently support a more active CO2 cycle in high northern latitude ecosystems with both enhanced productivity and increased respiration. Evidence points to increased uptake by boreal forests and Arctic ecosystems. Evidence also points towards increasing respiration, especially late in the warm season. On the other hand, there is currently no strong evidence of increased CH4 emissions, across the region, although we demonstrated here using atmospheric observations that small increases cannot be ruled out. Sweeney et al. [100] pointed out that given the widely observed temperature dependence of microbial production of CH4 in Arctic wetlands, the response of atmospheric CH4 to temperature increases appeared to be much smaller than expected. They attributed this lack of response to a lack of understanding of processes...
leading to emissions. However, it is also possible that microbial consumption of atmospheric CH$_4$ in drier upland soils is also increasing as temperatures rise and that this process has been significantly underestimated as proposed by Oh et al. [88]. Alternatively, a reduction in wetland extent and increased lake drainage may have played a role.

Finally, we point out that long-term observations help us to understand what has or is changing, but they are also critical for improving projections of future emissions. Long-term observations provide the valuable opportunity to test predictive models and their sensitivity to change. Increasing observational coverage of flux measurements, in situ atmospheric sampling, and remote sensing data from satellites and committing to maintaining data records over decades will improve our understanding of the Arctic carbon cycle and how it is changing over time.

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Data Availability All data used in this study are freely available for download from https://www.esrl.noaa.gov/gmd/.

Compliance with Ethical Standards

Conflict of Interest The authors declare that they have no conflict of interest.

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References

1. Meredith MM, Sommerkorn S, Cassotta C, Derksen A, Ekaykin A, Hollowed et al. In: H.-O. Pörtner, D.C. Roberts, V. Masson-Delmotte, P. Zhai, M. Tignor, E. Poloczanska, K. Mintenbeck, A. Alegría, M. Nicholai, A. Okem, J. Petzold, B. Rama, N.M. Weyer (eds.) Polar Regions. IPCC Special Report on the Ocean and Cryosphere in a Changing Climate 2019. https://www.ipcc.ch/srocc/chapter/chapter-3-2/.
2. Overland JE, Hanna E, Hannsen-Bauer I, Kim S-J, Walsh JE, Wang M, et al. In: The NOAA Arctic Report Card, Surface Air Temperature 2019. https://arctic.noaa.gov/Report-Card/ReportCard 2019/ArtMID/7916/ArticleID/835/Surface-Air-Temperature.
3. Goose H, Kay JE, Armour KC, et al. Quantifying climate feedbacks in polar regions. Nat Commun. 2018;9(2018):1919. https://doi.org/10.1038/s41467-018-04173-0.
4. Kay JE, et al. Recent advances in Arctic cloud and climate research. Curr Clim Change Rep. 2016;2:159.
5. Pithan F, Mauritsen T. Arctic amplification dominated by temperature feedbacks in contemporary climate models. Nat Geosci. 2014;7:181–4.
6. Qu X, Hall A. What controls the strength of snow-albedo feedback? J Clim. 2007;20:3971–81.
7. Steecker MF, Bitz CM, Armour KC, et al. Polar amplification dominated by local forcing and feedbacks. Nat Clim Chang. 2018;8:1076–81. https://doi.org/10.1038/s41558-018-0339-y.
8. Taylor PC, et al. A decomposition of feedback contributions to polar warming amplification. J Clim. 2013;26:7023–43. https://doi.org/10.1007/s00382-009-0535-6.
9. Vihma T, Screen J, Tjernström M, Newton B, Zhang X, Popova V, et al. The atmospheric role in the Arctic water cycle: A review on processes, past and future changes, and their impacts. J Geophys Res Biogeosci. 2016;121:586–620. https://doi.org/10.1002/2015JG003132.
10. Mudryk LR, Gordon T, Stuefer M. On the precipitation and precipitation change in Alaska. Atmosphere. 2017;8(12):253. https://doi.org/10.3390/atmos8120253.
11. Peterson BJ, Holmes RM, McClelland JW, Vörösmarty CJ, Lamers RB, Shiklomanov AI, et al. Increasing river discharge to the Arctic Ocean. Science. 2002;292:217. https://doi.org/10.1126/science.1077445.
12. Metzger MJ, Artaxo P, de Oliveira DC, et al. Large carbon cycle sensitivities to climate across a permafrost biome. Nat Geosci. 2011;4:747–50. DOI: https://doi.org/10.1038/ngeo2345.
13. Jones BM, et al. Modern thermokarst lake dynamics in the continental Arctic. Geophys Res Lett. 2017;44:919–26. https://doi.org/10.1002/2016GL071789.
30

Parmentier FJW, Christensen TR, Rysgaard S, Bendtsen J, Glud RN, Else B, et al. A synthesis of the arctic terrestrial and marine carbon cycles under pressure from a dwindling cryosphere. Ambio. 2017;46(1):53–69. https://doi.org/10.1007/s13280-016-0872-8.

Tarnocai C, Canadell JG, Schuur EAG, Kuhry P, Mazhigova V, Zimov S. Soil organic carbon pools in the northern circumpolar permafrost region. Glob Biogeochem Cycles. 2009;23:GB2023. https://doi.org/10.1029/2009GB003327.

Hugelius G, Strauss J, Zubrzycki S, Harden JW, Schuur EAG, Ping C-L, et al. Estimated stocks of circumpolar permafrost carbon with quantified uncertainty ranges and identified data gaps. Biogeosciences. 2014;11:6573–93. https://doi.org/10.5194/bg-11-6573-2014.

Schuur E, McGuire A, Schädel C, Grosse G, Harden JW, Hayes DJ, et al. Climate change and the permafrost carbon feedback. Nature. 2015;520:171–9. https://doi.org/10.1038/nature14338.

Ruppel CD, Kessler JD. The interaction of climate change and methane hydrates. Rev Geophys. 2017;55:126–68. https://doi.org/10.1002/2016RG000534.

Romanovskii NN, Hubberten HW, Gavrilov AV, Eliseeva AA, Tipenko GS. Offshore permafrost and gas hydrate stability zone on the shelf of East Siberian seas. Geo-Mar Lett. 2005;25:167–82.

Dmitrenko IA, Kirillov SA, Tremblay LB, Kassens H, Anisimov OA, Lavrov SA, et al. Recent changes in shelf hydrography in the Siberian Arctic: potential for subsea permafrost instability. J of Geophys Res C: Oceans. 2011;116(C10):C10027. https://doi.org/10.1029/2011JC007218.

Ferré B, Miemiet J, Feseker T. Ocean temperature variability for the past 60 years on the Norwegian-Svalbard margin influences gas hydrate stability on human time scales. J Geophys Res C: Oceans. 2012;117:C110017. https://doi.org/10.1029/2012CC003800.

Stranne C, O’Regan M, Jakobsson M. Overestimating climate-warming-induced methane gas escape from the seafloor by neglecting multiphase flow dynamics. Geophys Res Lett. 2016;43:8703–12. https://doi.org/10.1002/2016GL070049.

Elmendorf S, Henry G, Hollister R, et al. Plot-scale evidence of tundra vegetation change and links to recent summer warming. Nat Clim Chang. 2012;2:453–7. https://doi.org/10.1038/nclimate1465.

Myers-Smith IH, Hik DS. Climate warming as a driver of tundra shrubline advance. J Ecol doi. 2018. https://doi.org/10.1111/1365-2745.12817.

Myers-Smith I, Elmendorf S, Beck P, et al. Climate sensitivity of shrub growth across the tundra biome. Nat Clim Chang. 2015;5:887–91. https://doi.org/10.1038/nclimate2697.

Bhatt US, Walker DA, Raynolds MK, Bieniek PA, Epstein HE, Comiso JC, et al. Changing seasonality of pan-Arctic tundra vegetation in relationship to climatic variables. Environ Res Lett. 2017;12:055003.

Myers-Smith I, Kerby JT, Phoenix GK, Bjerke JW, Epstein HE, Assmann JJ, et al. Complexity revealed in the greening of the Arctic. Nat Clim Chang. 2020;10:106–17. https://doi.org/10.1038/s41558-019-0688-1.

van der Werf GR, Randerson JT, Giglio L, van Leeuwen TT, Chen Y, Rogers BM, et al. Global fire emissions estimates during 1997–2016. Earth Syst Sci Data. 2017;9:697–720. https://doi.org/10.5194/essd-9-697-2017.

Amiro BD, et al. Direct carbon emissions from Canadian forest fires, 1959–1999. Can J For Res. 2001;31:512–25.

Kasischke ES, Johnstone AF. Variation in post-fire organic layer thickness in a black spruce forest complex in Interior Alaska and its effects on soil temperature and moisture. Can J For Res. 2005;35:2164–77.

Yi S, et al. Interactions between soil, thermal and hydrological dynamics in the response of Alaska ecosystems to fire disturbance. J Geophys Res G: Biogeosci. 2009;114:G02015.

Turetsky M, Kane E, Harden J, Ottmar RD, Mannies KL, Hoy E, et al. Recent acceleration of biomass burning and carbon losses in Alaskan forests and peatlands. Nat Geosci. 2011;4:27–31. https://doi.org/10.1038/ngeo1027.

McCarty JL, Smith TEL, Turetsky MR. Arctic fires re-emerging. Nat Geosci. 2020;13:658–60. https://doi.org/10.1038/s41561-020-00645-5.

Bond-Lamberty B, Peckham SD, Ahl DE, Gower ST. Fire as the dominant driver of central Canadian boreal forest carbon balance. Nature. 2007;450(7166):89–92. https://doi.org/10.1038/nature06272.

Kelly R, Chipman ML, Higuera PE, Stefanova I, Brubaker LB, Hu FS. Recent burning of boreal forests exceeds fire regime limits of the past 10,000 years. PNAS. 2013. https://doi.org/10.1073/pnas.1305090110.

Coops NC, Hennonilla S, Walder MA, White JC, Bolton DK. A thirty year, fine-scale, characterization of area burned in Canadian forests shows evidence of regionally increasing trends in the last decade. PLoS One. 2018;13(5):e0197218. https://doi.org/10.1371/journal.pone.0197218.

Ponomarev EI, Kharkvi VI, Ranson KJ. Wildfires dynamics in Siberian larch forests. Forests. 2016;7:125.

Andela N, Morton DC, Giglio L, Chen Y, van der Werf GR, Kasibhatla PS, et al. A human-driven decline in global burned area. Science. 2017;356:6345, 1356–1362. https://doi.org/10.1126/science.aal4108.

Veraverbeke S, Rogers B, Goulden M, Jandt RR, Miller CE, Wiggins EB, et al. Lightning as a major driver of recent large fire years in North American boreal forests. Nat Clim Chang. 2017;7:529–34. https://doi.org/10.1038/nclimate3329.

SIMIP Community (2020) Arctic sea ice in CMIP6. Geophys Res Lett, 47, e2019GL086749. https://doi.org/10.1029/2019GL086749.

Lantuit H, Overduin PP, Wetterich S. Recent progress regarding permafrost coasts. Permaf Periglac Process. 2013;24:120–30. https://doi.org/10.1002/ppp.1777.

Bintanja RK, Van der Vel E, Van der Linden J, Reusen L, Boger F et al. Strong future increases in Arctic precipitation variability linked to poleward moisture transport. Sci Adv. 2020 12FEB2020:EAAX6869.

Hansen BB, Isaksen K, Benestad RE, Kohler J, Pederson ÅØ, Loe LE, et al. Warmer and wetter winters: characteristics and implications of an extreme weather event in the High Arctic. Environ Res Lett. 2014;9:11. https://doi.org/10.1088/1748-9326/9/11/014021.

Peters G, Andrew R, Boden T, et al. The challenge to keep global warming below 2 °C. Nat Clim Chang. 2013;3(13):4–6. https://doi.org/10.1038/nclimate1783.

Overland JE, Wang M, Walsh JE, Stroeve JC. Future Arctic climate changes: adaptation and mitigation time scales. Earth’s Future. 2014. https://doi.org/10.1002/2013EF000162.

McGuire AD, Lawrence DM, Koven C, Clein JS, Burke E, Chen G, et al. Dependence of the evolution of carbon dynamics in the northern permafrost region on the trajectory of climate change. PNAS. 2018;30:201719903. https://doi.org/10.1073/pnas.1719903115.

Nitzbon J, Westermann S, Langer M, Martin LCP, Strauss J, Laboor S, et al. Fast response of cold ice-rich permafrost in northeast Siberia to a warming climate. Nat Commun. 2020;11(1):2201. https://doi.org/10.1038/s41467-020-15725-8.
73. Pastick NJ, et al. Historical and projected trends in landscape drivers affecting carbon dynamics in Alaska. Ecol Appl. 2017;27(5):1383–402. https://doi.org/10.1002/eap.1538.

74. Young AM, Higuera PE, Duffy PA, Hu FS. Climatic thresholds shape northern high-latitude fire regimes and imply vulnerability to future climate change. Ecography. 2017;40(5):606–17. https://doi.org/10.1111/ecog.02205.

75. Walter Anthony K, et al. 21st century modeled permafrost carbon emissions accelerated by abrupt thaw beneath lakes. Nat Commun. 2018;9(1):326. https://doi.org/10.1038/s41467-018-05738-0.

76. Pearson RG, Phillips SJ, Loranty MM, Beck PSA, Damoulas T, Knight SJ, et al. Shifts in Arctic vegetation and associated feedbacks under climate change. Nat Clim Chang. 2013;3:673–7.

77. Swann AL, Fung IV, Levis S, Bonan GB, Doney SC. Changes in Arctic vegetation amplify high-latitude warming through the greenhouse effect. PNAS. 2009;107(4):1295–300. www.pnas.org/cgi/doi/10.1073/pnas.0913846107.

78. Parmentier F JW, Christensen TR, Sørensen LL, Rysgaard S, Gustafsson Ö. Extensive methane venting to the atmosphere from sediments of the East Siberian Arctic Shelf. Nature. 2010;463:195–202.

79. Terhaar J, Orr JC, Ethé C, Regnier P, Bopp L. Simulated Arctic greenhouse-gas exchange. Nat Clim Chang. 2013;3:195–202.

80. Redmann K, Smith R, Berchet A, Bousquet P, Pison I, Locatelli R, Chevallier F, Paris J-D, et al. The impact of a lower sea-ice extent on Arctic greenhouse-gas exchange. Nat Clim Chang. 2013;3:195–202.

81. Thornton BF, Prytherch J, Andersson K, Brooks IM, Salisbury DJ, Tjernström M, et al. Shipborne eddy covariance observations of methane fluxes constrain Arctic sea emissions. Sci Adv. 2019;5(7):eaay7934. https://doi.org/10.1126/sciadv.aay7934.

82. Shakhova N, Semiletov I, Salyuk A, Yusupov V, Kosmach D, Gustafsson Ö. Extensive methane venting to the atmosphere from sediments of the East Siberian Arctic Shelf. Science. 2010;327:1246.

83. Berchet A, Bousquet P, Pison I, Locatelli R, Chevallier F, Paris J-D, et al. Atmospheric constraints on the methane emissions from the East Siberian Shelf. Atmos Chem Phys. 2016;16:4147–57. https://doi.org/10.5194/acp-16-4147-2016.

84. Thomson BF, Pyrhtech J, Andersen BS, Brooks IM, Salisbury DJ, Tjernström M, et al. Shipborne eddy covariance observations of methane fluxes constrain Arctic sea emissions. Sci Adv. 2020;6(5):eaay7934. https://doi.org/10.1126/sciadv.aay7934.

85. Piao S, Ciais P, Friedlingstein P, et al. Net carbon dioxide losses of northern ecosystems in response to autumn warming. Nature. 2008;451:49–52. https://doi.org/10.1038/nature06444.

86. Lund M, Falk JM, Frigborg T, Mbuuong MN, Siggsgaard C, Soegaard H, et al. Trends in CO2 exchange in a high Arctic tundra heath, 2000-2010. J Geophys Res G: Biogeosci. 2012;117(G2):G02001. https://doi.org/10.1029/2011JG001901.

87. Parmentier F JW, van Huissijt J, van der Molen MK, Schaepman-Strub G, Karsanaev SA, Maximov TC, et al. Spatial and temporal dynamics in eddy covariance observations of methane fluxes at a tundra site in northeastern Siberia. J Geophys Res Biogeosci. 2011a;116(G3):G03016. https://doi.org/10.1029/2010JG001637.

88. Roach J, Griffith B, Verbyla D, Jones J. Mechanisms influencing changes in lake area in Alaskan boreal forest. Glob Chang Biol. 2011;17:2567–83. https://doi.org/10.1111/j.1365-2486.2011.02446.x.

89. Lawrence DM, Koven CD, Swenson SC, Riley WJ, Slater AG. Permafrost thaw and resulting soil moisture changes regulate high-latitude CO2 and CH4 emissions. Environ Res Lett. 2015;10(9):094011.

90. Oh Y, Zhuang Q, Liu L, Welp LR, Lau MCY, Onstott TC, et al. Reduced net methane emissions due to microbial methane oxidation in a warmer Arctic. Nat Clim Chang. 2020;10(4):317–21. https://doi.org/10.1038/s41558-020-0734-z.

91. Whalen SC, Reeburgh WS, Barber VA. Oxidation of methane in boreal forest soils: a comparison of seven measures. Biogeochemistry. 1992;16:181–211. https://doi.org/10.1007/BF00002818.

92. Myhre GD, Shindell D-F, Bréon W, Collins J, Fuglestvedt J, Huang D et al. Anthropogenic and natural radiative forcing. In: 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 (eds.) Climate Change 2013: The physical science basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change, Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA. 2013.

93. Tursetky MR, Abbott BW, Jones MC, Walter Anthony K, Olefeldt D, Schuur EAG, et al. Permafrost collapse is accelerating carbon release. Nature. 2019;569:32–4. https://doi.org/10.1038/s41558-019-01313-4.

94. Koven CD, Schuur EAG, Schädel C, Bohn TJ, Burke EJ, Chen G, et al. A simplified, data-constrained approach to estimate the permafrost carbon–climate feedback. Phil Trans R Soc London: Ser A. 2015;373:20140423. https://doi.org/10.1098/rsta.2014.0423.

95. Schuur EAG, Abbott BW, Bowden WB, Brovkin V, Camill P, et al. Expert assessment of vulnerability of permafrost carbon to climate change. Clim Chang. 2013;119:359–74.

96. Graven HD, Keelng RF, Piper SC, Patra PK, Stephens BB, Wofsy SC, et al. Enhanced seasonal exchange of CO2 by northern ecosystems since 1960. Science. 2013;341(6150):1085–9. https://doi.org/10.1126/science.1239207.

97. Thompson RL, Sasakawa M, Machida T, Aalto T, Worthy D, Lavric JV, et al. Methane fluxes in the high northern latitudes for 2005–2013 estimated using a Bayesian atmospheric inversion. Atmos Chem Phys. 2017;17:3553–72. https://doi.org/10.5194/acp-17-3553-2017.

98. Commare R, Lindaa J, Benmergui J, Luska KA, Chang RY-W, Daube BC, et al. Increasing early winter CO2 from Alaskan tundra. PNAS. 2017;114(21):5361–6. https://doi.org/10.1073/pnas.1618567114.

99. Jeong SJ, Bloom AA, Schimel D, Sweeney C, Parazoo N.C, Medvigy, et al. Accelerating rates of Arctic carbon cycling revealed by long-term atmospheric CO2 measurements. Sci Adv 2018 4(7) eaao1167. https://doi.org/10.1126/sciadv.aao1167.

100. Sweeney C, Dlugokencky E, Miller CE, Wofsy S, Karion A, Kaplan K, et al. No significant increase in long-term CH4 emissions on North Slope of Alaska despite significant increase in air temperature. Geophys Res Lett. 2016;43(12):6604–11. https://doi.org/10.1002/2016GL069292.

101. Dlugokencky EJ, Houweling S, Wofsy S, Karion A, Darnold S, et al. Non significant increase in long-term CH4 emissions on North Slope of Alaska despite significant increase in air temperature. Geophys Res Lett. 2003;30:1949. https://doi.org/10.1029/2003GL018126.

102. Dlugokencky EJ, Nisbet EG, Fisher R, Lowry D. Global atmospheric methane: budget changes and dangers. Philos Trans R Soc London Ser A. 2011;369:2058–2072. https://doi.org/10.1098/rsta.2010.0341.

103. Holzer M, Waugh DW. Interhemispheric transit time distributions and path-dependent lifetimes constrained by measurements of SF6, CFCs, and CFC replacements. Geophys Res Lett. 2015;42:4581–9. https://doi.org/10.1002/2015GL064172.

104. Dimndore-Miles OB, Palmer PI, Brohulier LP. Detecting changes in Arctic methane emissions: limitations of the inter-polar
difference of atmospheric mole fractions. Atmos Chem Phys. 2018;18:17895–907. https://doi.org/10.5194/acp-18-17895-2018.

105. Bruhwiler L, Dlugokencky E, Masarie K, Ishizawa M, Andrews A, Miller J, et al. CarbonTracker-CH₄: an assimilation system for estimating emissions of atmospheric methane. Atmos Chem Phys. 2014;14:8269–93. https://doi.org/10.5194/acp-14-8269-2014.

106. Ueyama M, Ichii K, Iwata H, Euskirchen ES, Zona D, Rocha AV, et al. Upscaling terrestrial carbon dioxide fluxes in Alaska with satellite remote sensing and support vector regression. J Geophys Res Biogeosci. 2013;118:1266–81. https://doi.org/10.1002/jgrg.20095.

107. Natali SM, Watts JD, Rogers BM, Potter S, Ludwig SM, Jung M, Reichstein M, Schwalm CR, Huntingford C, Sitch S, Walter KM, Smith LC, Chapin FS. Methane bubbling from northern European lakes based on high-resolution satellite imagery. Geophys Res Lett. 2014;41:6396–403. https://doi.org/10.1002/2014GL063544.

108. AMAP Assessment 2015: Methane as an Arctic climate forcer. Norway. vii + 139 pp.

109. Saunois M, Stavert AR, Poulter B, Bousquet P, Canadell JG, Ciais P, Le Quéré C, Marland G, Tans P, et al. Anthropogenic emissions of methane: comparison of different inventories. Geophys Res Lett. 2016;43:12,569–77. https://doi.org/10.1002/2016GL069772.

110. Thornton BF, Wik M, Crill PM. Double-counting challenges the accuracy of high-latitude methane inventories. Geophys Res Lett. 2016;43:12,569–77. https://doi.org/10.1002/2016GL069772.

111. Wik M, Varner R, Anthony KW, Bastviken D, Selhofer S, Marchesini L, et al. Upscaling terrestrial carbon dioxide fluxes in Alaska with satellite remote sensing and support vector regression. J Geophys Res Biogeosci. 2013;118:1266–81. https://doi.org/10.1002/jgrg.20095.

112. Verpoorter C, Kutser T, Seekell DA, Tranvik LJ. A global inventory of methane bubbling from northern peatlands: present and future contributions to the global methane budget. Phil Trans R Soc London: Ser A. 2007;365:1657–70. https://doi.org/10.1038/s41558-019-0592-8.

113. Walter KM, Zimov SA, Chapin FS. Methane bubbling from Siberian Thaw Lakes as a positive feedback to climate warming. Nature. 2006;443:71–5. https://doi.org/10.1038/nature05040.

114. Walter KM, Smith LC, Chapin FS. Methane bubbling from northern lakes: present and future contributions to the global methane budget. Phil Trans R Soc London: Ser A. 2007;365:1657–76. https://doi.org/10.1098/rsta.2007.2036.

115. Wik M, Crill PM, Bastviken D, Danielsson Å, Norbäck E. Bubbles trapped in arctic lake ice: potential implications for methane emissions. J Geophys Res. 2011;116:G03044. https://doi.org/10.1029/2010GG003917.

116. Sepulveda-Jauregui A, Walter Anthony KM, Martinez-Cruz K, Greene S, Thalasso F. Methane and carbon dioxide emissions from small ponds in the Arctic. Geophys Res Lett. 2014;41:6396–403. https://doi.org/10.1002/2014GL063544.

117. Jorgensen CJ, Lund Johansen KM, Westergaard-Nielsen A, Elbert B. Net regional methane sink in High Arctic soils of northeastern Greenland. Nat Geosci. 2014;8:20–3. https://doi.org/10.1038/NGEO2305.

118. Cox PM, Betts RA, Jones CD, Spall SA, Totterdell IJ, Le Treut H, et al. Positive feedback between future climate change and the carbon cycle. Geophys Res Lett. 2001;28(8):1543–6. https://doi.org/10.1029/2000GL012015.

119. Holgerson M, Raymond P. Large contribution to inland water carbon dioxide fluxes from small ponds. Biogeosciences. 2015;12:3197–3208. https://doi.org/10.5194/bg-12-3197-2015.

120. Hayes DJ, McGuire AD, Kicklighter DW, Gurney KR, Burnside TJ, Melillo JM. Is the northern high-latitude land-based CO₂ sink weakening? Global Biogeochem Cy. 2011;25(3):GB3018. https://doi.org/10.1029/2010GB003813.

121. Parmentier F-JW, Rasse DP, Lund M, Bjerke JW, Drake BG, Weldon S, et al. Vulnerability and resilience of the carbon exchange of a subarctic peatland to an extreme winter event. Curr Clim Change Rep. 2021;7:14–34. https://doi.org/10.1007/s40795-021-00205-8.
169. Peters W, Jacobson AR, Sweeney C, Andrews AE, Conway TJ, Masarie K, et al. An atmospheric perspective on North American carbon dioxide exchange: CarbonTracker. PNAS. 2007;104(48):18925–30. https://doi.org/10.1073/pnas.0708986104.

170. van der Laan-Luijkx IT, van der Velde IR, van der Veen E, Tsuruta A, Stanislawska K, Babenhauserheide A, et al. The CarbonTracker Data Assimilation Shell (CTDAS) v1.0: implementation and global carbon balance 2001–2015. Geosci Model Dev. 2017;10(7):2785–800. https://doi.org/10.5194/gmd-10-2785-2017.

171. Parazoo NC, Commane R, Wofsy SC, Koven CD, Sweeney C, Lawrence DM, et al. PNAS. 2016;113(28):7733–8. https://doi.org/10.1073/pnas.1601085113.

172. Leonard, M. et al. (2020) Examining the global terrestrial carbon cycle using 'top-down' and 'bottom-up' models. in prep.

173. Welp LR, Patra PK, Rödenbeck C, Nemani R, Bi J, Piper SC, et al. Increasing summer net CO₂ uptake in high northern ecosystems inferred from atmospheric inversions and comparisons to remote-sensing NDVI. Atmos Chem Phys. 2016;16:9047–66. https://doi.org/10.5194/acp-16-9047-2016.

174. Potter CS, Randerson JT, Field CB, Matson PA, Vitousek PM, Mooney HA, et al. Terrestrial ecosystem production: a process model based on global satellite and surface data. Global Biogeochem Cycles. 1993;7(4):811–41. https://doi.org/10.1029/93GB02725.

175. Randerson JT, Van Der Werf GR, Giglio L, Collatz GJ, Kasibhatla PS. Global fire emissions database, version 4.1 (GFEDv4). ORNL DAAC. 2015. https://doi.org/10.3334/ORNLDAAC/1293.

176. Schaefer K, Collatz GJ, Tans P, Denning AS, Baker I, Berry J, et al. Combined simple biosphere/Carnegie-Ames-Stanford approach terrestrial carbon cycle model. J Geophys Res G: Biogeosci. 2008;113(G3):G03034. https://doi.org/10.1029/2007JG000603.

177. Haynes K, Baker IT, Denning S, Stöckli R, Schaefer K, Lokupitiya EY, et al. Representing grasslands using dynamic prognostic phenology based on biological growth stages: 1. Implementation in the Simple Biosphere Model (SiB4). J Adv Model Earth Syst. 2019a;11:4423–39. https://doi.org/10.1029/2018MS001540.

178. Haynes KD, Baker IT, Denning AS, Wolf S, Wohlfahrt G, Kiely G, et al. Representing grasslands using dynamic prognostic phenology based on biological growth stages: 2. Carbon cycling. J Adv Model Earth Syst. 2019b;11:4440–65. https://doi.org/10.1029/2018MS001541.

179. Schaefer K, Lantuit H, Romanovsky VE, Schuur EAG, Witt R. The impact of permafrost carbon feedback on global climate. Environ Res Lett. 2014;9:085003. https://doi.org/10.1088/1748-9326/9/8/085003.

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