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1. Supplementary Methods

1.1 Holocene* nomenclature

We refer to organic matter produced *via* photosynthesis in and around the thermokarst basins as 'Holocene*' since the majority (93%) accumulated from 11.7 kya to present (Fig. 3d); however, it should be noted that 7% of the non-yedoma, peat-rich carbon (C) pool indicated by 'Holocene*' actually accumulated in thermokarst basins that formed prior to the Holocene during the deglacial warming between 14 and 11.7 kya. This follows terminology common to peatland studies[12,14]. Without the *, Holocene refers to the period of 11.7 kya to present.

1.2 Macrofossils

The distinctly different climates of the late Pleistocene (cold, dry) *vs*. Holocene (relatively warmer and wetter) supported different types of environments and ecosystems, with distinct, representative plant functional types. The steppe tundra environment of the late Pleistocene resulted in plant macrofossils preserved in permafrost and lake sediments consisting primarily of graminoid taxa[59,76], while warmer, wetter Holocene climate, driven in part by thawing permafrost, resulted in plant macrofossils consisting of aquatic and wetland vegetation[77], which in these alas settings represent thermokarst activity that resulted from the warmer Holocene climate[59]. The organic material in the Pleistocene yedoma was much more detrital than the Holocene organic matter.

To characterize macrofossil assemblages representing facies F1-F7, we washed with deionized water approximately 5 cc of wet soil from each of 225 field samples collected in alas and yedoma exposures through a 150-µm sieve. We recorded the occurrence of 61 different types of macrofossils collected in sieves. Some macrofossils were identified to species level (Table SI1). Pleistocene *vs*. Holocene macrofossil attributions were first made in the field laboratory and later confirmed by radiocarbon dating [Extended Data (ED) Table ED1]. Within each field sample, macrofossils were weighted with a 0 (absent), 1 (present, not dominant), or 5 (present, dominant)[78]. Each macrofossil was assigned to one of nine functional groups: Other aquatics, submerged aquatic mosses, wet aquatic moss (mosses that grow both submerged and emergent), wet sedge, other emergent vegetation, terrestrial, graminoid, unidentified, and dominating detritus in a silty matrix. Unidentified refers to large (>>150-µm), distinct macrofossils which we could not identify as terrestrial *vs*. aquatic. Dominating detritus refers to pieces of organic matter too small to visually identify, but which dominated the >150-µm particle size fraction retained by the sieve. We scored dominating detritus in samples with a silty matrix with a 5 since the detritus was the dominant macrofossil and since we could not visually determine if the detritus has a Pleistocene-steppe tundra (yedoma) origin or a Holocene thermokarst ecosystem origin. We ignored non-dominating detritus in samples with non-silty (peaty) matrices, assuming that the detritus had the same composition as the identifiable macrofossils in these samples.

Different types of plants, organisms, and their respective habitats result in differential preservation of macrofossils depending on the amount of cellulose *versus* lignin and preservation conditions such as redox and pH after the organisms died. The fact that a macrofossil was preserved at all, even if not abundant, signifies that it was present in the environment, which is an important distinction from pollen that could have blown in from elsewhere. In order to represent the observed macrofossils, we summed the number of 1's and 5's in each sample. This approach weights the more abundant macrofossils, but also shows the occurrence of the less abundant ones. To assess the relative contribution of each macrofossil functional group to the average alas permafrost exposure,

we weighted the relative abundances of the functional groups by facies' organic matter content (Fig. 2a) and thickness.

Since the main purpose of this analysis was to provide secondary evidence for Holocene* *vs*. Pleistocene organic matter attribution in alas profiles, which is the basis for our calculation of 159 Pg Holocene* carbon in alases, we conservatively assumed that when detritus dominated a silty sample, that 100% of the detritus was of Pleistocene (yedoma) origin. This assumption is conservative because graminoid material in lacustrine deposits could also have been sedge, which is common to littoral wetlands. We found that on average, graminoid and detritus in a silty matrix (assumed to represent the main Pleistocene component) comprised 6% of the macrofossils in alas profiles (F1-F5). This suggests that other macrofossils indicative of warmer, wetter Holocene* environments[59,77], such as thermokarst lakes and their watersheds, were ≈94% of the alas profile macrofossils. The Holocene* macrofossil fraction would be larger than 94% if some of the detritus in silt matrices was considered as sedge from thermokarst shores.

To demonstrate that our results were not an artifact of the macrofossil weighting system (1=present, not dominant; 5=present, dominant), we also conducted the analysis (a) on dominants (5's) only, and (b) by removing the weighting altogether and instead giving all observed macrofossils a score of 1 regardless of their relative abundance in the samples. Using these alternative methods, the main Pleistocene macrofossils (graminoid and detritus in silt) were 9% and 3% of the macrofossils in the average alas profile, respectively. Using values greater than 5 for dominants, further devalues the 1's leading to results closer to those of method *a*; conversely, using values of 4, 3 or 2 instead of 5 for the dominants, relatively inflates the 1s, leading to results closer to those of method *b*. Thus, methods *a* and *b* provide upper and lower bounds (3-9%) on the Pleistocene, yedoma-derived component of macrofossil assemblages in alas profiles. This suggests the Holocene* component is 93-99% of total alas macrofossils.

1.3 Facies description

The sedimentology of deep thermokarst-lake basins has been described in several previous works[68,79-81]. For deep yedoma thermokarst lakes of North Siberia and Alaska, specifically, Hopkins & Kidd[68] identified a basal unit consisting of coarser-grained mineral sediments and detrital organic matter that forms near migrating thermokarst margins. As the lake expands and deepens due to ground-ice melt, an organic-rich, fine-grained sedimentary unit forms above the basal unit, characteristic of a quieter deep-water environment. Lacustrine peat often forms thick deposits when detrital organic matter accumulates along the lee shore of a lake. Finally, when lakes drain or partially drain, autochthonous peat forms in association with aquatic and terrestrial vegetation colonization of the basin floor.

In this study, we observed this general stratigraphic pattern in alas sediments and distinguished eight types of facies described here sequentially: F1 (Terrestrial peat), located at the surface of most exposures, consisted of well-preserved to humified terrestrial peat, representing post-drainage carbon accumulation (Fig. 2). This facies was similar in content and organic carbon bulk density to the terrestrial peat described in detail for alases formed in the yedoma deposits of the Northern Seward Peninsula, Alaska[69]. The roots of colonizing vegetation often extended into underlying deposits. In some exposures, mineral sediment at the base of F1 reflected either aeolian deposition or mineral-dominated lacustrine sediments. The thickness of F1 was 17 ± 2 cm (mean ± s.e., n = 33 sites; range 5-40 cm) in the exposures where it was distinguished separately from F1.5.

F2 (Benthic moss/ littoral peat), located above mineral-dominated lake sediments and beneath terrestrial peat sequences, consisted of the remains of benthic lake moss and littoral vegetation, including wet sedges and horsetail (*Equisetum fluviatile*), which grow along lake

margins and on floating mats at all stages of lake development. Benthic moss and other macrophytes have been reported to be particularly prolific along protected shorelines and bays in thermokarst lakes[22,68,79], forming thick autochthonous peat. Contrary to thermokarst lakes in the Mackenzie River Delta region, Canada, in which the strong disturbance of sedimentation associated with retrogressive thaw-slumping prevents moss growth along thermokarst margins[22], we observed benthic, brown moss growing abundantly in all littoral zones of actively expanding yedoma thermokarst lakes in Siberia and Alaska (unpublished data). Our observations were consistent with previous studies of benthic moss ecology, in that mosses were most prolific in environments with less disturbance of active sedimentation[22,82]; however, even along the thermokarst margins with regular erosion and sedimentation, mosses were often well-established. The densest crops of benthic moss we observed were growing to the lake surface adjacent to floating mats in partially drained, yet still deep (8 to 12-m maximum depth) thermokarst lakes in Siberian yedoma. We also observed dense benthic moss stands on the bottoms of smaller (20-30 m diameter), actively expanding thermokarst ponds. In these ponds, the mosses grew from the sediments to the pond surface around all margins. The intact, undecomposed strands of moss that comprised the thick, benthic moss facies in drained, refrozen alas sequences suggests moss peat formation occurred *in situ* (autochthonously) in lakes during the Holocene and not as a result of sediment focusing of eroded organic matter. We commonly observed intact leaves on the moss stems in refrozen paleolake sediments. Preservation of moss may be enhanced relative to vascular plants, given that moss tissues are more resistant to decomposition[83,84]. Among permafrost exposures, the thickness of F2 was 73 ± 21 cm (mean ± s.e., n = 15 sites; range 5 to 250 cm). Outside of F2, thinner peat horizons dominated by benthic moss (0.5 to 5 cm) were commonly observed and included with calculations of the stratified muddy peat (F3) facies. Benthic moss also often comprised thicker buried peat horizons (F4).

In nine permafrost exposures, where the transition from aquatic to terrestrial vegetation was not delineated in fieldwork, the F1.5 facies refers to the combination of organic matter produced in wet environments (benthic lake moss and/or sedge/horsetail peat) that transitioned to humified and well-preserved terrestrial peat.

Stratified muddy peat (F3), on average 3.1 m thick in exposures, consisted of alternating layers of light-colored mineral horizons and dark, organic-rich horizons. Individual horizons within this facies typically ranged from 1 cm to 30 cm thickness; however, this facies often included finer (millimeter to centimeter scale) laminations as well. Murton[79] referred to this facies as 'mud/muddy peat' to distinguish it from detrital peat by the abundance of mud. In F3, we identified macrofossil remains of allochthonous and autochthonous productivity, including brown moss leaves intact on moss stems protruding from fine laminations, wood fragments and mollusk shells. The strata were horizontal to sharply dipping, depending on their proximity to ice-wedge casts. Strata were laterally continuous for 10^1 to 10^3 m in permafrost exposures across drained, refrozen lake basins. F3 forms by suspension settling of fine, low-density material typically in the deeper water zones of thermokarst lakes[68,79]; thus F3 was thickest (≤12 m) beneath basin centers; however, we observed laminated F3 lake sediments >2 m thick within 15 m from former thermokarst-lake shores.

Buried peat horizons (F4) were organic-rich, horizontally continuous peat layers with a thickness of 24 ± 9 cm (mean ± s.e., n = 23 sites; range 5-190 cm) buried beneath mineral-dominated lake sediments. In some cases, these well-preserved to humified peat-rich horizons originally formed as terrestrial soils, littoral wetland soils, or benthic moss mats in lakes. They were subsequently submerged either intact or as peat blocks as a result of thermokarst subsidence, and then buried by lake sedimentation. In other cases, buried peat horizons in F4 formed when coarse and fine organic detritus or peat blocks drifted to small embayments and protected shores. Such

beach-like accumulations of detrital organic matter were reported to be more than a meter thick in deep yedoma lakes in Alaska[68], consistent with our observations in Siberia. When they occur as basal horizons, F4 peats are often detrital, containing a mixture of terrestrial and aquatic remains and woody debris that thicken and thin across the lake basin at semi-regular intervals (usually 10-m scale), where they fill in voids left by permafrost ice-wedge melting (Fig. 2b). These resulting undulating structures are known as ice-wedge casts[68,85].

We identified Lacustrine silt (F5) as massive grey silt containing autochthonous and allochthonous macrofossils, woody debris, and occasional peat blocks (usually ≤25 cm^2, but up to 500 cm^2 in cross section). This facies represents a near-shore depositional environment, in which yedoma silt that thawed subaerially on the lake bluff subsided and slumped into the lake bottom. This process of re-working from the bluff into the lake allows mixing of Holocene-aged terrestrial and aquatic organic matter with Pleistocene remains of thawed yedoma[86].

Taberite (F6) comes from a Russian term that refers to permafrost sediments thawed beneath a water body[5]. In this study, *taberite* refers specifically the diagenetically-altered component of Pleistocene yedoma that previously thawed *in situ* beneath the lake or stream and which is still present there today[5,76]. Taberites re-form permafrost together with other alas facies F2-F5 following lake drainage. Taberites have a low ice content that usually does not significantly exceed the sediment pore space. Taberites occurred beneath ice-wedge casts, and were distinguished from lacustrine grey silts based on the absence of autochthonous aquatic macrofossils or macrofossils characteristic of the Holocene terrestrial ecosystem [e.g. *Larix cajanderi*, ericaceous shrubs (*Vaccinium* spp., *Ledum* spp., *Salix* spp., *Betula nana*), *Eriophorum* spp., *Carex* spp., and *Sphagnum* spp. in drier (non-lake) settings and *Menyanthes trifoliata, Carex* spp., *Eriophorum* spp., *Drepanocladus* spp., *Scorpidium* spp. in wetter settings].

Yedoma (F7) refers to organic-rich, silt-dominated, loess, slope, and alluvial deposits with massive, syngenetic ice wedges that have not thawed since formation in the late Pleistocene[10,53,76]. High sedimentation rates that formed yedoma resulted from aeolian, slopewash and alluvial deposition of materials on the soil surface during the Pleistocene. Relatively undecomposed graminoid roots and other labile organic matter at the bottom of the unfrozen layer of soil were incorporated into permafrost. F7 was identified in exposures adjacent to deep, drained thermokarst lake basins.

Paleosols (F8; not shown) are Pleistocene-aged [>47 kcal yr before present (BP), n=1] organic-rich (106 ± 12 kg C m^{-3}, n=4) buried soils found occasionally in yedoma and taberite deposits. Although they were documented at a few exposure sites, due to low sample sizes and their rare occurrence, we ignored paleosols in site-level and regional carbon assessments.

1.4 Pleistocene *vs*. Holocene carbon in facies

Our upscaling calculations were based on the following assumptions: (a) 100% of the organic matter in facies F1-F2 and F4 was of non-yedoma origin, but rather was fixed by photosynthesis in plants associated with a warmer, wetter thermokarst-affected land surfaces during the deglacial warming and Holocene periods [Supplementary Information (SI) 1.1], (b) F3 facies organics are 83% Holocene* and 17% Pleistocene, (c) F5 facies organics are 53% Holocene* and 47% Pleistocene, and (d) 100% of organic matter in F6 and F7 is the result of photosynthesis in the steppe-tundra biome associated with yedoma formation in the Pleistocene[10,76].

We used three independent approaches to estimate these Holocene* *vs*. Pleistocene carbon fractions in the alas facies: (1) Macrofossil assemblages (Fig. 2a, Table SI1); (2) Radiocarbon ages (Fig. 2a, Table ED1); and (3) carbon bulk density mass balance equations.

Macrofossil analysis (SI 1.2) showed that fine graminoid leaves and roots, indicative of the Pleistocene-yedoma steppe-tundra biome, were observed only in the mineral-dominated facies: Stratified muddy peat (F3), lacustrine silt (F5), taberites (F6) and yedoma (F7). The peat-dominated facies (F1-F2, F4) contained only noticeable macrofossils indicative of Holocene environments in and around thermokarst-lakes. On average, graminoid remains and detrital organic matter found in the silt-dominated samples, which we assumed was 100% Pleistocene aged yedoma origin, comprised 6% (range 3-9%) of the macrofossils throughout the full F1-F5 thermokarst lake-basin sediments. Conversely, macrofossils characteristic of Holocene climates and environments comprised 94% (range 91-97%).

Scaling the Pleistocene macrofossil fraction of each facies by the facies' organic carbon contents and thicknesses, we determined that on average, 3% of the macrofossils in the alas facies (excluding F6) are Pleistocene-aged of yedoma origin. Since sample selection for radiocarbon dating was biased toward larger terrestrial macrofossils (Tables SI2 and SI3), potential underrepresentation of smaller and more decomposed Pleistocene graminoid macrofossils would lead to artificially low estimation of the Pleistocene carbon fraction in alas sediments. In an independent analysis, the radiocarbon age of bulk, mineral-dominated surface sediments collected from a present-day study lake (1.9 kcal yr BP), indicates that Pleistocene carbon (20–40 kya) constitutes 5–10% of the lake sediment carbon. This is within the same order of magnitude as the 3% Pleistocene carbon contribution to alas sediments determined from the macrofossil dating approach.

Radiocarbon dating of macrofossils picked from specific facies showed that 100% of the dates obtained on macrofossils collected from facies F1-F4 were younger than 13.8 kcal yr BP (Fig. 2a, Table ED1). This suggests that carbon fixation associated organic matter in these facies was contemporary with deglacial and Holocene thermokarst development on the landscape. Macrofossils collected from the lacustrine silt (F5) facies, representing yedoma that thawed and sloughed off of steep lake margins into lakes, gathering with it Holocene* terrestrial and aquatic organic matter prior to burial in the lake sediments, were 60% Pleistocene-aged (15.3-47.6 kcal yr BP). The majority of alas macrofossils dated were collected from basal units for the purpose of age-dating lake initiation and drainage events; thus the radiocarbon ages are biased toward the maximum ages of facies (Table ED1).

Finally, since the inorganic-rich facies, F3 and F5, comprised 75% of the alas sediment profile thickness (excluding F6) (Table ED1, Fig. ED2), and since the silt-dominated mineral matrix of F3 and F5 suggests a yedoma origin, determining the Pleistocene *versus* Holocene* carbon fraction for these facies has a large impact on upscaling calculations. We derived our Holocene* *versus* Pleistocene organic carbon ratios for F3 and F5 using a carbon mass balance approach based on conservative assumptions about the magnitude of yedoma carbon decomposed in these facies prior to sequestration in alas sediments (SI 1.7.2). We assumed that the thawed yedoma component of F5 lost the same amount of organic matter to decomposition as taberites (28 ± 12%) and that decomposition in the thawed yedoma component of F3 was twice as high (56 ± 24%) due to intensive reworking under conditions of prolonged exposure to oxygen prior to burial in anaerobic lake sediments[88,89]. Our calculation also considers that the thawed yedoma fraction of the F3 and F5 facies comprises 68 ± 7% and 73 ± 8% of the facies' volume, which we determined by solving the system of equations:

$$D_f = D_y \cdot V_y + D_p \cdot V_p \quad \text{Eq. 1}$$

$$V_y + V_p = 1 \quad \text{Eq. 2}$$

where D is dry bulk density, V is volumetric fraction, f is facies F3 or F5, y is thawed yedoma (taberites), and p is buried peat. Uncertainties are based on the standard errors of the means.

The conclusion that Holocene* carbon comprises a significant fraction of F3 and F5 total organic matter is corroborated by observations of macrofossil assemblages in these facies characteristic of organisms living in the Holocene*-aged lakes and their watershed ecosystems (Fig. 2a, Table SI1). Unlike taberite (F6) and yedoma (F7) facies that were dominated by terrestrial graminoid remains characteristic of the Pleistocene steppe-tundra ecosystem, the stratified muddy peat (F3) and lacustrine silt (F5) facies contained few terrestrial graminoid remains in the >150-µm size fraction. Instead, F3 and F5 were dominated by macrofossils characteristic of Holocene thermokarst environments: emergent wetland vegetation, benthic brown moss, zooplankton remains, and wood. Finally, the radiocarbon ages of macrofossils near the base of the F3 facies (7.93 ± 0.69 kcal yr BP, n=23; Table ED1) and bulk sediments generally in the upper two meters of the facies (1.58 ± 0.57 kcal yr BP, n = 7) suggested a dominance of Holocene-aged organic matter in F3. Section SI 1.7 provides an uncertainty analysis of the Pleistocene *vs*. Holocene* carbon attribution for the alas facies and the impact on the regional upscaling calculations.

1.5 Downstream export of thawed yedoma

Our calculations assumed small rivers and streams associated with thermoerosional gullies exported 70% of yedoma volume thawed beneath them to the sea, including to deltas and continental shelves, based on field observations of yedoma thickness at the thermoerosional gully site, DUV-26. The remaining 30% of thawed yedoma was partially decomposed *in situ* in F5 and F6 facies, with mean thicknesses of 1.2 m and 2.6 m, respectively, consistent with the geomorphology and stratigraphy observed in Duv-26. The organic carbon mass balance of the Pleistocene carbon in thermoerosional gullies is associated with high uncertainty since it is based on only one field site. However, similar stratigraphies described for thermoerosional gullies in other yedoma subregions[57-59] suggest that the calculation parameters are reasonable. Since yedoma organic matter is highly labile, it is likely that a fraction of the material exported from the land surface by fluvial processes was metabolized and converted to greenhouse gases[90] before or after reaching the sea; however due to insufficient information we did not estimate the magnitude of this process.

1.6 Radiative forcing impact of deep thermokarst-lake carbon fluxes

We adapted an atmospheric perturbation model[12] to construct a first-order quantification of the radiative forcing generated by organic carbon accumulation in thermokarst-lake basins and methane and carbon dioxide emissions from the basins. Flux trajectories used as input to the model were generated through the assessment of thermokarst-lake initiation (basal) dates, mass balance constraints of the total yedoma carbon lost to the atmosphere from lakes as carbon dioxide and methane (100 ± 34 Pg), total accumulated Holocene* carbon (159 ± 24 Pg), and observed contemporary methane fluxes.

1.6.1 Thermokarst-lake basal dates

We estimated rates of carbon loss to the atmosphere from lakes *versus* carbon gain from the atmosphere in lakes in 100-year time steps from 20 kya to the present based on the distribution of 85 thermokarst-lake basal dates compiled from previous publications and our own data for Beringia (Fig. 3a, Table SI2). We omitted data from profiles where the bottom of the Holocene* deposits were not reached in field sampling. To avoid introducing bias in binning dates by choosing arbitrary boundaries associated with measured basal ages, we calculated the number of lake initiation dates

within 1000-year time steps centered on each century following Walter *et al.*[2]. The one-thousand year time step for each date takes into account stratigraphical and spatial uncertainties in estimating basal ages (usually <1000 years). Similar methods are commonly used in peatland reconstructions[91,92]; however, the approach used here and by Walter *et al.* [2] and Brosius *et al.*[4] has the advantage that dates with larger age errors are not over-weighted in the binning. Radiocarbon dating procedures are described in Methods.

1.6.2 Yedoma-derived methane and carbon dioxide flux trajectories

To determine the flux trajectories of Pleistocene-aged methane and carbon dioxide emissions associated with thaw and decay of yedoma from thermokarst lakes in the yedoma region (Fig. 3b) we estimated instantaneous flux rates in 100-year intervals following these steps:

(1) We applied the mean trajectory on a per lake basis of methane and carbon dioxide produced from thawed yedoma deposits in thermokarst lakes from the time of lake initiation to 1.2 kyr after initiation following Kessler *et al.*[70]. The numerical simulation of thermokarst-lake methane and carbon dioxide production *versus* time is depth-integrated, accounting for three-dimensional expansion rates of an individual thermokarst lake and methane and carbon dioxide production since time of incorporation of thawed yedoma into the lake sediments[70].

(2) We initiated this trajectory of Pleistocene-aged methane and carbon dioxide production in each 100-year bin from 20 kya to the present. Each trajectory was weighted by the fraction of total lakes that formed in that bin. For each 100-year bin, we summed the individual-weighted methane and carbon dioxide production trajectories to determine total thermokarst-lake Pleistocene-aged methane and carbon dioxide production per year in each 100-year time step. Cumulative Pleistocene-aged methane and carbon dioxide production from 20 kya to the present was constrained by the mass-balance derived estimate of 100 ± 34 Pg C (Table ED3).

(3) Following previous literature[2,70,93], our calculations assumed a 1:1 stoichiometric relationship between carbon dioxide and methane produced from the labile fraction of thawed yedoma. The 1:1 production ratio [$CH_4/(CH_4+CO_2) = 0.5$] is not soil specific, but based upon theoretical chemistry of steady state methanogenesis with cellulose as primary substrate[94]. It can safely be assumed that cellulose and hemicellulose together are the dominating component of bulk plant material, particularly the non-woody steppe-tundra vegetation that dominated formation of yedoma soil organic matter. If alternative electron acceptors are present (e.g. O_2, nitrate, sulfate, ferric iron), the ratio shifts toward smaller values (CH_4 production < CO_2 production). It may also happen that the oxidation state of the remaining soil organic matter itself changes, allowing deviations of the ratio to smaller or higher values. We incubated yedoma soil collected from a permafrost exposure near Cherskii, Siberia at the Max Planck Institute (MPI) for Microbiology. Soil was incubated anoxically at 25°C for up to 300 days; temperature optima for methanogenesis in boreal and subarctic sites were found to be ≥ 25°C (95,96). Headspace gas concentrations were followed regularly by a GC-FID with methanizer[95]. The steady-state ratio of $CH_4/(CH_4+CO_2)$, after correcting for dissolved carbon dioxide, was about 0.6 and was reached after 90 days. Due to a small amount of available material, we had three replicate vials in the incubation for the first 21 days, and only one vial for 300 days. To test the sensitivity of the radiative forcing model (SI 1.6.6) to the production ratio, $CH_4/(CH_4+CO_2)$, we considered an uncertainty range of 40% (0.3 to 0.7). Results are shown in SI 1.6.6. Isotopic data from a separate pulse labeling experiment at the MPI with ^{13}C-acetate revealed that the ^{13}C signal was found in methane with only a minute effect on carbon dioxide. The ^{13}C experiment verifies that acetate, if available, was quantitatively converted to methane ruling out an effect of alternative electron acceptors that would otherwise drive the methane to carbon dioxide production ratio towards values less than 0.5. These findings were

consistent with ion chromatography results that showed that nitrite and nitrate were undetectable at the beginning of the incubation and that sulfate occurred in trace concentration (15 µM). Concentrations of all three species were below detection limit (<10 µM) after the incubation.

(4) Our calculations also assume that all methane and carbon dioxide produced from decomposed yedoma organic matter is emitted from lakes. Little is known about methane oxidation rates in yedoma lakes, a process that would effectively lower methane emissions and lead to the possibility of Pleistocene carbon assimilation by aquatic plants in lakes. Since the majority of simulated methane production at a given time is from a narrow zone of high production in deep talik sediments[97], ebullition is favored as the primary means of methane transport[100] and the opportunity for methane oxidation in transit is small[70]. Furthermore, $\delta^{13}C$ values of submerged mosses collected from a profile of paleolake sediments (-29.9 ± 0.7 ‰, n = 5), and submerged aquatic plants (benthic moss and *Potamageton* spp., mean ± s.e.) growing in two present-day Siberian study lakes with modern ^{14}C ages (104 ± 2 % modern carbon, n = 3) and $\delta^{13}C$ values (-29.5 ± 3.7‰, n = 3) showed no indication of yedoma carbon recycling in lakes (SI 1.7.1), including no evidence of methane oxidation influencing the dissolved inorganic carbon pool in lakes[101].

1.6.3 Holocene*-aged methane flux trajectory

Emission of methane formed from decomposition of non-yedoma organic matter fixed by photosynthesis in and around thermokarst basins during deglaciation and the Holocene is less well constrained than yedoma-derived greenhouse gases. This is because there is no equivalent direct record, such as the difference in carbon content between undisturbed yedoma and yedoma that thawed, partially decomposed in lakes, and then refroze after lake drainage. Similarly, carbon uptake also provides a more robust direct record, which is peat.

We estimated the instantaneous rates of Holocene* methane emissions in 100-year time steps from thermokarst lakes in the yedoma region (Fig. 3b) by assuming that modern lakes and drained lake basins are an analog for the past. This approach is similar to that used in previous modeling of peatland impacts on radiative forcing in the Holocene[12]. Year-round measurements of ebullition (daily measurements) and diffusion (biweekly measurements) on North Siberian yedoma thermokarst lakes revealed that mean annual emissions from late-stage and partially-drained lakes were 7.5 ± 1.3 g $C\text{-}CH_4$ m^{-2} a^{-1} (mean ± SE, n=4). Biweekly chamber-based measurements made from June through October 2003 in eight drained lake-basin fen and bog sites[1] showed that these environments emitted 4.8 ± 0.9 g $C\text{-}CH_4$ m^{-2} a^{-1} (mean ± **s.e.**). This is similar to the emissions measured in vegetated lake margins and shoals near the Lena River Delta, which is the far western extent of the yedoma region (2.9 g $C\text{-}CH_4$ m^{-2} a^{-1}) (67). Assuming that 100% of the methane emitted from these environments was Holocene-aged[102], we applied these methane emission rates to the distribution of thermokarst basins from 20 kya to present. Based on ^{14}C analysis of sediment facies (Table SI3), the Holocene*-methane emission trajectory assumes that during their open-water stage, lakes emit 7.5 g $C\text{-}CH_4$ for 5.2 kyr; after complete drainage, emissions in drained-lake basins are 4.8 g $C\text{-}CH_4$ m^{-2} a^{-1}. This approach assumes, like in peatland modeling[103], that Holocene*-aged methane emissions are constant over millennial timescales, ignoring possible century-scale to millennial-scale variations in these fluxes that could be driven by climatic shifts and natural lake successional development. For instance, methane emissions in lakes may be bimodal, with an initial emission peak associated with yedoma permafrost thaw and a second smaller peak associated with high plant productivity during the rapid peat-accumulating phase. Our calculations account for the yedoma-thaw peak, but due to a small sample size of later-stage lakes, we did not attempt to resolve Holocene* emissions from different open-water lake phases.

1.6.4 Carbon uptake flux trajectory

We calculated long-term apparent rates of Holocene* carbon accumulation by dividing the total Holocene* organic carbon mass in individual exposures by the total number of years the column represented. Multiple dates per column at some sites revealed consistency in the chronology of the profiles (Table SI3). We acknowledge that climate likely played a role in variable carbon accumulation rates during the Holocene; however we lacked temporal resolution in ^{14}C dates within the exposures to properly assess the inter-millennial carbon accumulation rate differences. Thus we did not draw any inferences from our data about the role of climate at different times during the Holocene in carbon accumulation rates in the deep yedoma lakes. The carbon uptake trajectory for all deep thermokarst basins in Beringia (Fig. 3b) was constructed from instantaneous carbon accumulation rates determined through these steps:

(5) Based on measured carbon accumulation rates and dated profiles, we determined the mean trajectory of Holocene* carbon accumulation in a thermokarst-lake basin from initiation to the present.

(6) We initiated this trajectory of carbon accumulation in each 100-year bin from 20 kya to the present. Each trajectory was weighted by the fraction of total lakes that formed in that bin. For each 100-year bin, we summed the individual weighted carbon accumulation trajectories to determine total thermokarst-lake Holocene* carbon accumulation per year in each 100-year time step.

1.6.5 Cumulative pools

We estimated the cumulative pool of Pleistocene-aged yedoma carbon decomposed in facies F3, F5, and F6 in thermokarst basins and loss to the atmosphere for the entire yedoma territory (Fig. 3d) by summing instantaneous carbon decomposition rates determined in step 2, taking into account the assumptions described in steps 3 and 4. The cumulative pool of Holocene* carbon accumulation in deep thermokarst basins in the entire yedoma territory (Fig. 3d) was estimated by summing the instantaneous carbon accumulation rates determined in step 6.

1.6.6 Modeling radiative forcing impacts

We adapted the simple five box atmospheric carbon dioxide model and one box first order methane oxidation model established for northern peatlands[12,103] to derive the net radiative effect of deep thermokarst basins from the onset of their formation during deglacial warming to the present (Fig. 3c). In this model, the competing radiative forcing impacts of sustained carbon uptake and methane and carbon dioxide emissions are modeled in a manner analogous to the Global Warming Potential (GWP) methodology[71,104,105]. Our adaptation to the peatland model consisted of considering the net carbon dioxide flux from thermokarst basins in 100-year time steps as equal to carbon dioxide uptake (peat accumulation) minus total carbon emissions from the decay of thawed yedoma. The methane that is emitted from yedoma carbon mineralization will be oxidized to carbon dioxide after a short (decades) residence time in the atmosphere. Since essentially all yedoma carbon was removed from the atmosphere in the late Pleistocene, this CO_2 resulting from methane oxidation must be included in the radiative forcing perturbation, along with the radiative forcing perturbation from the methane itself. This is not the case for the Holocene* fixed carbon that is emitted as methane, as the CO_2 flux budget for this carbon is based only on accumulated peat. In the model budgeting for this case, the carbon emitted as methane was not removed from the atmospheric CO_2 pool, so it should not be added back to the atmospheric CO_2 pool upon methane oxidation. In the model, the net methane flux perturbation equaled the combined flux of both yedoma-derived and Holocene* peat-derived carbon.

As in previous peatland carbon assessments[12,103], we considered peat accumulation in drained lake basins to represent net CO_2 uptake over the long-term. Vegetation biomass carbon per unit area in this region is quite small (≈1%)[106-110] relative to permafrost soil carbon; thus, the radiative impact of net accumulation/loss of carbon in vegetation biomass would be insignificant over long time scales compared to that of peat. Peat accumulation is the net of inputs and decay, with net peat loss expressed as a negative accumulation.

We used a simple representation of the GWP methodology; fluxes were modeled as atmospheric perturbations (positive or negative) to linear non-interacting, first-order reservoirs (e.g., 111). Net methane flux goes into a single atmospheric reservoir, while net carbon dioxide flux (usually uptake) is taken in different portions from five reservoirs with different lifetimes[72,112]. Unlike GWP calculations, this modeling approach can consider time series inputs and calculate time series radiative forcing. The total radiative forcing, RF_{total}, at any time t is calculated as the sum of the individual gas contributions, and can be written as

$$RF_{total}(t) = \sum_{i=0}^{5}\left(\varepsilon_i A_i f_i \cdot \int_0^t \Phi_i(t') e^{(t'-t)/\tau_i}\, dt'\right) \qquad \text{Eq. 3}$$

where ε_i is a multiplier for indirect effects, A_i is the radiative efficiency of greenhouse gas i (W m^{-2} of radiative forcing per kg of gas in the atmosphere), f_i is the fractional multiplier for the net flux into or from reservoir i, $\Phi_i(t')$ is the net flux of greenhouse gas i into the atmosphere at time t', and τ_i is the adjustment or residence time of the reservoir i. The integral term in Eq. 3, $\int_0^t \Phi_i(t') e^{(t'-t)/\tau_i} dt'$, is the concentration of gas i at time t due to all previous perturbations (since $t = 0$) and their partial to nearly complete removal from the atmosphere, modeled as first order removal from a collection of non-interacting reservoirs. Note that carbon dioxide is the greenhouse gas for reservoirs i = 0-4, and methane for reservoir i = 5. Parameters values (Table ED4) are from Ramaswamy *et al.*[71], Joos *et al.*[72], and Prather *et al.*[73].

The model assumes that net emissions of carbon dioxide and methane are small perturbations to the global atmosphere, so that lifetimes and radiative efficiencies can be considered to be constant, as is done in the GWP methodology[104]. Methane has a relatively short lifetime – long enough to be well-mixed in the global atmosphere, but short enough that within several decades a pulse input is almost completely removed from the atmosphere. A constant (or slowly-changing) methane source (or sink) will thus cause a temporary dynamic period (≈50 years) before stabilizing as a constant (or slowly-changing) radiative forcing perturbation; continued constant flux only maintains this new, constant state[12]. Carbon dioxide uptake (or emission) leaves a persistent negative (or positive) residual in the atmosphere, on time scales of up to millennia or longer (e.g., 113). Therefore, the atmosphere cannot come into equilibrium with constant carbon dioxide source or sink over the time scales we are considering. As a result, the magnitude of this residual offset continually increases. Eventually, this accumulating carbon dioxide impact overcomes the stronger radiative efficiency per unit mass of methane, and the instantaneous radiative forcing due to the impact on atmospheric composition of long-term emissions from thermokarst systems switches from net warming to ever-increasing net cooling.

Specifically, model results showed that deep yedoma thermokarst lakes had largely a warming effect on climate, constituting a net positive feedback to climate warming during deglaciation. Net radiative forcing associated with lake carbon fluxes peaked at 0.06 ± 0.03 W m^{-2} ≈9.5 kya (Fig. 3c). Net radiation switched from positive to negative values ≈5 kya, and since that time the lake basins have had an increasing net cooling impact on climate. The present net radiation associated with deep thermokarst lake basins is -0.06 ± 0.02 W m^{-2}.

Radiative forcing error estimates are based on the uncertainties in the carbon budget, which we assume are the dominant factors of uncertainty. Other important parameters controlling radiative forcing dynamics are the methane lifetime and the fraction of carbon dioxide partitioned into the very slow response pool (17.6%), as this has the strongest control on the rate of residual accumulation. This parameter is likely most related to the geologic carbon cycle. Model response is linearly proportional to radiative efficiency parameters for both gases. Large uncertainty in the methane lifetime will not change the general temporal evolution of the net radiative forcing (initial warming and eventual cooling), but will affect both the timing of the switchover and the magnitude of the forcing. For example, a shorter lifetime for methane (e.g., 114) would lead to a lower peak warming impact and an earlier transition to cooling. Results are also based on assumptions outlined in SI 1.6.2, including a 1:1 stoichiometric methane to carbon dioxide production ratio [$CH_4/(CH_4+CO_2) = 0.5$] associated with anaerobic decomposition of yedoma organic matter thawed beneath lakes. The sensitivity analysis showed that changing the ratio by ±40% (0.3-0.7) resulted in a +3% to -4% difference in the mid-Holocene switchover date from lakes having a positive warming impact to a negative cooling impact on climate. The maximum positive radiative forcing value was ±17% of the value based on a 0.5 ratio and the timing of the climax changed by +0.5% to -1%. Present day radiative forcing values were ±3% of the value based on a 0.5 ratio.

1.7 Uncertainty

This section assesses potential sources of variability in our estimates of yedoma thaw, degradation, and greenhouse gas release from thermokarst lakes (100 ± 34 Pg C) and of Holocene* carbon accumulation in the thermokarst basins (159 ± 24 Pg C). It also explains why we based our calculations on specific conservative assumptions. A summary of this uncertainty analysis is shown in Table ED3. Error terms here and throughout the manuscript are propagated errors based on the standard error of the mean, unless otherwise noted.

1.7.1 Pleistocene carbon recycling in lakes

In our attribution of Pleistocene *vs*. Holocene* carbon in the alas deposits we considered the possibility of Pleistocene carbon recycling in lakes. Submerged aquatic plants (including benthic mosses) could conceivably assimilate ^{14}C-depleted dissolved inorganic carbon originating from decomposition of Pleistocene-aged organic carbon and/or oxidation of methane produced from Pleistocene yedoma. Our field and lab data suggest that Pleistocene carbon recycling plays a minor to insignificant role in the deep thermokarst lakes. First, macrofossil analysis showed that ≈2/3 of macrofossils found in the lake sediments represented subaerial primary production (Fig. 2a), in which plants assimilated atmospheric carbon dioxide with contemporary Holocene ^{14}C ages. Second, submerged aquatic plants comprised approximately 1/3 of the macrofossils in the lake sediments. Radiocarbon dates of present-day submerged aquatic plants growing in the late-stage lake environments, where most of the *in situ* peat forms, had modern radiocarbon ages (104 ± 2 % modern carbon, n=3). Modern ^{14}C ages were also measured on submerged aquatic plants growing in the deep, rapid peat-accumulating lakes in Alaska[115]. The only location where we found that submerged aquatic plants had assimilated any ^{14}C-depleted carbon was along the actively expanding thermokarst margin of a present-day lake on the northern Seward Peninsula, Alaska. In this case ^{14}C ages of a benthic moss plant and a *Potamageton* spp. were 2.5 ± 0.02 kcal yr BP and 2.3 ± 0.02 kcal yr BP, respectively, signifying that Pleistocene carbon deposited 20–40 kya may be partially recycled in this thermokarst-margin environment. However, the thermokarst margins are not the major peat-forming environment in the lakes. We used an average ^{14}C age of all measured submerged aquatic plants in all environments of the three yedoma lakes studied in Siberia and

Alaska (0.78 ± 0.02 kya, n=5 plants), weighted by the ≈30% contribution of submerged aquatic plants to the macrofossils in the alas deposits, to determine that recycled Pleistocene carbon could contribute 0.6% to 1.2% of the organic carbon stock in alases that was fixed by photosynthesis during the Holocene. Much of the Pleistocene-age yedoma CO_2 would probably have been emitted, like the Pleistocene-aged methane was, during early stages of lake expansion, such that this ^{14}C-depleted CO_2 source would likely have been flushed from lakes by the time lakes had matured, partially drained and entered a stage that is more conducive to submerged plant growth. Finally, microbial oxidation of Pleistocene-aged methane could also potentially supply ^{14}C-depleted and ^{13}C-depleted inorganic carbon to submerged plant photosynthesis. Stable carbon isotope values of submerged aquatic plants in present-day lakes and as measured down an entire alas profile dating back 10.5 kya showed no indication of methane oxidation as a source of DIC in the lake (SI 1.6.2).

1.7.2. Uncertainty assessment for mineral-dominated F3 and F5 carbon composition

The assumption that decomposition of yedoma organic matter in F5 is the same as in taberites (F6, 28 ± 12%) is conservative because presumably some of the F5 yedoma sediment is subject to aerobic decomposition when it thaws and is exposed subaerially on the lake margin before slumping into the lake. Applying the upper limit of anaerobic decomposition observed in taberites (40%) to yedoma decomposition in F5 would increase the estimate of landscape scale Holocene* carbon pool in alases from 159 Pg to 163 Pg (Table ED3).

Our calculations also assume that for F3, 56 ± 24% of the organic matter fraction of yedoma decomposed during prolonged periods of oxygen exposure on thermokarst-lake bluffs and during re-working by waves and currents throughout the lake water column prior to storage in the F3, stratified muddy peat facies. This assumption is conservative because the abundance of graminoid macrofossils (indicative of Pleistocene steppe tundra, Fig. 2a) and isotopic mixing ratios of mineral-dominated (90% mineral) surface lake bulk sediments (^{14}C age 1.2 kcal yr BP, $\delta^{13}C$ -31.1‰, n=1) collected from a present-day lake suggested that modern submerged plants (^{14}C age 0.78 ± 0.66 kcal yr BP, δ^{13} -30.7 ± 2.4 ‰, n=5) and terrestrial plant macrofossils in surface sediments (^{14}C age 0.44 ± 0.12 kcal yr BP, δ^{13} -28.0 ± 0.7 ‰, n=3) comprised ≈97% of the F3 facies, while Pleistocene-aged yedoma carbon (^{14}C age 20-40 kcal yr BP; δ^{13} -24.9 ± 1.5 ‰, n = 2) were only ≈3%. Given the low sample size in the isotopic analysis and the likelihood that the macrofossil analysis missed a smaller particle-size graminoid fraction that would have washed through the 150 μm sieve, we used the conservative value of 56 ± 24% yedoma carbon decomposition (2 times the observed rate of anaerobic decomposition of yedoma organic matter) in our analysis. Using 95% yedoma organic matter decomposition in F3 instead of 56% would have increased the Holocene* carbon stock in deep thermokarst lake basins to 175 Pg (Table ED3).

1.7.3 Uncertainty in geospatial analysis

The uncertainties associated with the estimates of core yedoma permafrost area in Beringia (1,322,000 km^2) and the fraction of yedoma degraded since the early Holocene* (70%) (Methods) are difficult to quantify because many factors influence the accuracy of the maps on which the geospatial analysis was based: aerial image interpretation and field studies by field geologists and cartographers; scaling this information to 1:1 million scale maps, which effectively reduces its resolution; accuracy of map digitization; interpretation the digitized units as yedoma, and degraded yedoma or non-yedoma; and the occurrence of younger units overlying not fully degraded yedoma. Table ED3 shows the impact on the Holocene* and Pleistocene pool sizes for the yedoma-dominated region of Beringia based on a very conservative (20%) uncertainty and less conservative (10%) uncertainty. Table ED3 also shows the impact on upscaled carbon pool estimates of the

range of values for the fraction of yedoma that has been degraded by thermokarst (65-78%) observed among different regions of Beringia (Laptev Sea coast[44]; Kolyma region[45], and the Lena Delta yedoma region[47]. Future efforts to compare existing maps with higher resolution maps with complete coverage of the yedoma region and modern remote sensing data will reveal more quantitative differences in boundaries and areas depicted as yedoma and degraded yedoma.

1.7.4. Conservative calculation of deep-lake carbon stocks

Our estimate for the Holocene* deep yedoma lake carbon pool size (159 Pg) is conservative for the following additional reasons: (1) We conducted field work along river and coastal bluffs, landscape features that enhance drainage and slow modern peat accumulation on top of the bluffs. Drained, thermokarst-lake basins with lower drainage gradients further away from the bluffs were undersampled in our study, but are likely to retain higher levels of soil moisture leading to larger post-drainage carbon accumulation rates. (2) In boreal alases, we assumed woody biomass of dead trees buried in lake sediments (2.3 kg C m^{-2}) equivalent to the biomass observed in the present-day mid-succession *Larix* forest[110] and a 1:1 aboveground/belowground woody biomass ratio[116]. Due to uncertainties in its pool size, we did not include woody biomass of trees in tundra sites, despite our observation of large woody remains buried in some tundra lake sediments and although the boreal forest advanced over much of today's Siberian tundra region during the Holocene Optimum[117]. Applying the same woody biomass to the tundra region alases would increase the Holocene* carbon pool size in the yedoma-region alases by 0.5% (Table ED3). If we assumed instead a range of woody biomass observed among early succession, low-density (0.7 kg C m^{-2}) to mid-succession, high density larch forests (5.1 kg C m^{-2}) (110), the landscape scale-estimate of Holocene* carbon in alases would also change very little: 158-161 Pg. (3) Our boreal lake field sites were at the far northern boundary of the boreal zone. Given the apparent climate-driven gradient in carbon accumulation rates (Fig. 2f), it is possible that our boreal lake sites represent a minimum for boreal-zone yedoma lake carbon accumulation during the Holocene*. (4) Benthic mosses are known to dominate macrophyte communities in other non-yedoma high-latitude lakes[19,20,118-120]. To our knowledge no estimate of their cumulative carbon stocks in these lakes exists; however, carbon in these lakes would further increase the estimate of the high-latitude lake carbon pool.

Other sources of uncertainty have been quantitatively assessed for macrofossil weighting procedures (SI 1.2), yedoma thickness and excess ice content, facies' thickness, and variability in calculated carbon stocks among alas profiles (Methods, Table ED3).

1.8 Terrestrial soils and vegetation as indicators of yedoma lake fertilization

We sampled terrestrial soils and vegetation from four non-yedoma, Holocene floodplain sites and six Pleistocene yedoma upland sites to determine differences in plant and soil indices of nitrogen (N) and phosphorus availability on these two surface types. Sites were selected from road- or river-accessible areas in the Cherskii area (Fig. ED1) that had similar willow species (primarily *Salix pulchra, S. alaxensis, and S. glauca*). All sites were shrublands with a very low density of larch (*Larix cajanderi*).

In each site, fully expanded leaves of *Salix* spp. were sampled at peak biomass from 10 randomly chosen plants. At leaf senescence, the same plants were revisited and leaves that had undergone color change but had not yet fallen from the plant were sampled for litter analyses. Live leaf samples were dried at 60 °C for 48 hours and returned to the University of Florida (UF) for analyses. Litter was dried at 25 °C and returned to UF where subsamples were extracted for soluble C, nitrogen and phosphorus by submerging them in deionized water for 24 hours at a water to litter ratio of 100ml:10g. Extracts were filtered through a GF-F filter and analyzed immediately for

soluble C, nitrogen or phosphorus as described below. For analyses of total C, nitrogen and phosphorus, live leaf and litter samples were re-dried at 60 °C, ground on a Thomas-Wiley cutter mill (Thomas Scientific, Swedesboro, NJ, USA) fitted with a 40 screen and analyzed as described below.

In each site, soils were sampled in three randomly chosen locations. Organic soils were sampled by digging a small pit to the organic-mineral interface with a serrated knife and volumetrically sampling one of the exposed faces of the pit. At the bottom of the pit, mineral soils were sampled to 5 cm depth with a 7 cm diameter soil corer. Soils were returned to the lab in Cherskii, where they were homogenized by hand to remove coarse woody debris, large roots, and rocks. On organic and mineral soils, subsamples were dried at 60 °C for analyses of C, N and phosphorus (organic and mineral) or gravimetric water content (organic). Water content of mineral soils was determined on subsamples dried at 110 °C. Dried subsamples were then returned to the University of Florida (UF) for analyses. In Cherskii, a 20 g fresh weight subsample was extracted with 100 ml deionized water and filtered under vacuum through a Whatman GF-F filter. Extract subsamples for soluble phosphorus were acidified for transport to UF, while subsamples for carbon and nitrogen were frozen for transport.

At UF, litter and organic soil total carbon and nitrogen concentrations were analyzed on a Costech Analytical ECS 4010 Elemental Analyzer (Valencia, CA, USA). Total plant and organic soil phosphorus was prepared via a dry ash digestion method[121] and then analyzed on a colorimetric autoanalyzer (Astoria-Pacific, Clackamas, OR, USA). Mineral soil total phosphorus was digested via a four acid near-total method (MEICP-61) and analyzed with ICP-AES at ALS Geochemistry (Reno, Nevada, USA). Soluble litter and organic soil N in water extracts were analyzed on a Shimadzu Vcpn, (Shimadzu Corp. Kyoto, Japan) at the University of Minnesota. For soluble phosphorus, extracts were oxidized via persulfate digestion and then analyzed on the colorimetric autoanalyzer.

Samples were analyzed on a per-plant or per-core basis and averaged by site. Values tended to have heterogeneous variances, so differences between upland yedoma and Holocene floodplain surfaces were determined via Mann-Whitney U tests using Systat statistical software (Systat Software Inc., Chicago, IL, USA).

We found that soluble reactive phosphorus (P) concentrations in thawed yedoma ice wedges, which make up 50% of permafrost soil volume in the region[10], were approximately 0.28 mg P L^{-1} of ice-wedge melt water (Table ED5). In addition, water-extractable dissolved organic and inorganic phosphorus was three times higher in never-thawed yedoma than in thawed surface soils and produced 50% more soluble phosphorus over a one-year laboratory incubation (M.C.M. unpublished data). Finally, terrestrial plants on landscape surfaces with thawing Pleistocene-aged yedoma permafrost had higher phosphorus concentrations and lower phosphorus resorption from senescing leaves compared to those on adjacent Holocene floodplain sediments (Table ED5), suggesting greater phosphorus availability in yedoma. Together, this supports the hypothesis of phosphorus transport from thawed yedoma soils as the source of phosphorus driving high lake productivity (Fig. 1).

2. Supplementary Tables

Supplementary Table 1. Macrofossil identification in 225 field samples representing facies F1-F7 were grouped into nine functional groups: Other aquatics, submerged aquatic mosses, wet aquatic moss (mosses that grow both submerged and emergent), wet sedge, other emergent vegetation, terrestrial, graminoid, unidentified, and dominating detritus in a silty matrix (SI 1.2). The number of field samples analyzed for each facies is shown in the first row. Values in the cells show the number of occurrences of each macrofossil by facies (no parentheses) and the relative frequency with which any particular macrofossil dominated a sample (percentages in parentheses). For instance, *Scorpidium revolvens* was present in ten field samples classified as F2 (Benthic moss/ littoral peat), and it was the dominant macrofossil in 70% of these samples.

			Facies							
			F1	F1.5	F2	F3	F4	F5	F6	F7
			Terrestrial	Mixed	Benthic moss/ littoral peat	Stratified muddy peat	Buried peat	Lacustrine grey silt	Taberite	Yedoma
		Total number of field samples analyzed	13	5	39	78	36	32	15	7
Other aquatic		Aquatic plant (genus unidentified)						1 (0%)		
		Blue-green algae (genus unidentified)					1 (0%)			
		Daphnia spp. ephippia				10 (10%)	2 (0%)	7 (0%)		
		Chironomid head capsule (genus unidentified)			4 (0%)	11 (0%)	3 (0%)	5 (0%)		
		Ostracod (genus unidentified)				2 (0%)	2 (0%)	4 (0%)		
		Shells: bivalve (genus unidentified)						1 (0%)		
		Shells: (genus unidentified)				1 (0%)				
		Bryozoa (genus unidentified)				1 (0%)				
		Oribatid mite (genus unidentified)				2 (0%)		1 (0%)		
		Seeds: *Potamageton* spp.				2 (0%)		2 (0%)		
		Aquatic insect (genus unidentified)				1 (0%)				
Submerged aquatic moss		*Drepanocladus fluitans* (now: *Warnstorfia fluitans*)			2 (50%)		3 (100%)			
		Drepanocladus exannulatus (now: *Warnstorfia exannulata*)			2 (50%)	3 (67%)				
		Scorpidium scorpiodes		1 (0%)	10 (60%)	2 (50%)	6 (50%)	2 (100%)		
		Drepanocladus revolvens (now: *Scorpidium revolvens*)		1 (0%)	10 (70%)	3 (33%)	3 (33%)	2 (50%)		
		Submerged aquatic moss (genus unidentified)				1 (0%)	1 (100%)			
Wet aquatic moss		Moss -Amblystegiaceae (may also contain sumberged aq. moss)								
		Calliergon spp.					1 (0%)			
		Campylium spp.				1 (0%)	1 (0%)			
		Drepanocladus spp.			3 (33%)	12 (33%)	3 (33%)			
		Drepanocladus aduncus			7 (57%)		1 (100%)			
		Moss: wet type (genus unidentified)	3 (67%)		5 (40%)	10 (10%)	2 (0%)	4 (50%)		
		Wet brown moss (genus unidentified)			12 (83%)	7 (0%)	5 (40%)	4 (25%)		
Wet sedge		Sedge	3 (0%)	4 (75%)	31 (45%)	48 (42%)	27 (19%)	18 (72%)		1 (0%)
		Eriophorum spp.				2 (0%)				
		Seeds: *Carex* spp.				1 (0%)	1 (0%)			
		Seeds: Sedge		1 (0%)	3 (33%)	5 (0%)	2 (0%)			
Other emergent		*Equisetum* spp.		1 (100%)	8 (50%)	20 (40%)	10 (30%)	5 (0%)		
		Menyanthes trifoliata								
		Tomethypnum nitens						1 (0%)		
		Sphagnum spp.		2 (0%)	6 (0%)	11 (9%)	10 (90%)	11 (90%)	1 (0%)	
		Sphagnum riparium								
		Seeds: *Menyanthes trifoliata*		1 (0%)	1 (0%)		1 (0%)	1 (0%)		
Unidentified habitat		Roots: medium, fine (not necessarily upland, could be fen)	3 (67%)		4 (0%)	7 (29%)	2 (50%)	1 (0%)	1 (0%)	
		Seed: unidentified			2 (0%)	3 (0%)	3 (0%)	1 (0%)		
		Fecal material					1 (0%)			
		Mycorrhizae	1 (0%)			1 (0%)	1 (0%)			
		Insect remains: Unidentified, some possible aquatic, a beetle, chitin			1 (0%)	7 (0%)	1 (0%)	7 (0%)	3 (0%)	1 (0%)
		Roots: herbaceous					1 (0%)			
Dry upland		*Sphagnum fuscum*					1 (0%)	2 (0%)		
		Seeds: *Betula* spp.				5 (0%)		3 (0%)		
		Fungal scerlotia	1 (0%)	1 (0%)		4 (0%)	1 (0%)	2 (0%)		1 (0%)
		Moss: Upland, dry type (genus unidentified)	3 (100%)							
		Polytrichum spp.	2 (100%)				1 (0%)			
		Dicranum spp.	1 (100%)							
		Aulacomnium spp.				1 (0%)		1 (0%)		
		Hypnum spp.		1 (0%)						
		Mnium spp.			1 (0%)					
		Wood, bark	1 (0%)	1 (0%)	5 (40%)	18 (39%)	8 (13%)	8 (0%)	2 (0%)	3 (0%)
		Sphagnum section *Acutifolium*				1 (100%)	1 (0%)	1 (100%)		1 (0%)
		Vascular / ericacous leaves	1 (0%)		3 (0%)	10 (0%)	7 (0%)	5 (20%)		
		Vaccinium spp. leaves			2 (0%)		1 (0%)			
		Ledum palustre leaf		1 (0%)						
		Betula spp. leaf		1 (0%)	3 (0%)	3 (0%)	2 (0%)	2 (0%)		
		Salix spp. leaf			1 (0%)		1 (0%)			
		Larix cajanderi needles			2 (0%)	6 (0%)	3 (0%)			
		Seeds: Ericaceous (i.e. *Vaccinium uliginosum* or *Empetrum nigrum*)				1 (0%)				
		Charcoal	1 (0%)		1 (0%)	2 (0%)	1 (0%)	2 (0%)		1 (0%)
		Ericaceous roots	3 (100%)	2 (50%)	4 (25%)	13 (31%)	10 (40%)	5 (20%)	3 (0%)	
Dry graminoid		Graminoid: fine stems				2 (50%)		3 (33%)	12 (25%)	7 (100%)
		Graminoid: fine roots				1 (100%)			4 (25%)	7 (100%)
Detritus		Detritus in a silty matrix				32 (100%)	2 (100%)	15 (100%)	15 (100%)	2 (100%)

Supplementary Table 2. Basal ages of thermokarst lakes North Siberia, Alaska and Northwest Canada. Basal ages were compiled from the literature[2,4,59,79,101,122-137] and from AMS radiocarbon dates we acquired (see *) for macrofossils exposed at the base of lake cross sections along river and costal cut banks in Northeast Siberia, or from cores of modern lakes. Radiocarbon ages were calibrated to calendar 2-σ years BP using Calib 6.0 (40). Initiation dates of three natural thermokarst lakes within the last 40 years were observed by S.Z. and reported previously by Walter *et al.*[2] (see †). In some other lakes, basal sediments were not reached by coring or digging exposures (see minimum ages, ‡). In the later lakes, radiocarbon dates were used to quantify organic carbon accumulations rates above the dated material, but these minimum dates were omitted from Holocene*-scale analysis of carbon loss and gain (Fig. 3) since the basal dates were not obtained.

Reference	Reference	Lab ID	Location	Region	Lake Type	^{14}C Age (Yrs. BP)	Cal. Age (Yrs. BP)	Basal	Material dated
Walter et al. 2007	2	-	Kolyma, Yakutia	Siberia	yedoma	- -	40	†	-
Walter et al. 2007	2	-	Kolyma, Yakutia	Siberia	yedoma	- -	40	†	-
Walter et al. 2007	2	-	Kolyma, Yakutia	Siberia	yedoma	- -	40	†	-
This study	*	UCIAMS7064	Airport Lake-2	Siberia	non-yedoma	1,015 ± 20	940	‡	Fine light roots, rhyzomes, detritus
This study	*	OS-96395	Plaxhanski Yar (Pla-33-10)	Siberia	yedoma	1,200 ± 20	1,120		Plant
Lynch et al. 2003	122	Cams-22001	Interior Alaska (Duece Lake)	Alaska	non yedoma	1,300 ± 60	1,261		Wood
This study	*	UCIAMS-70668	Cape Chukochi (Dtlb-4-3)	Siberia	yedoma	2,070 ± 25	1,956		Wood
Hopkins & Robinson 1979	123	USGS-509	Beaufort Sea coast	Alaska	non yedoma	2,270 ± 20	2,324		Peat
Burn & Smith 1990	124	BGS-843	Mayo, Yukon Territory	NW Canada	yedoma	2,340 ± 100	2,431		Wood
This study	*	OS-96422	Cherskii, Yakutia (Cher-6)	Siberia	yedoma	2,530 ± 25	2,547		Wood
This study	*	UCIAMS-7058	Cherskii, Yakutia (Dry L.)*	Siberia	yedoma	2,885 ± 20	3,013	‡	Wood
This study	*	UCIAMS-7056	Cherskii, Yakutia (Grass L.)*	Siberia	yedoma	2,890 ± 20	3,016	‡	Moss
This study	*	UCIAMS-70683	Cape Chukochi (Chuk-11-2)	Siberia	yedoma	2,975 ± 20	3,148		Moss
This study	*	UCIAMS-7069	Cherskii, Yakutia (Tube Dispenser L.)	Siberia	yedoma	3,070 ± 20	3,224	‡	Organic detritus
Hopkins & Robinson 1979	123	USGS-501	Beaufort Sea coast	Alaska	non yedoma	3,130 ± 70	3,321		Peat
This study	*	OS-96396	Duvannii Yar (Duv-26-17)	Siberia	yedoma	3,170 ± 25	3,402	‡	Charcoal
Brosius et al. 2012	4	UCIAMS-70664	Cape Chukochi (Dtlb-5-2)	Siberia	yedoma	3,550 ± 20	3,862	‡	Plant
Brosius et al. 2012	4	UCIAMS-70663	Cape Chukochi (Chuk-17-1)	Siberia	yedoma	3,590 ± 20	3,884		Herbaceous
Anderson & Lozhkin 2002	125	MAG-177	Yana-Kolyma Lowland	Siberia	yedoma	3,885 ± 60	4,294		Peat
Burn & Smith 1990	124	WAT-2150	Mayo, Yukon Territory	NW Canada	yedoma	3,890 ± 80	4,306		Wood
This study	*	UCIAMS-7053	Cherskii, Yakutia (Shuchi L.)*	Siberia	yedoma	4,000 ± 25	4,438		Twigs, peat
Anderson & Lozhkin 2002	125	MAG-161	Kolyma lowland	Siberia	yedoma	3,955 ± 80	4,446		Peat
Brosius et al. 2012	4	UCIAMS-70627	Krestovski Cape (Kres-1-1)	Siberia	yedoma	4,370 ± 15	4,919		Herbaceous
Brosius et al. 2012	4	UCIAMS-70679	Krestovski Cape (Kres-12-5)	Siberia	yedoma	4,375 ± 25	5,023	‡	-
This study	*	OS-96397	Duvanni Yar (Duv-23-8)	Siberia	yedoma	4,740 ± 40	5,358	‡	Wood
Katamura et al. 2006	126	NUTA2-4699	Central Yakutia	Siberia	yedoma	4,641 ± 28	5,419		Plant
Brosius et al. 2012	4	UCIT21195	Seward Peninsula (Lake Rhonda)	Alaska	non yedoma	4,660 ± 20	5,419	‡	Plant
Brosius et al. 2012	4	UCIT21194	Seward Peninsula (Jaeger Lake)*	Alaska	yedoma	4,825 ± 20	5,591	‡	Plant
Brosius et al. 2012	4	UCIAMS-70637	Krestovski Cape (Kres-8-3)	Siberia	yedoma	5,045 ± 25	5,812		Peat
MacIntosh 1997	127	-	Yukon Territory	NW Canada	non yedoma	5,270 ± 80	6,061		-
This study	*	OS-96426	Duvanni Yar (Duv-13-17)	Siberia	yedoma	5,330 ± 25	6,097		Wood
This study	*	OS-96412	Duvanni Yar (Duv-11-13)	Siberia	yedoma	5,340 ± 30	6,105		Wood
Andreev & Klimanov 1989	128	-	Yakutia (Madjagara Lake)	Siberia	yedoma	5,480 ± 70	6,294		Bulk sediment
Andreev & Klimanov 1989	128	-	Yakutia (Nuochaga Lake)	Siberia	yedoma	5,550 ± 70	6,376		Bulk sediment
Brosius et al. 2012	4	UCIAMS-70645	Cape Chukochi (Chuk-3-2)	Siberia	yedoma	5,770 ± 20	6,568		Wood
This study	*	OS-96389	Duvanni Yar (Duv-27-9)	Siberia	yedoma	5,980 ± 40	6,700	‡	Plant
Hopkins & Robinson 1979	123	I-10329	Beaufort Sea coast	Alaska	non yedoma	6,234 ± 20	7,203		Wood
Brosius et al. 2012	4	UCIAMS-70681	Cape Chukochi (Chuk-1-1)	Siberia	yedoma	6,305 ± 20	7,220	‡	Moss
Anderson & Lozhkin 2002	125	MAG-156	Kolyma lowland	Siberia	yedoma	6,300 ± 60	7,242		Peat
Brosius et al. 2012	4	UCIAMS-70650	Cape Chukochi (Chuk-7-4)	Siberia	yedoma	6,695 ± 25	7,583		Herbaceous
Kaufmann & Hopkins 1985	129	W-1250	Seward Peninsula	Alaska	non yedoma	7,270 ± 350	8,125		Wood
Andreev & Klimanov 1989	128	-	Yakutia (Chabada 1 Lake)	Siberia	yedoma	7,740 ± 70	8,518		Bulk sediment
This study	*	OS-96749	Duvanni Yar (Duv-29-17)	Siberia	yedoma	7,930 ± 50	8,613		Wood
Katamura et al. 2006	126	NUTA2-4692	Central Yakutia	Siberia	yedoma	7,975 ± 32	8,856		Wood
Andreev et al. 2009	59	KIA12544	Bolshoy Lyakhovsky Island	Siberia	yedoma	8,020 ± 40	8,885		Wood
Edwards & Brigham-Grette 1990	130	-	Beaufort Sea coast	Alaska	non yedoma	8,110 ± 80	9,022		Organic detritus
Anderson & Lozhkin 2002	125	MAG-479	Kolyma lowland	Siberia	yedoma	8,370 ± 100	9,329		Peat
Brosius et al. 2012	4	UCIAMS-70646	Cape Chukochi (Chuk-4-5)	Siberia	yedoma	8,345 ± 25	9,370	‡	Wood

Supplementary Table 2 cont.

Hopkins & Robinson 1979	123	I-10332	Beaufort Sea coast	Alaska	non yedoma	8,435	± 160	9,396		Peat
Anderson & Lozhkin 2002	125	MAG-472	Kolyma lowland	Siberia	yedoma	8,450	± 100	9,397		Organic detritus
Anderson & Lozhkin 2002	125	MAG-138	Yana-Kolyma Lowland	Siberia	yedoma	8,450	± 160	9,405		Wood
Katamura et al. 2006	126	NUTA2-4690	Central Yakutia	Siberia	yedoma	8,453	± 33	9,482		Wood
Anderson & Lozhkin 2002	125	MAG-865	S. Chukotka	Siberia	yedoma	8,450	± 490	9,506		Peat
Burn & Smith 1990	124	BGS-842	Mayo, Yukon Territory	NW Canada	yedoma	8,520	± 120	9,569		Wood
Burn & Smith 1990	124	BGS-841	Mayo, Yukon Territory	NW Canada	yedoma	8,560	± 130	9,593		Wood
Tomidiaro 1982	131	-	Berelekh River, Yakutia	Siberia	yedoma	8,670	± -	9,600		-
This study /Brosius et al. 2012	*	UCIAMS-70662	Cape Chukochi (Chuk-16-3)	Siberia	yedoma	8,730	± 30	9,677		Wood
Anderson & Lozhkin 2002	125	MAG-243	Yana-Kolyma Lowland	Siberia	yedoma	8,620	± 200	9,721		Wood
Anderson & Lozhkin 2002	125	MAG-237	Yana-Kolyma Lowland	Siberia	yedoma	8,650	± 650	9,779		Wood
This study	*	OS-96429	Plaxhanski Yar (Pla-32-17)	Siberia	yedoma	9,020	± 40	9,975	‡	Wood
This study	*	OS-96469	Duvanni Yar (Duv-MJ15-11)	Siberia	yedoma	8,890	± 60	9,982	‡	Plant
Edwards & Brigham-Grette 1990	130	-	Beaufort Sea coast	Alaska	non yedoma	8,950	± 150	10,001		Organic detritus
Brosius et al. 2012	4	UCIAMS-70677	Krestovski Cape (Kres-4-2)	Siberia	yedoma	8,870	± 35	10,029	‡	Herbaceous
Kaufmann & Hopkins 1985	129	W-1255	Seward Peninsula	Alaska	non yedoma	9,020	± 350	10,290		Wood
Hopkins & Robinson 1979	123	I-10328	Beaufort Sea coast	Alaska	non yedoma	9,125	± 150	10,292		Peat
Hopkins & Robinson 1979	123	I-19368	Beaufort Sea coast	Alaska	non yedoma	9,180	± 50	10,339		Peat
Andreev & Klimanov 1989	128	-	Yakutia (Boduga Lake)	Siberia	yedoma	9,130	± 120	10,352		Bulk sediment
Brosius et al. 2012	4	UCIAMS-70640	Krestovski Cape (Kres-15-11)	Siberia	yedoma	9,225	± 25	10,359		Wood
Spiker et al. 1978	132	W-2619	Seward Peninsula	Alaska	non yedoma	9,190	± 350	10,377		Wood
Anderson & Lozhkin 2002	125	MAG-165	Kolyma lowland	Siberia	yedoma	9,200	± 150	10,444		Peat
This study	*	OS-96728	Plaxhanski Yar (Pla-31-37)	Siberia	yedoma	9,280	± 110	10,484		Plant
Edwards & Brigham-Grette 1990	130	-	Beaufort Sea coast	Alaska	non yedoma	9,350	± 80	10,518		Organic detritus
Anderson & Lozhkin 2002	125	MAG-123	Yana-Kolyma Lowland	Siberia	yedoma	9,315	± 50	10,523		Wood
Andreev et al. 2009	59	KIA12551	Bolshoy Lyakhovsky Island	Siberia	yedoma	9,320	± 60	10,531		-
Wooller et al. 2012	102	OS-86081	Qalluuraq Lake, Alaska Coastal Plain	Alaska	non yedoma	9,370	± 45	10,577		Plant
Brosius et al. 2012	4	UCIT21205	Seward Peninsula (Kit-22-2)	Alaska	yedoma	9,465	± 25	10,710		Wood
Katamura et al. 2006	126	Beta-201140	Central Yakutia	Siberia	yedoma	9,610	± 40	10,907		Wood
Murton 1996	79	-	Tuktoyaktuk Coastlands, Yukon	NW Canada	non yedoma	9,620	± 100	10,956		Peat
Spiker et al. 1978	132	W-2620	Seward Peninsula	Alaska	non yedoma	9,625	± 350	11,140		Wood
Anderson & Lozhkin 2002	125	MAG-257	Yana-Kolyma Lowland	Siberia	yedoma	9,910	± 50	11,313		Wood
Andreev et al. 1989	133	-	Yakutia	Siberia	yedoma	10,400	± 600	11,935		-
Walter et al. 2007	2	-	Southern Yukon Flats	Alaska	yedoma	10,320	± 140	12,148		-
Edwards & Brigham-Grette 1990	130	-	Beaufort Sea coast	Alaska	non yedoma	10,430	± 150	12,308		Organic detritus
Brosius et al. 2012	4	UCIT21189	Seward Peninsula (Kit-7-9)	Alaska	yedoma	10,375	± 25	12,315		Wood
Hopkins & Robinson 1979	123	USGS-517	Beaufort Sea coast	Alaska	non yedoma	10,600	± 180	12,445		Wood
Edwards & Brigham-Grette 1990	130	-	Beaufort Sea coast	Alaska	non yedoma	10,630	± 160	12,490		Organic detritus
Anderson & Lozhkin 2002	125	MAG-244	Yana-Kolyma Lowland	Siberia	yedoma	10,730	± 230	12,556		Wood
Harry et al. 1988	135	GSC-3986	Sabine Point, Yukon Territory	NW Canada	non yedoma	11,000	± 100	12,968		Peat
Brosius et al. 2012	4	UCIAMS-70628	Krestovski Cape (Kres-6-1)	Siberia	yedoma	11,295	± 25	13,196		Plant
This study	*	OS-96398	Duvanni Yar (Duv-22-15)	Siberia	yedoma	11,300	± 55	13,204		Plant
Kaufmann & Hopkins 1985	129	W-1254	Seward Peninsula	Alaska	non yedoma	11,340	± 400	13,251		Wood
Andreev 1996	135	-	Yakutia	Siberia	yedoma	11,550	± 120	13,441		-
Andreev et al. 2009	59	KI-4851	Bolshoy Lyakhovsky Island	Siberia	yedoma	11,570	± 90	13,446		-
Brosius et al. 2012	4	UCIAMS-70642	Krestovski Cape (Kres-16-9)	Siberia	yedoma	11,645	± 35	13,504		Herbaceous
Spiker et al. 1978	132	W-1205	Seward Peninsula	Alaska	non yedoma	11,550	± 350	13,506		Wood
Hill 1990	136	RIDDL 768	King Point, Yukon Territory	NW Canada	non yedoma	11,850	± 150	13,697		Wood
Brosius et al. 2012	4	UCIAMS-70644	Cape Chukochi (Chuk-2-2)	Siberia	yedoma	11,940	± 30	13,808		Herbaceous
This study	*	OS-96729	Duvanni Yar (Duv-21-15)	Siberia	yedoma	12,800	± 300	15,331		Plant
This study	*	OS-96392	Anuiy (Inu-3-20)	Siberia	yedoma	13,550	± 80	16,671		Plant
Anderson & Lozhkin 2002	125	MAG-1026	S. Chukotka	Siberia	yedoma	14,045	± 180	16,782		Wood
Harry et al. 1988	134	GSC-1792	Sabine Point, Yukon Territory	NW Canada	non yedoma	14,400	± 180	17,312		Oranic detritus
Mackay 1972	137	-	Tuktoyaktuk Coastlands, Yukon	NW Canada	non yedoma	17,860	± 240	21,222		Organic detritus

Supplementary Table 3. AMS radiocarbon dates and calibrated ages[40] of macrofossils sampled for determination of long-term apparent rates of carbon accumulation in North Siberian thermokarst lake basins, including present-day lakes (see *). Each carbon accumulation value (g C m^{-2} a^{-1}) was determined for a unique sedimentary sequence by dividing the carbon stock (g C m^{-2}) by the length of time the carbon accumulated (years). Carbon stocks were the sum of products of bulk density and organic carbon content measured on individual samples (organic carbon bulk density, g C m^{-3}), multiplied by the thickness (m) of the horizons from which the samples were taken. We determined the mean rate of carbon accumulation during the lake phase in our study lakes by averaging all rates that represented facies F2-F5 (see ‡): 47 ± 10 g C m^{-2} a^{-1}, mean ± s.e., n=20, 95% confidence interval 27-67 g C m^{-2} a^{-1} (138). We conducted an additional uncertainty analysis to consider errors in assumptions that are not accounted for in the population statistics (s.e.). These include (1) the assumption that carbon bulk density values measured on subsamples of horizons represent the carbon bulk density of the full horizon, and (2) that the dates which bookend the calculated carbon stocks accurately represent the deposition events. We assessed the uncertainty associated with assumption 1 using two independent field data sets: At one permafrost alas exposure site, we collected an integrated wedge sample containing a uniform volume of material from the full length of the 130-cm horizon. We determined a relative standard error of 4.0% in the organic carbon bulk density estimate based on four subsamples collected within the same horizon *versus* that based on the integrated sample from the full horizon. In another permafrost alas exposure, we sampled 90 cm of lake sediments at 1-cm intervals. We found a relative standard error of 2.1% in the organic carbon bulk density estimate based on subsampling approximately every 30 cm *vs.* using the high spatial resolution (1-cm) sampling. To assess the uncertainty associated with assumption 2, we radiocarbon dated two independent macrofossils collected from the same horizons in each of four different exposures (see †). Propagating errors associated with AMS dates, field sampling for ^{14}C dating, and subsampling horizons for carbon bulk density revealed that the cumulative error for these factors not accounted for in the s.e. was smaller (± 5 g C m^{-2} a^{-1}) than the s.e. of the sample population (± 10 g C m^{-2} a^{-1}). Of the total we estimate that Holocene* carbon accumulated at a rate of 42 ± 10 g C m^{-2} a^{-1}, n=20; however, since other studies do not distinguish carbon from different epochs, we presented the total carbon accumulation rate in Fig. 4 . Radiocarbon-dated lake sediment and peat deposits in yedoma alases in the Laptev Sea subregion[59] and in deep, non-yedoma lakes in Alaska[120] corroborated our findings of high organic carbon accumulation during the early Holocene. We applied the mean organic carbon bulk densities observed in 232 field samples of F1-F4 in this study (calculated from Table ED1), to the column thickness of lacustrine and terrestrial stratigraphic units described and dated by Andreev *et al.*[59], to show that carbon accumulation rates in our Kolyma subregion study sites were similar to those of the Laptev Sea subregion's yedoma alases (see §): (mean lake phase 75.2 g C m^{-2} a^{-1}, median 44.2 g C m^{-2} a^{-1}, range 1.3 to 182 g C m^{-2} a^{-1}). These deep lake carbon accumulation rates for Siberian lakes were similar to those studied in deep lakes in northern Alaska (30 and 130 g C m^{-2} a^{-1}) (120).

			Start date					End date			
Field ID	Depth (cm)	Lab ID	^{14}C age (Yrs. BP)	Calibrated age (Cal. Yrs. BP 2σ 95%)	Average age (Cal. Yrs. BP)	Material dated	Description	(Cal. Yrs. BP)	Represented facies	Thermokarst carbon accumulation (g C m^{-2} a^{-1})	
Grass L.-4*	93	UCIAMS-7082	505 ± 25	507 - 547	527	Plant	Moss, macrophyte	Present	F2	77.7	‡
Dry L.*	135	UCIAMS-7058	2,885 ± 20	2,948 - 3,078	3,013	Wood	-	Present	F3	7.6	‡
Shuchi L.*	202	UCIAMS-7055	1,485 ± 20	1,320 - 1,321	1,321	Organic detritus	-	Present	F3	26.2	‡
Tube Dispenser L.*	64	UCIAMS-7069	3,070 ± 20	3221 - 3226	3224	Organic detritus	-	Present	F3	6.2	‡
Tower L.*	131	UCIAMS-7060	290 ± 25	290 - 333	312	Plant	-	Present	F2, F3	60.5	‡
Cher-6	470	OS-96422	2,530 ± 25	2,496 - 2,597	2,547	Wood	Outer wood	Present	F1.5, F3, F4, F5	110.1	
Inu-1-3	76	OS-96423	8,490 ± 45	9,445 - 9,539	9,492	Plant	Sedge seeds	Present	F1, F2	5.0	
Inu-3-5	150	OS-96394	5,850 ± 30	6,566 - 6,588	6,577	Plant	Sedge	Present	F1, F2	10.0	
Inu-3-20	870	OS-96392	13,550 ± 80	16,413 - 16,929	16,671	Plant	Sedge, *Equisetum* spp., birch seed	6,577	F3, F4, F5	21.7	‡
Duv-11-14	52	OS-96393	425 ± 20	468 - 516	492	Wood	Bark	Present	F1, F2	53.7	
Duv-11-13	205	OS-96412	5,340 ± 30	6,000 - 6,210	6,105	Wood	Bark	492	F3, F4, F5	6.3	‡
Duv-13-17	305	OS-96426	5,330 ± 25	6,000 - 6,193	6,097	Wood	Bark, outer wood	Present	F1, F3, F4	23.7	
Duv-MJ15-11	300	OS-96469	8,890 ± 60	9,767 - 10,196	9,982	Plant	*Equisetum* spp., *Betula nana* leaf	Present	F3, F4, F5	20.3	‡
Duv-21-15	475	OS-96729	12,800 ± 300	14,123 - 16,538	15,331	Plant	Sedge	Present	F1, F3, F5	10.4	
Duv-22-11	150	OS-96390	1,760 ± 20	1,608 - 1,724	1,666	Plant	*Larix* spp. needles	Present	F1.5	76.9	
Duv-22-15	423	OS-96398	11,300 ± 55	13,093 - 13,314	13,204	Plant	Sedge	1,666	F3, F4, F5	9.6	‡
Duv-23-7	45	OS-96391	1,450 ± 25	1,302 - 1,382	1,342	Plant/wood	Seed, wood, sedge	Present	F1.5	24.8	
Duv-23-8	240	OS-96397	4,740 ± 40	5,326 - 5,389	5,358	Wood	Bark	1,342	F3, F5	19.2	‡
Duv-26-17	445	OS-96396	3,170 ± 25	3,359 - 3,445	3,402	Charcoal	-	Present	F1, F2, F5	42.5	
Duv-27-9	245	OS-96389	5,980 ± 40	6,699 - 6,700	6,700	Plant	*Larix* spp. needles	Present	F1, F2, F3	15.1	
Duv-29-11	280	OS-96406	1,860 ± 20	1,729 - 1,865	1,797	Plant	Sedge	Present	F1, F3, F4	72.7	
Duv-29-17	730	OS-96749	7,930 ± 50	8,610 - 8,616	8,613	Wood	Bark	1,797	F3	31.6	‡
Pla-31-6	75	OS-96475	6,600 ± 40	7,433 - 7,524	7,479	Plant	Seeds, sedge seeds, leaves	Present	F1.5	7.0	
Pla-31-8	125	OS-96450	3,300 ± 35	3,448 - 3,618	3,533	Plant	Larix spp. needles, *Betula nana* leaf	-	F2	-	
Pla-31-10	165	OS-96366	6,940 ± 40	7,679 - 7,853	7,766	Plant	*Betula nana* leaves, *Vaccinium* spp. leaf	-	F2	-	
Pla-31-15	265	OS-96457	6,800 ± 45	7,574 - 7,701	7,638	Plant	*Vaccinium* spp. Leaves	-	F2	-	
Pla-31-18	425	OS-96470	7,570 ± 55	8,207 - 8,262	8,235	Plant	*Larix* spp. needles	7,479	F2	185.0	‡
Pla-31-37	800	OS-96728	9,280 ± 110	10,230 - 10,737	10,484	Plant	Vascular plant leaves	8,235	F3	36.6	‡
Pla-32-17†	655	OS-96429	9,020 ± 40	9,966 - 9,984	9,975	Wood	*Betula* spp. bark	Present	F1, F3, F4	24.1	
Pla-32-21†	700	OS-96370	8,900 ± 55	9,780 - 9,850	9,815	Plant	*Betula* spp. katkins, seeds, leaves	Present	F1, F3, F4	25.7	
Pla-33-10	155	OS-96395	1,200 ± 20	1,063 - 1,176	1,120	Plant	*Larix* spp. needles	Present	F3, F4, F5	78.3	‡
Chuk-1-1	300	UCIAMS-70681	6,305 ± 20	7,171 - 7,268	7,220	Herbaceous	Moss	Present	F1, F3, F4, F5	15.0	
Chuk-2-2	51	UCIAMS-70644	11,940 ± 30	13,688 - 13,927	13,808	Herbaceous	Sedge, moss	Present	F1, F3, F4	1.3	
Chuk-3-2	560	UCIAMS-70645	5,770 ± 20	6,500 - 6,636	6,568	Wood	Twigs	Present	F1, F3, F4	31.2	
Chuk-4-5	220	UCIAMS-70646	8,345 ± 25	9,294 - 9,450	9,372	Wood	Wood	Present	F1, F3	7.7	
Chuk-7-1	60	UCIAMS-70649	3,740 ± 20	3,990 - 4,043	4,017	Wood	Sticks	Present	F1, F2	15.4	
Chuk-7-4	700	UCIAMS-70650	6,695 ± 25	7,509 - 7,544	7,527	Herbaceous	-	4,017	F2, F3, F5	54.7	‡
Chuk-8-2	19	UCIAMS-70651	995 ± 20	802 - 810	806	Plant/Wood	Sticks, sedge	Present	F1, F2	13.9	
Chuk-10-2a†	40	UCIAMS-70653	530 ± 20	515 - 555	535	Herbaceous	Sedge	Present	F1, F2	71.2	
Chuk-10-2b†	40	UCIAMS-70654	905 ± 20	744 - 752	748	Wood	Wood	Present	F1, F2	50.9	
Chuk-10-8	340	UCIAMS-70686	2,740 ± 20	2,779 - 2,871	2,825	Plant	Moss, vascular plant	642	F2, F3, F4, F5	48.4	‡
Chuk-11-4	43	UCIAMS-70658	765 ± 20	672 - 726	699	Plant	Sedge leaves	Present	F1.5	27.0	
Chuk-11-2	800	UCIAMS-70683	2,975 ± 20	3,075 - 3,220	3,148	Plant	Moss	699	F3, F4, F5	107.7	‡
Chuk-12-4	440	UCIAMS-70660	3,535 ± 20	3,723 - 3,797	3,760	Wood	Wood	Present	F1, F3, F4	36.4	
Chuk-12-1	480	UCIAMS-70659	3,670 ± 20	3,926 - 3,950	3,938	Plant	Sedge	3,760	F4	74.0	‡
Chuk-16-2†	690	UCIAMS-70661	8,710 ± 25	9,555 - 9,710	9,633	Wood	Wood	3,938	F3, F5	36.0	
Chuk-16-3†	710	UCIAMS-70662	8,730 ± 30	9,557 - 9,797	9,677	Wood	Wood	3,938	F3, F5	35.7	‡
Dtlb-3-1	150	UCIAMS-70622	5,080 ± 20	5,749 - 5,830	5,790	Herbaceous	Sedge	Present	F1.5	9.4	
Dtlb-4-3a†	200	UCIAMS-70624	1,820 ± 20	1,710 - 1,818	1,764	Herbaceous	Plant	Present	F1, F3, F4, F5	44.8	
Dtlb-4-3b†	200	UCIAMS-70668	2,070 ± 25	1,952 - 1,959	1,956	Wood	Wood	Present	F1, F3, F4, F5	40.4	
Dtlb-5-2	600	UCIAMS-70664	3,550 ± 20	3,727 - 3,749	3,738	Plant	-	Present	F1, F3, F5	43.7	
Kres-1-1	290	UCIAMS-70627	4,370 ± 15	4,866 - 4,971	4,919	Herbaceous	Plant roots	Present	F1, F3, F4	21.7	
Kres-4-2	165	UCIAMS-70677	8,870 ± 35	9,787 - 9,847	9,817	Herbaceous	Fine roots	Present	F1, F3, F5	7.8	
Kres-5-1	150	UCIAMS-70678	5,740 ± 20	6,473 - 6,572	6,523	Herbaceous	Sedge, fine roots	Present	F1, F2	15.5	
Kres-6-1	388	UCIAMS-70628	11,295 ± 25	13,109 - 13,283	13,196	Plant	Sedge, seed	Present	F1, F3, F4	6.6	
Kres-8-3	212	UCIAMS-70637	5,045 ± 25	5,729 - 5,895	5,812	Peat	Moss/ graminoid peat	Present	F1, F2, F3, F4, F5	16.1	
Kres-12-2	35	UCIAMS-70639	1,800 ± 25	1,628 - 1,655	1,642	Moss/Herbaceous	Stems	Present	F1	12.0	
Kres-12-5	300	UCIAMS-70679	4,375 ± 25	4,861 - 4,978	4,920	-	-	1,642	F3, F4, F5	25.7	‡
Kres-15-11	620	UCIAMS-70640	9,225 ± 25	10,275 - 10,443	10,359	Wood	Wood	Present	F1, F3, F4, F5	20.7	
Kres-16-9	265	UCIAMS-70642	11,645 ± 35	13,356 - 13,651	13,504	Herbaceous	-	Present	F1, F3, F4, F5	7.7	
L21-50-S21	20	-	7,590 ± 60	8,306 - 8,541	8,424	-	-	Present	F1	1.3	§
L21-50-S15	45	-	7,690 ± 60	8,395 - 8,586	8,491	-	-	8,424	F2	182.0	§
L21-50-S13/15	115	-	8,525 ± 65	9,422 - 9,628	9,525	-	-	8,491	F3, F4, F5	30.4	§
L21-50-S5	565	KI-4851'	11,730 ± 105	13,356 - 13,805	13,581	-	Peat and twigs	9,525	F4	42.0	§
L17-OS-63	135	KIA12545	3,700 ± 30	3,967 - 4,100	4,034	-	Peat	Present	F1, F2, F3	13.6	§
L17-OS-62	635	KIA12544	8,020 ± 35	8,753 - 9,017	8,885	-	Wood	4,034	F3, F4, F5	46.3	§
Mean ± SE lake-phase carbon accumulation										47 ± 10, n=20 (see ‡)	

3. Supplementary Discussion

3.1. Non-yedoma lake and peatland carbon

Long-term organic carbon accumulation rates numbered in Fig. 4 among lakes (#1-9) and peatlands (#10-42) were synthesized for the following northern hemisphere regions: (#1) Toolik Lake, Alaska, USA[139]; (#2) Greenland[140]; (#3) Quebec, Canada[35]; (#4) Alberta, Canada[141,142]; (#5-6) Finland[143,144]; (#7) Sweden[145]; (#8) Minnesota, USA[146,147]: (#9) Michigan, USA[148]; (#10) Elsmere Island, Canada[149]; (#11-14) Nunavut, Canada[150]; (#15 and 27) Saskatchewan, Canada[151,152]; (#16) NWT, Canada[153]; (#17 and 22-25) Alaska, USA[152,154,155]; (#18-19,26, and 28) West Siberian Lowlands, Russia[156,157]; (#20-21, 29-31, 35) Finland[158-160]; (#32-34) Alberta, Canada[161-163]; (#36) New Brunswick, Canada[164]; (#37) Québec, Canada[165]; (#38) Nova Scotia, Canada[164]; (#39-41) Scotland[166]; (#42) British Columbia, Canada[167].

3.2 Benthic-moss peat accumulation in yedoma lakes

Despite a paucity of benthic moss productivity data, particularly in the Arctic, and reports of slow growth rates in Char Lake[168], an ultraoligotrophic Canadian lake, moss production can be quite high under the right conditions[169]. Arscott *et al*.[170] reported high benthic moss productivity (≈99 g C m^{-2} a^{-1}) in phosphorus-enriched riffles of a tundra stream in north-central Alaska. Bowden (171) also presented relatively high values for benthic moss net production in streams (up to 109 g C m^{-2} a^{-1}). While our north Siberian lake moss-peat facies accumulation numbers are high (89 ± 15 g C m^{-2} a^{-1}, mean ± SE, n = 8, maximum 185 g C m^{-2} a^{-1}), they are not unprecedented.

We contend that nutrient availability in the yedoma thermokarst lakes contributed to high benthic brown moss productivity. Previous work in other non-yedoma/non-thermokarst lake systems has shown a strong response in benthic brown moss growth to phosphorus additions[20-22,82,172]. We assume that benthic brown mosses in the deep yedoma thermokarst lakes also respond to high phosphorus availability. The yedoma thermokarst-lake phosphorus concentrations (Figs. ED3 and ED4) are much higher than in other arctic lakes in Alaska and Canada[62] suggesting high phosphorus mobility in yedoma soils (SI 1.8). Furthermore, phosphorus and nitrogen concentrations in benthic brown mosses of yedoma thermokarst lakes were well-above critical concentrations (≈0.09% P, ≈1% N)[20] (Table ED5). Our field observations of benthic mosses in both present-day lakes and paleolake sediments in the northern boreal zone revealed that benthic mosses were not simply tolerating the harsh northern climate conditions in these boreal lakes, but they were thriving.

Benthic brown moss growth in the yedoma thermokarst lakes may also have been enhanced by a strong continental climate regime. During the early Holocene, when thermokarst-lake carbon was accumulating rapidly, orbital parameters were different[30] and resulted in higher summer insolation in high latitudes. High rates of peatland carbon accumulation in Alaska in the early Holocene were explained by higher seasonality (warmer summers, colder winters) driven by orbital parameters[92].

In addition to seasonality, moss photosynthesis can continue following freeze-up given their adaptation to low temperatures and their low light requirement. This can increase the growing season for these plants. We have observed this in numerous arctic lakes when winter lake ice grows down to the lake bed, encapsulating mosses in the ice column. Tiny bubbles released from photosynthesis and respiration surround the moss tissues, making a bright white halo in the ice around the plants.

Finally, peat accumulation is a function of both production and decomposition. Because the mosses were extremely well preserved (leaves intact on stems in refrozen lake sediments), we

suggest that it is not only production driven by greater nutrient availability that led to high peat accumulation, but also resistance to decomposition, especially compared to the other vascular plant material[83,84]. Conditions fostering organic matter preservation, cold and anoxia, also contribute to high carbon accumulation in lake bottoms. When lakes drain completely, organic matter in lake sediments rapidly freezes[25,173] , locking this carbon pool into permafrost.

3.3 Potential for a strong, future tundra-lake carbon sink

Holocene carbon accumulation and macrofossil records show that aquatic mosses and littoral vegetation contributed more to the lake carbon sink in the boreal zone than they did in the tundra zone. Carbon accumulation rates in the Holocene were 60% higher in the boreal lakes than in the tundra lakes (Fig. 2f), owing primarily to larger stocks of lake peat facies in boreal alases (Fig. 2e). Specifically, organic carbon stocks of F2 (benthic moss/ littoral peat facies) was 28 ± 9 kg C m^{-2} in boreal alases *vs*. 4 ± 2 kg C m^{-2} in tundra alases. For F4 (buried peat horizons), the carbon stocks were 21 ± 8 (boreal) *vs*. 10 ± 3 (tundra) kg C m^{-2}. Mean August water temperature measured in present-day lakes was also >5 °C warmer in boreal lakes (16.2 ± 1.0°C, n = 8 lakes) compared to tundra lakes (10.8 ± 0.6°C, n=5 lakes). Warmer lake surface temperatures and longer ice free seasons likely increased nutrient cycling and benthic moss primary productivity, leading to higher carbon accumulation in boreal lake sediments compared to the tundra lake sites (Fig. 2f). This suggests that the projected 2-7.5 °C warming[27] at high latitudes by 2100 AD could intensify this deep lake carbon sink in the future, particularly in tundra regions.

3.4 Future permafrost thaw

Organic-rich Holocene soils with air-filled pore space provide added protection against thaw to the deeper ice-rich permafrost[174], such as Pleistocene-aged yedoma. The protection of peat overlying mineral soils was far less available in the early Holocene. Despite this protection, at a localized scale, new thermokarst lakes have formed throughout the Holocene, including within the past few decades (Table SI2). These localized thermokarst features will likely continue to form in the future as temperature rises and disturbances occur.

Thermokarst-lake formation is an ongoing process that began primarily at the onset of deglaciation and continues today, including in regions with a permafrost-forming climate. Future widespread permafrost thaw is predicted under increasingly warmer climate conditions. Model projections of future widespread permafrost thaw in the yedoma region take into account thermal properties and moisture for distinct soil and ground layers, surface vegetation, snow cover depth and density, and air temperature[9,175]. Widespread surface permafrost loss is predicted as early as 2100 in some yedoma subregions[9,27]. Such models do not take into account any local-scale thermokarst or thermo-erosion and purely treat gradual top-down thaw for very large grid cells. Permafrost thaw is a complex process over multiple spatiotemporal scales, thus we cannot expect a uniform response everywhere. The resulting landscape will also be subject to complex process interactions, including carbon accumulation in local areas of wetting, but regionally we expect overall drying and increased decomposition associated with widespread permafrost thaw[176].

3.5. Reconciling previous carbon-stock estimates for the yedoma region

The size of the present-day Pleistocene-aged yedoma carbon pool was originally estimated to be 450 Pg (25) based on a mean deposit thickness of 25 m, 1 x 10^6 km^2 areal extent, 2.6% total organic carbon content, 1.65 x 10^3 kg m^{-3} dry bulk density, and 50% volumetric ice wedge content. This estimate assumed that 17% of the Last Glacial Maximum yedoma carbon stock was lost to greenhouse gas production and emission when 50% of yedoma thawed beneath lakes during the

Holocene*. The regional scale yedoma carbon pool estimate of Zimov *et al*.[10] did not include any Holocene* carbon.

In subsequent global permafrost carbon syntheses[6,13,177], soil organic carbon content (SOCC, kg C m^{-2}) data from the Northern Circumpolar Soil Carbon Database (NCSCD) and Zimov *et al*.[10] were used to estimate the soil organic carbon pool for the yedoma region (450 Pg), assuming only Pleistocene-aged yedoma carbon from 3 to 25 m (407 Pg), and predominately Pleistocene yedoma carbon in the 0 to 3 m interval (43 Pg).

Based on more extensive sampling of yedoma's ground ice content, Schirrmeister *et al*.[5] converted ground ice content to dry bulk density using a transfer function with dry bulk density and ground ice content measured on 13 samples collected near Cherskii, Russia by Dutta *et al*.[178]. Results suggested that the carbon bulk density of yedoma should be 25-50% lower than the value used by Zimov *et al*.[10]. A more recent synthesis of yedoma-region carbon stocks[11], taking into account the lower carbon bulk density values of yedoma, higher organic carbon concentrations, a larger landscape fraction of thermokarst (70% of yedoma region area) and its carbon content, and remote-sensing based quantification of ice-wedge volumes produced a lower mean-based estimate of yedoma-region carbon[179] (352 Pg). However, this study did not include taberite deposits, which are the re-frozen remains of yedoma previously thawed beneath lakes. Since the NCSCD global permafrost carbon synthesis was published prior to Strauss *et al*.[11] and focuses on the 0-3m depth range, revised results for deep yedoma from Schirrmeister *et al*.[5] were only partially taken into account in these new inventories[13,177,180].

In our study, we measured the dry bulk density directly on 89 yedoma and 311 thermokarst-basin samples collected in four yedoma subregions of the North Siberian Kolyma Lowlands. Multiplying the organic matter content of an individual sample by the same sample's measured bulk density yielded an organic carbon bulk density data set for yedoma samples that was normally distributed. Combining our subregion-specific organic carbon bulk density results with those of Schirrmeister *et al*.[5] for other yedoma subregions extending to the far western extent of Siberian yedoma, we determined a mean organic carbon bulk density of yedoma for the total yedoma region (26 ± 1.5 kg C m^{-3}, Table ED2). Our estimate of the organic carbon pool size of undisturbed yedoma permafrost (129 ± 30 Pg Pleistocene C) in the 396,600 ± 39,700 km^2 area that has not been degraded by thermokarst since the Last Glacial Maximum (Table ED3) is based on this regional-mean carbon bulk density value. Our calculation also assumes an average yedoma deposit thickness of 25 m and 50% volumetric massive ice wedge content (Methods), as in previous estimates[6,10,13,177] (Table ED3). Similar results found in the recent study of the yedoma-region carbon inventory by Strauss *et al*.[11] corroborate our estimate of the undisturbed yedoma carbon inventory[181].

Based on a larger number of thermokarst-basin sample sites (49 in this study *vs*. 10 in Strauss *et al*.[11]), a larger sample size (311 in this study *vs*. 41 in Strauss *et al*.[11]), and differentiation of thermokarst-lake facies, including taberite deposits, we estimate that an additional 155 Pg Pleistocene-aged organic carbon is stored in thermokarst-lake basins and thermoerosional gullies in the yedoma region of Beringia in facies F3, F5 and F6 (Table ED3). This Pleistocene-aged carbon represents the remains of yedoma that thawed and partially decomposed beneath and in thermokarst lakes and streams. Altogether we estimate a total Pleistocene-carbon pool size of 284 ± 40 Pg for this region in the present day as the sum of Pleistocene carbon in undisturbed yedoma and thermokarst basins (Table ED3).

Separately, Holocene*-aged organic carbon assimilated and sequestered in deglacial thermokarst basins in the yedoma-region is 159 ± 24 Pg. Our upscaling is based on the mean carbon stocks of individual permafrost exposures (Fig. 2e), which were normally distributed. We did not measure the carbon content of Holocene terrestrial soils overlying undisturbed yedoma permafrost;

however, applying values from the NCSCD in Siberia for Histels (44.3 kg C m^{-2}, 9% of yedoma region area), Orthels (26.0 kg C m^{-2}, 17% of yedoma region area) and Turbels (38.4 kg C m^{-2}, 63% of yedoma region area) to the extent of 1-m surface deposits overlying the area of undisturbed yedoma permafrost (396,000 ± 39,600 km^2), results in 12.9 ± 1.3 Pg of Holocene carbon. This calculation assumes that the 70/30 ratio of thermokarst to undisturbed yedoma (Methods) applies across the Histel, Orthel and Turbel cover classes.

Altogether, we estimate the Holocene* and Pleistocene organic carbon pool size in the yedoma region of Beringia as 456 ± 45 Pg (38% Holocene*, 62% Pleistocene) (Table ED3, Fig ED5). Despite the differences in approaches[179,181] and locations of study sites, similarities in the mean-based estimates of the yedoma-region organic carbon pool size between Strauss *et al*.[11] and this study corroborate our findings. Not accounting for diagenetically altered organic carbon from yedoma thawed *in situ* beneath lakes (taberites), Strauss *et al*.[11] estimated 352 Pg C for the regional pool size. Without taberite carbon, our estimate would be similar (342 Pg C). However, we argue that an accurate assessment of yedoma-region carbon must include taberite deposits because they are a large carbon pool that represents diagenetically-altered organic carbon from yedoma thawed *in situ* beneath lakes (Fig. ED5). Our estimate of yedoma-derived taberite deposits underlying thermokarst basins (114 Pg C), would bring the yedoma-region carbon pool estimate by Strauss *et al*.[11] up to 466 Pg C, which is similar to our estimate of 456 Pg C.

In summary, the yedoma-region organic carbon value (456 ± 45 Pg C, consisting of Pleistocene and Holocene* carbon) determined by this study is similar to that calculated originally by Zimov *et al*.[10] to represent only the Pleistocene yedoma carbon pool (450 Pg). Pleistocene-aged yedoma carbon was considered to be >90% of the regional pool by Tarnocai *et al*.[6] as well, and this yedoma regional carbon pool size (450 Pg) was subsequently assimilated into the NCSCD synthesis for quantification of circumpolar permafrost carbon [13,177]. The primary difference between the yedoma-region carbon pool estimate presented here *versus* by previous studies[6,10,13,177] is that in this study net carbon gains associated with a widespread thermokarst process are taken into account. The component of Pleistocene yedoma carbon was reduced in this study by 38% and a new Holocene*-thermokarst carbon pool (159 Pg) was introduced. We lowered the Pleistocene-aged yedoma carbon pool based on larger, more recent data sets on yedoma's dry bulk density by this study, Schirrmeister *et al*.[5], and Dutta *et al*.[178] and based on our more recent map-based analysis showing a 20% larger areal extent of deep thermokarst activity in the yedoma region (Methods).

Finally, we maintain that the deep thermokarst-basin Holocene* carbon pool estimate (159 ± 24 Pg) is a newly recognized soil organic carbon pool that has not been captured in the previous pan-arctic assessment by Tarnocai *et al*.[6] and Hugelius *et al*.[177] for four reasons:

(1) Upland soil (non-alas) pedons are disproportionately represented in past field data sets for the region. Within the 1,141,000 km^2 Siberian yedoma region (based on Romanovskii[41]; Fig. ED1a) the current NCSCD update for the 0-3 m depth range[177] lists 60 pedons representing 16 study sites; of these, only nine pedons (seven sites) are listed as the soil suborder Histel (permafrost peat soil). This apparent bias in the NCSCD data set toward sampling undisturbed upland soils, which we determined represent only 30% of the regional land surface (Methods), is likely explained by different scientific objectives of the field researchers. The basal depth of these 9 Histel pedons ranges from 1.65 m to 4.20 m. Of the NCSCD pedons, 11 are located in our field study region Kolyma lowland (four sites) and four of these pedons represent Histels (two sites) ranging in basal depth from 1.5 m to 1.9 m. Based on the level of detail available in the NCSCD, none of these existing pedons in the yedoma region appears to be interpreted as dominated by subaquatic mosses that accumulated in thermokarst lacustrine settings.

(2) Upscaling of the NCSCD pedons was done with transfer functions and landscape polygons that for Siberia are based on historical soil maps in the scale 1:2,500,000 (13). The level of detail provided at this scale is useful for pan-arctic assessments; however, it is insufficient to represent thermokarst-affected areas at regional scales and individual thermokarst basins are not resolved. Comparison between NCSCD polygons that at least partially contain Histels (5-100% Histels) indicates that the current NCSCD map scale is insufficient to represent peat soil carbon pools associated with widespread thermokarst landforms. Of the 1,141,000 km^2 Siberian yedoma region[41], only about 107,000 km^2 are covered with Histels based on the NCSCD (ca. $^1/_{10}$ of the total area). For the upscaling, the NCSCD assumes a uniform soil organic carbon stock of 44.3 kg m^{-2} for Histels in Siberia. The NCSCD Histels in the Siberian yedoma region store a total of 4.7 Pg C down to 1 m depth in this region, compared to our finding of 31 Pg Holocene* peat-carbon down to 1 m depth in the Siberian yedoma region's alases. Based on more detailed map information (Methods), we have learned that alases are 70% of the yedoma region land surface area. If the Histel-associated carbon stocks used in the NCSCD (44.3 kg m^{-2} in the surface 1-m) were scaled up to 70% of the area (area of alases) instead of 10% of the area, the pool size would increase to 32 Pg, which is similar to our estimate of 31 Pg in alases.

(3) Although the deep thermokarst-basin land-cover type was not specifically sampled or systematically accounted for by the NCSCD synthesis over the yedoma region - the whole region was assumed to be underlain by homogenous yedoma - the carbon stock for the top 1 m of the ground surface in Histel soils (44.3 kg m^{-2}) was not different from that measured in deep-thermokarst lake basins in this study (44.4 kg m^{-2}, assuming 10% ice wedge volume in the surface two meters in our study). This implies overlap in the near surface carbon stocks between this study and Tarnocai *et al*.[6]. For the 0-300 cm soil interval, our estimate for the soil organic carbon mass in deep thermokarst basins (114 Pg of which, 102 Pg C are Holocene*, across 925,400 km^2 thermokarst basins) is more than two times higher than that used by Tarnocai *et al*.[6] and Hugelius *et al*.[13] for the Siberian yedoma region (43 Pg across 1,141,000 km^2). Our field data show that Holocene*-aged carbon has accumulated at depths up to 13.7 m in thermokarst landscape features such as present-day lakes, drained and re-frozen thermokarst-lake basins, and thermoerosional gullies (Fig. ED2). It should also be noted that F3 and F5, facies that comprise the largest fraction of sedimentary carbon, tend to be located deeper in the alas profiles; therefore maps of surface soil deposits could easily miss them.

(4) Yedoma-region alas deposits have largely been studied in the context of geomorphology, cryostratigraphy, sedimentary facies, and paleoenvironment, lacking carbon data[59,68,80,182]. Very few studies have investigated the general organic carbon content of a small number of alases without taking into account the alas sedimentary facies[5,11,183]. One recent study, also with a paleoenvironment focus, presented carbon and some developmental stage descriptions from a single alas in Siberia[184]; this study was published after the permafrost region carbon inventories were completed. Another study quantified the organic carbon pool of peatlands that form in drained lake basins in a yedoma subregion of Alaska[69], without including the deeper lacustrine deposits. It is likely that additional unpublished alas carbon data sets exist, or that some occur only in Russian-language literature, which have not been taken into account in the NCSCD. To our knowledge, this is the first study to combine a geomorphologic classification of alas facies with carbon content, including the deeper lacustrine deposits, for the purpose of systematically upscaling to a regional alas carbon inventory.

The major implications of this study pertain to the nature and fate of greenhouse gas emissions associated with permafrost thaw in the yedoma region. Differentiation of the carbon pool in the yedoma region (yedoma *vs*. thermokarst basins) is critical to understanding past and future

carbon dynamics and climate feedbacks. Since a larger fraction of the landscape has already been degraded by thermokarst during the Holocene* (70% instead of 50%), the size of the anaerobically-vulnerable yedoma carbon pool for the production of methane is 40% lower than that calculated by others[6,10,13,177]. Second, there is concern that permafrost thaw will mobilize and release to the atmosphere 'ancient' organic carbon. Assuming average radiocarbon ages of Pleistocene-yedoma and Holocene* deposits of 30 kya and 6.5 kya respectively, accounting for the new Holocene*-aged thermokarst carbon pool (159 Pg C) lowers the average age of the current yedoma-region soil carbon pool by about one third. This result is important to global carbon-cycle modeling since carbon isotope signatures provide valuable constraints in models. Finally, given differences in permafrost soil organic matter origins for the Pleistocene-aged steppe-tundra yedoma carbon pool [accumulated under aerobic conditions; froze within decades to centuries after burial; and remained frozen for tens of thousands of years] and the lacustrine Holocene*-aged carbon pool [accumulated predominately under anaerobic conditions and remained thawed for centuries to millennia prior to freezing after lakes drained], it is likely that soil organic matter degradability differs substantially between these two pools. This has implications for differences in their vulnerability to decomposition and greenhouse gas production under scenarios of permafrost thaw in the future.

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