



Newly dated permafrost deposits and their paleo-ecological 1 inventory reveal a much warmer-than-today Eemian in Arctic 2

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1 2 Abstract. Fossil proxy records in Last Interglacial (LIG, ca. 130-115 ka) lacustrine thermokarst deposits now 3 preserved in permafrost can provide insights into terrestrial Arctic environments during a period when northern 4 hemisphere climate conditions were warmer than today and which might be considered a potential analog for a 5 near-future warmer Arctic. Still, such records are scarce on a circum-Arctic scale and often poorly dated. Even 6 more, the quantitative climate signals of LIG permafrost-preserved deposits have not yet been systematically 7 explored. 8 Here, we synthesize geochronological, cryolithological, paleo-ecological, and modeling data from one of the most 9 thoroughly studied LIG sites in NE Siberia, the permafrost sequences along the coasts of the Dmitry Laptev Strait, 10 i.e., on Bol'shoy Lyakhovsky Island and at the Oyogos Yar coast. We provide chronostratigraphic evidence by 11 new luminescence ages from lacustrine deposits exposed at the southern coast of Bol'shoy Lyakhovsky Island. The infrared-stimulated luminescence (IRSL) ages of 127.3±6.1 ka, 117.8±6.8 ka, and 117.6±6.0 ka capture the 12 13 MIS 5e sub-stage, i.e., the LIG. 14 The LIG lacustrine deposits are mostly preserved in ice-wedge pseudomorphs of 1-3 m thickness with alternating 15 layers of peaty plant detritus and clayish silt. Ripples and synsedimentary slumping structures indicate shallow-16 water conditions. The rich fossil record was examined for plant remains (macro-fossils, pollen, sedaDNA), lipid 17 biomarkers, and aquatic and terrestrial invertebrates (cladocera, mussels, snails, ostracods, chironomids, and beetles). 18 19 Most proxy data and also paleoclimate model results indicate a regional LIG climate significantly (ca. 5 to 10 °C) 20 warmer than today. Plant macrofossil data reflect mean temperatures of the warmest month (MTWA) of 12.7-15.3 21 °C for Oyogos Yar and 10.3-12.9 °C for Bol'shoy Lyakhovsky, while pollen-based reconstructions show mean 22 MTWA of 9.0±3.0 °C and 9.7±2.9 °C as well as mean annual precipitation (MAP) of 271±56 mm and 229±22 23 mm, respectively. The biomarker-based reconstruction of the Air Growing Season Temperature (Air GST) using 24 GDGTs is 2.8±0.3 °C. The fossil beetle-based mutual climatic range is 8 to 10.5 °C for MTWA and -34 to -26 °C 25 for the mean temperature of the coldest month (MTCO) on Bol'shoy Lyakhovsky Island and 8 to 14 °C for MWTA 26 and -38 to -26 °C for MTCO on Oyogos Yar. The chironomid-based MTWA varies between 9.4±1.7 and 15.3±1.5 27 °C and the water depth (WD) between 1.7±0.9 and 5.6±1.0 m on Bol'shoy Lyakhovsky Island. Prior findings from 28 Oyogos Yar in the literature suggest an MTWA of 12.9±0.9 °C and a WD of 2.2±1.1 m. The first-time application 29 of clumped isotopes to permafrost-preserved biogenic calcite of ostracods and bivalves reconstruct near-surface 30 water temperature of 10.3±3.0 °C and bottom water temperatures of 1.5±5.3 °C in thermokarst lakes during 31 summers. PaleoMIP Model simulations (PIobs+(lig127k-PI)) of the LIG show warmer MTWA compared to 32 modern conditions (by 4.4±1.0 °C for Bol'shoy Lyakhovsky and 4.5±1.2 °C for Oyogos Yar) but currently 33 underestimate the Eemian warming reconstructed from our multiple paleoecological proxies. 34 The LIG warming mainly affected summer conditions, whereas modern and future warming will rather impact 35 winter conditions. As the LIG annual mean temperature is often used as an analog for the future climate in the

36 High Arctic, the proxy-model mismatch highlights the urgent need for more systematic quantitative proxy-based

37 temperature reconstructions in the Arctic and more sophisticated Earth system models capable of capturing Arctic

38 paleoenvironmental conditions.





1 1 Introduction

2 The climate control on permafrost dynamics during the late Quaternary is reflected in large-scale permafrost 3 aggradation during glacial periods and extensive thaw in interglacial periods (Shur and Jorgenson, 2007; Jones et 4 al., 2023; Opel et al., 2024). These broader climate-driven dynamics were superimposed by local factors, including 5 topography, hydrology, and vegetation cover, as well as natural disturbances causing localized rapid thaw such as 6 thermokarst lakes or wildfires. During warm periods, rising air temperatures and, consequently, rising ground 7 temperatures and active-layer thickening promote ground-ice melting, surface subsidence, and the formation of 8 thermokarst lakes and basins in areas underlain by ice-rich permafrost (Czudek and Demek, 1970; Grosse et al., 9 2013; Brosius et al., 2021). Shallow thermokarst lakes might develop that can preserve traces of landscape 10 evolution, paleoclimate, and paleoecology in lacustrine sediments (Murton, 1996; Lenz et al., 2016; Bouchard et 11 al., 2017). Thawing ice-wedge polygons below the lake-water level form ice-wedge casts (pseudomorphs), which 12 may also preserve laminated lacustrine deposits (Farquharson et al., 2016). Lake drainage or desiccation over time 13 promotes the formation of typically palustrine (peaty) deposits above the lacustrine sequences in thermokarst 14 basins (e.g., Morgenstern et al., 2013). However, permafrost aggradation and degradation are not restricted to 15 glacial and interglacial periods, respectively. At least on the local to regional scale, permafrost formation is also 16 reported for interglacial times such as associated with pingo formation (Wetterich et al., 2018) or peat growth 17 during the Holocene (Kaplina, 2011a, 2011b; Wetterich et al., 2009) and permafrost degradation occurred during 18 interstadial stages of glacial periods (Vaks et al., 2020, 2013). 19 The globally warmer-than-today Last Interglacial (LIG, ca. 130-115 ka) is commonly seen as a potential analog 20 for future climate warming. Due to summer insolation higher than today and additional feedback effects such as 21 the retreat of ice sheets, reduction of summer sea ice, and expansion of boreal forests, the LIG warming in the 22 Arctic was amplified compared to the Northern Hemisphere as a whole (CAPE-LIG Project Members, 2006). 23 Recent studies combining proxy evidence across the Arctic (mainly from terrestrial and lacustrine pollen and plant 24 macrofossils and Greenland ice cores) and paleoclimate modeling largely agree on 4-5 °C higher summer 25 temperatures than today and a nearly sea-ice free Arctic Ocean during summers (Guarino et al., 2020; Sime et al., 26 2023; Vermassen et al., 2023), accompanied by a High Arctic greening (Crump et al., 2021). For a reduced 27 Greenland Ice Sheet, up to +5 °C regional warming is modeled for the LIG (Pfeiffer and Lohmann, 2016).

28 However, it is important to note that the warmer than today conditions during the LIG were predominantly driven 29 by increased summer solar insolation, unlike modern Arctic warming, which is most pronounced in winter due to 30 anthropogenic forcing. Despite this difference, many of the consequences of summer warming in the LIG - such 31 as ice sheet retreat, reduction of sea ice, and permafrost degradation - are observable in the changing Arctic today, 32 supporting the continued relevance of the LIG as an analog setting. There are only limited quantitative paleoclimate 33 data on the terrestrial interglacial MIS 5e conditions in the Arctic (e.g., CAPE-LIG Project Members, 2006; Sime 34 et al., 2023), with sparse sites that are widely spaced and which often have only single or few selected paleoproxies 35 and rather poor temporal constraints. Part of the mismatch between model and proxy data can be reconciled by 36 considering the potential seasonal bias of the proxy record and/or the uncertainties in the dating of the proxy 37 records for the LIG thermal maximum (Pfeiffer and Lohmann, 2016). Many terrestrial records of the LIG in the 38 Arctic are found in fluvial deposits exposed in river bluffs or artificial placer mining cuts in Alaska (Hamilton & 39 Brigham-Grette, 1991; Edwards et al., 2003; Jensen et al., 2013), Siberia (Velichko et al., 2008), or NW Canada 40 (Reyes et al., 2010). As interglacial climate conditions degraded pre-existing ice-rich permafrost deposits and also 41 promoted the formation of thermokarst basins and lakes, the interglacial legacy in permafrost regions is also





commonly represented by thaw unconformities and lacustrine and palustrine deposits. Some of these sites
 attributed to the LIG are known from eastern Siberia in the Yana-Indigirka Lowland (site Achagy-Allaikha,
 Kaplina, 1980, 1981) and the Kolyma Lowland (site Duvanny Yar; Kaplina, 2011a). Furthermore, the world's
 currently largest permafrost degradation feature, the Batagay megaslump in the Yana Upland in eastern Siberia,
 exposes a distinct woody debris layer below an erosional disconformity of Marine Isotope Stage (MIS) 5e age,
 i.e., the LIG that is overlain by MIS 4 to MIS 2 Yedoma Ice Complex deposits (Ashastina et al., 2017; Murton et al., 2022).

8 Extensive late Pleistocene paleoecological studies on ice-wedge pseudomorphs and other lacustrine sequences 9 were conducted on coastal exposures at both coasts of the Dmitry Laptev Strait that connects the Laptev and the 10 East Siberian seas (Figure 1). Both the southern coast of Bol'shoy Lyakhovsky Island near the Zimov'e River 11 mouth and the Oyogos Yar mainland coast near the Kondrat'eva River mouth have been studied for LIG pollen, 12 plant macrofossils, fossil insect remains including beetles and chironomids, lacustrine invertebrates such as 13 ostracods, cladocera, and mollusks, and testate amoebae and sedimentary ancient DNA (Andreev et al., 2004, 14 2011; Ilyashuk et al., 2006; Kienast et al., 2008, 2011; Wetterich et al., 2009; Schneider, 2010; Zimmermann et 15 al., 2017). However, only scarce chronological control is available (Andreev et al., 2004; Opel et al., 2017) for 16 lacustrine deposits, which are locally named the Krest-Yuryakh stratum (Tumskoy and Kuznetsova, 2022) and 17 commonly interpreted as deposits of the LIG, i.e., MIS 5e (Eemian). Mammal bones belonging to the late 18 Pleistocene Mammoth fauna in Krest-Yuryakh deposits are very rare and poorly dated (Kuznetsova et al., 2022). 19 Ancient thermokarst deposits and their paleoenvironmental inventory can provide interesting analogs for modern 20 and (near-)future warming and its impact on periglacial landscapes and ecosystems. During the Lateglacial to 21 Holocene transition, thermokarst processes re-shaped vast areas of the Beringian periglacial landscapes by thawing 22 the MIS 4 to MIS 2 Yedoma Ice Complex deposits (Jones et al., 2022; Walther Anthony et al., 2014, Morgenstern 23 et al., 2013), and paleoecological records from past warming episodes such as the Lateglacial Interstadials (e.g., 24 Allerød) and the early Holocene with rapid permafrost degradation are fairly well characterized, helping to 25 understand interactions between elimate, permafrost, and ecosystem dynamics. For example, previous paleobotanical studies associated with thermokarst deposits from NE Siberia revealed quantitative estimates of the 26 27 Lateglacial-early Holocene warming with a pollen-based mean temperature of the warmest month (MTWA) of 8-28 12 °C (Andreev et al., 2009, 2011). Likewise, the LIG elimate warming led to the degradation of previously 29 aggraded ice-rich permafrost deposits by thermokarst processes. A LIG (MIS 5e) macrofossil-based reconstruction 30 of MTWA reached >12.5 °C (Kienast et al., 2008, 2011), suggesting the potential for more intense warming during 31 MIS 5e, which in turn could be considered - at least in the amplitude - a representative analog for stronger modern 32 warming in the Arctic than during the Lateglacial or early Holocene.

33 According to Rovere et al. (2016), the global sea level of MIS 5e might have reached levels 5 to 9.4 m higher than 34 today. For north-eastern Siberia, especially for the Laptev Sea and the East Siberian Sea coastal regions, only 35 scarce information on the MIS 5e coastline is available and outlined below. According to Ivanenko (1998), a 36 distinctive feature of the Fadeevsky and Novaya Sibir islands (especially at their northern coasts; Figure 1) are 37 widely distributed marine deposits (called the Kanarchak Formation), which are overlain by terrestrial Yedoma 38 Ice Complex or, rarely, by terrestrial Holocene deposits. A smooth boundary between the marine and terrestrial 39 strata is striking, indicating a continuous sedimentation regime and uninterrupted transition from marine to 40 terrestrial conditions. According to Alekseev et al. (1991a, 2001), the lower part of the sections consists of marine 41 terrace deposits, assumed to have formed during the LIG (Kazantsevo period in Russian). The sandy series =





1 corresponding to the Kazantsevo transgression overlays the marine terrace deposits, which are today situated at 8-2 10 m above sea level (a.s.l.). Remnants of the marine terrace deposits with mollusk fauna are widely distributed 3 and well expressed on the Novaya Sibir, Fadeevsky, and Kotel'ny islands, mainly in the estuarine parts of river 4 valleys. Later studies on Novaya Sibir and Fadeevsky islands were undertaken by Basilyan et al. (2010), Tumskoy 5 (2012), and Nikolskiy et al. (2017), including first detailed investigations of the Kanarchak Formation that contains 6 a prominent massive ground ice body. These studies recognized the massive ground ice as a relic of a late mid-7 Pleistocene (MIS 6) glaciation, and the upper part of the Kanarchak Formation was assigned to the LIG (Basilyan 8 et al., 2010). We conclude that the northern coast of the Fadeevsky and Novaya Sibir islands is characterized by 9 marine and coastal deposits of the LIG, which delineate the approximate position of the coastline during MIS 5e. 10 Linking the paleoecologic records from the different locations in order to understand the regional context requires 11 a robust geochronological framework. While Lateglacial and early Holocene thermokarst deposits are commonly 12 well-constrained via radiocarbon dating (Wetterich et al., 2009), the chronostratigraphy of MIS 5 deposits 13 attributed to the LIG suffers from large dating uncertainties of the available dating methods that include 14 radioisotope disequilibria (230Th/U) of peat (Schirrmeister et al., 2002; Wetterich et al., 2016) and optically stimulated luminescence of quartz (OSL) or infrared stimulated luminescence of feldspar (IRSL) (Andreev et al., 15 16 2004; Opel et al., 2017). Therefore, the highly variable millennial climate dynamics from about 130 to 80 ka during 17 MIS 5 (expressed as MIS 5 sub-stages 5e to 5a; Shackleton et al., 2003) are not yet resolved in terrestrial permafrost 18 records and hinder the paleoclimatic interpretation of permafrost-preserved fossil proxy records.

19 Our study summarizes previously published and newly obtained data from coastal permafrost exposures at both 20 coasts of the Dmitry Laptev Strait to (1) provide new luminescence dates that constrain the timing of the LIG and 21 thus to resolve regional MIS 5e climate variability better; (2) summarize cryolithological and geochemical 22 characteristics of LIG deposits that capture depositional processes and preservation conditions; (3) deduce the 23 ecological response and quantify the paleoclimatic parameters linked to LIG warming as reflected by fossil proxy 24 data of vegetation, terrestrial and aquatic invertebrates, and compare them with results of climate model 25 simulations; and (4) discuss LIG climate-ecology-permafrost dynamics and their potential as analogs for the 26 ongoing and future climate warming in the terrestrial Siberian Arctic.

27 2 Study sites

The study sites stretch along the Dmitry Laptev Strait at the southern coast of Bol'shoy Lyakhovsky Island and the opposite mainland coast of Oyogos Yar (Figure 1). Various coastal outcrops, thaw slumps, and drill sites were studied along an approximately 16.5 km long section west and east of the Zimov'e River mouth on Bol'shoy Lyakhovsky (Figure 1b; Figure 2a) and along a 5.5 km long section west of the Kondrat'eva River mouth at the Oyogos Yar mainland coast (Figure 1c; Figure 2b). A recent review of the permafrost research history of the Dmitry Laptev Strait shores is provided in Tumskoy and Kuznetsova (2022).

The modern climate of the study area is characterized by short, cold summers with a mean July temperature (MTWA) of 2.5 to 2.8 °C (WMO stations 216470, 216360). Long, harsh winters of eight months are characterized by low light availability and low temperatures, with a mean January temperature (mean temperature of the coldest month, MTCO) of -34.4 to -33.1°C. The annual precipitation varies from 243 to 262 mm, yet overall conditions are humid due to low evaporation rates and poor drainage of the wet active layer during summer (Hersbach et al., 2020, ERA5, 1990-2019). The area belongs to the Arctic tundra subzone (Chernov and Makarova, 2008), more





- 1 specifically, the moist to dry tundra vegetation zone with open to continuous plant cover (G2) on Bol'shoy
- 2 Lyakhovsky Island and sedge/grass, moss wetland (W1) on the Oyogos Yar coast (CAVM Team, 2003).
- 3 The region is underlain by continuous permafrost with a thickness of 400-600 m, and the mean annual ground
- 4 temperature is about -14 to -12 °C (Yershov, 1989). The mean thickness of the active layer is about 30-40 cm
- 5 (Schwamborn and Wetterich, 2015).



Figure 1. Study area (a) in northeastern Siberia along the Dmitry Laptev Strait, (b) at the southern coast of Bol'shoy
Lyakhovsky Island, and (c) the opposite mainland coast of Oyogos Yar. The locations of sampling profiles of LIG
deposits are also indicated in Table A1 and Figure 2. The maps were compiled by Sebastian Laboor, AWI Potsdam,
using World Imagery (Credits: Esri, Maxar, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS,
AeroGRID, IGN, and the GIS User Community) and World Ocean Base (Credits: Esri, Garmin, GEBCO, NOAA
NGDC, and other contributors).





In its western, central, and eastern parts, Bol'shoy Lyakhovsky Island is shaped by hills reaching elevations of 1 2 about 100 to 300 m a.s.l. In the central part and the coastal region, Yedoma uplands up to 40 m a.s.l. are present 3 and dissected by large thermokarst basins (alases), wide and flat thermo-erosional valleys (logs), gullies or ravines (ovrags). The southern coast of Bol'shoy Lyakhovsky Island is characterized by vast retrogressive thaw slumps 4 5 (thermo-cirques), the mouth of the Zimov'e River, and numerous smaller streams. Widespread thermokarst 6 characterizes the Oyogos Yar mainland coast (Günther et al., 2013), covered by polygonal peatlands, shallow 7 thermokarst lakes, and erosional remnants of Yedoma uplands. The general stratigraphy of both coastal sections 8 with deposits between MIS 7 and MIS 1 is presented in Figure 2.



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14 **3** Material and methods

15 3.1 Fieldwork

Field studies on both sides of the Laptev Strait were conducted in the summers of 1999, 2002, 2007, and 2014, as
well as in spring of 2014 (Schirrmeister et al., 2000, 2003; Boike et al., 2008; Schwamborn and Wetterich, 2015).
After an initial survey, selected coastal exposures (Figure 2) were sampled in detail. Vertical profiles were cleaned
with spades and hoes to remove the outermost thawed material. The exposed sequences were surveyed, described,
photographed, and sketched to document sediment structures, cryostructures, color, and visible organic content.
The frozen deposits were sampled for further studies using hammers and small axes. In spring 2014, a Russian





- 1 drill rig (KMB3-15M) mounted on an all-terrain vehicle was used to retrieve permafrost cores on Bol'shoy
- 2 Lyakhovsky Island using a rotary mechanism in dry holes.
- 3 Sections of Krest-Yuryakh deposits sampled at the southern coast of Bol'shoy Lyakhovsky Island included the
- 4 profiles R35, R22+60, R23+40, L11+40, L12+30, L13+80 and L14 in 1999; the profiles L7-14, L7-11 and L7-16
- 5 in 2007; and the profile L14-12 and the permafrost core L14-04 in 2014 (Figure 2; Table A1). On the Oyogos Yar
- 6 coast, the profiles Oya-3-10, Oya-3-11, and Oya 5-1 were obtained in 2002, and the profiles Oy7-01, Oy7-07, and
- 7 Oy7-08 A-C in 2007 (Figure 2; Table A1).

8 Except for the permafrost core, the ice content of all permafrost samples was determined in the field in closed 9 aluminum boxes. The samples were weighed while still frozen, dried in a field oven, and weighed again. The 10 absolute gravimetric ice content is the ratio of the ice mass in a sample to the dry sample mass, expressed as a 11 percentage (van Everdingen, 2005).

In 1999, screening for rodent remains using a woody screen box with a metallic screen (1mm mesh) and a motor pump was carried out. Although no rodents were found, the screened sediment was used to extract insects. In addition, insects were collected by screening the thawed sediment with a 0.4 mm mesh. Plant macrofossils were excavated from insect samples and large (up to 2 kg) bulk samples. Large mammal bones were collected from the section and below at the seashore. Some small rodent teeth were picked up from mineral and plant debris below the section.

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20 3.2 Luminescence dating

Previous luminescence sampling in 1999 on Bol'shoy Lyakhovsky is described in Andreev et al. (2004, 2007) and on Oyogos Yar in Opel et al. (2017). In 2014, Krest-Yuryakh deposits were sampled at the southern coast of Bol'shoy Lyakhovsky Island for luminescence dating (profile L14-12, 73.34055°N, 141.28498°E; Figure 1). After cleaning and cryolithological description, the ca. 7 m high steep exposure was sampled for luminescence dating at heights of 4.5 m a.s.l. (L14-12-OSL1) and 2.7 m a.s.l. (L14-12-OSL3) (Table A1). We used a HILTI TE6 - A36 cordless rotary hammer to obtain frozen cores protected from sunlight that were packed dark, stored in an ice cellar next to the camp at -4 °C, and kept frozen until arrival in the laboratory.

28 The processing of sample cores aimed at extracting K-feldspars with grain sizes of 40-63 µm (L14-12-OSL1, L14-29 12-OSL3) and 63-90 µm (L14-12-OSL1). Coarser material (>100 µm) was lacking, or only a minor component, 30 and the quartz OSL signals were close to saturation. Pure mineral extracts were obtained via carbonate and organic removal (10% HCl and 30% H₂O₂, respectively), feldspar flotation (0.2% HF, pH 2.4-2.7, dodecylamine) for 31 32 efficient separation from quartz, density separation to enrich K feldspars (2.53-2.58 g cm⁻³) and 5 min final etching 33 in 10% HF. Extracted medium-sized feldspar grains were used to prepare sets of 24 aliquots with a 2 mm diameter. 34 Measurements and analyses for age estimation were based on 20 aliquots, while four aliquots per sample and grain 35 size fraction were used for quality tests. For L14-12-OSL3, five additional aliquots were used in equivalent dose 36 screening sequences to optimize the regenerative dose points. The IRSL signals of feldspars were measured using 37 a TL/OSL DA-20 reader (Bøtter-Jensen et al., 2003) equipped with a 90Sr beta irradiation source (4.95 Gy min⁻¹). Signals were stimulated at 870 nm (IR diodes, 125°C for 100 s) and detected through a 410 nm optical interference 38 39 filter (Krbetschek et al., 1997).

- 40 The measurement sequence followed the single-aliquot regenerative dose (SAR) protocol according to Murray
- 41 and Wintle (2000), including cycles to record recycling ratios and recuperation and to correct for sensitivity





- 1 changes. Preheat and cut-heat temperatures were set to 230 °C and 160 °C, respectively, according to preheat tests.
- 2 Emitted signals were recorded for 100 s to ensure the acquisition of pure background signals at the end of each
- 3 measurement cycle. Dose-recovery tests (Murray and Wintle, 2003) confirmed suitable luminescence properties
- under the chosen conditions with coefficients of variations between 3.8% and 5.3%. The data processing was
 performed using the R package "Luminescence" (Kreutzer et al., 2012), version 0.9.20.

6 The datasets (n = 20 to 25) revealed equivalent dose distributions of low skewness (below 0.8%) and low standard

deviations (below 5%). No evidence of insufficient bleaching or significant post-depositional mixing was found, and hence, paleodose estimates were based on the Central Age Model (CAM) (Galbraith et al., 1999). The CAMbased paleodose was then processed together with all sample-specific dose rates (sediment-internal, mineralinternal, cosmic) and correction (grain sizes, water content, sediment cover, etc.) parameters using the online DRAC calculator (Durcan et al., 2015). For the mineral-internal dose rate of the K feldspars, a potassium content

- 12 of $12.5 \pm 0.5\%$ was assumed (Huntley and Baril, 1997).
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14 **3.3** Sediment analyses

15 In the laboratory, the sediment samples were freeze-dried, carefully manually homogenized, and split into sub-16 samples for sedimentological, geochemical, and paleo-ecological analyses. Grain-size distribution was analyzed using a laser-particle analyzer (Beckmann Coulter LS 200) and computed with GRADISTAT 4.0 software (Blott 17 18 and Pye, 2001). The mass-specific magnetic susceptibility (MS) was measured using a Bartington MS2 instrument (MS2B sensor), and values are given in SI units (Le Système International d'Unités; $10^{-8} \text{ m}^3 \text{ kg}^{-1}$). The total organic 19 carbon (TOC) and total nitrogen (TN) contents were measured by a carbon-nitrogen-sulfur (CNS) analyzer 20 21 (Elementar Vario EL III), and the total organic carbon to total nitrogen ratio was calculated as TOC/TN ratio. 22 Stable carbon isotopes (δ^{13} C) of TOC were measured until 2014 with a Finnigan DELTA S mass spectrometer 23 coupled to a FLASH element analyzer and a CONFLO III gas mixing system after the removal of carbonates with 24 10% HCl in Ag-cups and combustion to CO₂. The accuracy of the measurements was determined by parallel 25 analysis of internal and international standard reference material. The analyses were accurate to ±0.2 ‰. Later, the 26 measurement was undertaken using a Thermo Scientific Delta V Advantage isotope ratio MS equipped with a 27 Flash 2000 organic elemental analyzer using helium as a carrier gas. The accuracy was better than ±0.15 ‰. The δ^{13} C values are expressed in delta per mil notation (δ , ∞) relative to the Vienna Pee Dee Belemnite (VPDB) 28 29 standard.

Values are given as per mil (‰) difference from the Vienna Pee Dee Belemnite (VPDB) standard for δ^{13} C and from nitrogen in ambient air (AIR) for δ^{15} N. The accuracy was better than ±0.15 ‰ for δ^{13} C and ±0.2 ‰ for δ^{15} N.

33 3.4 Paleo-ecological analyses and paleoclimate reconstructions

Pollen data are available (Table A1) from Bol'shoy Lyakhovsky Island from Krest-Yuryakh deposits in profiles
R22+60, L11+40, L12+30 and L14 (Andreev et al., 2004), R23+40 (Andreev et al., 2009), R35 (Ilyashuk et al.,
2006), L7-14 (Wetterich et al., 2009), and in the drill core and hand pieces of the permafrost core L14-04
(Zimmermann et al., 2017). On Oyogos Yar, pollen data were obtained from profiles Oy7-08 (Wetterich et al.,
2009) and Oya 5-1 (Kienast et al., 2011). The pollen sample preparation followed standard methods (e.g., Andreev
et al., 2004).





Pollen-based climate reconstructions were based on a northern hemispheric modern pollen training dataset 1 2 comprising 15,379 sites in Eurasia and North America (Herzschuh et al., 2023). Only terrestrial pollen taxa (including Cyperaceae) were used for reconstructions, while aquatic pollen taxa, as well as spores from mosses, 3 4 ferns, fungi, and algae, were excluded. Woody taxa, as well as some very common herbaceous taxa (e.g., 5 Artemisia, Thalictrum, or Rumex), were harmonized to the genus level, and all other herbaceous taxa were 6 harmonized to the family level (Herzschuh et al., 2022). Site-specific mean July temperatures (T_{July}) and annual 7 precipitation (Pann) were derived from WorldClim 2 version 2.1 (https://www.worldclim.org; Fick and Hijmans, 8 2017) by extracting the climate data at the location of the modern samples. The pollen taxa in the fossil pollen 9 samples noted above were harmonized in the same way as the taxa in the modern training dataset. For each 10 location, we calculated the geographic distance between each sampling site in the modern training dataset and the 11 fossil pollen record. Climate reconstructions were performed using the modern analog technique (MAT, Overpeck et al., 1985) by applying the MAT function from the rioja package (version 0.9-21, Juggins, 2019) for R (R Core 12 13 Team, 2020) to the pollen percentages of the selected fossil pollen taxa, looking for seven analogs between the 14 pollen data and the calibration dataset. The dissimilarity between the fossil samples and the modern pollen 15 assemblages was determined by the squared-chord distance of the percentage data (Cao et al., 2014; Simpson, 16 2012). 17 Plant macrofossils were examined (Table A1) in profiles R22+60, L12+30, R35 (Kienast et al., 2008), and L7-11

18 (Schneider, 2010) on Bol'shoy Lyakhovsky Island and in profile Oya 5-1 on Oyogos Yar (Kienast et al., 2011). 19 Sample preparation followed standard methods (e.g., Kienast et al., 2008). The MTWA tolerances of plant species 20 identified by macrofossils were calculated by correlating their modern distribution in Yakutia, pooled in the online 21 database GBIF (2023), which comprises geocoded distribution data from maps published in the Flora of Siberia 22 (Artemov and Egorova, 2021), permanently updated iNaturalist research-grade observations (iNaturalist, 2023) 23 and records from literature on local floras of Russia (Bochkov and Seregin, 2022) with monthly mean temperatures 24 from the updated database of Leemans and Cramer (1991). We considered only the Yakutian distribution of 25 recovered plant species because of the relative climatic stability of

26 Yakutia throughout the late Quaternary and the related conservative genetic configuration of plant populations in 27 Yakutia with a low percentage of polyploidy and a narrower ecological tolerance in comparison with more western 28 populations. The temperature range of a certain species was determined by the correlation of dot occurrences 29 within Yakutia published in GBIF (2023) with the mean July temperature as MTWA at the closest grid point with 30 a resolution of 0.5° longitude/latitude (Leemans and Cramer, 1991). The temperature extremes within the Yakutian 31 distribution range, e.g., the northernmost occurrence as the minimum and the presence in the Central Yakutian 32 Plain with an MTWA of up to 18.4 °C as the possible maximum, reveal the temperature range of a species. The 33 minimum requirement for MTWA of the most thermophilous species, together with the maximum MTWA 34 tolerance of the most cold-adapted plant within a paleo-flora, reveal the temperature interval (or mutual climatic 35 range, MCR) for the coexistence of all species. We focused on species with particularly high (boreal) and low 36 (arctic) temperature demands (Table S1). 37 Sedimentary ancient DNA (sedaDNA) refers to the desoxyribonucleic acid (DNA) preserved in sedimentary

deposits that stem from biological material such as plants, animals, and microorganisms that live in or near the depositional environment. In permafrost, *seda*DNA is predominantly local in origin (Alsos et al., 2018), and its source can be derived from preserved plant tissues, from extracellular DNA bound to mineral particles, and from

41 feces, and only to a lesser degree from pollen (Crump, 2021). That allows for the reconstruction of past community





1 composition, diversity, and temporal dynamics up to geological timescales (Courtin et al., 2022; Kjær et al., 2022).

- 2 We used DNA metabarcoding to amplify and sequence a short plant-specific genetic marker (see details in
- 3 Zimmermann et al., 2017). DNA metabarcoding was successfully applied (Table A1) to seven samples of the
- 4 permafrost core L14-04, three samples from profile L14-04-B, and seven samples of profile L14-04-C
- 5 (Zimmermann et al., 2017).

6 Lipid biomarkers were analyzed in permafrost core L14-04. A total of 10 samples were processed, and microbial 7 ether lipids (branched and isoprenoid glycerol dialkyl glycerol tetraethers; brGDGTs, isoGDGTs) were analyzed 8 as described by Kusch et al. (2019). The methylation index of 5-methyl branched tetraethers (MBT'_{5ME}) was 9 calculated using MBT'_{5ME} = (Ia + Ib + Ic)/(Ia + Ib + Ic + IIa + IIb + IIc + IIIa) (de Jonge et al., 2014). The Isomer 10 Ratio (IR) of penta- and hexamethylated brGDGTs was calculated as IR = (IIa' + IIIa')/(IIa + IIIa + IIa' + IIIa') 11 (Yang et al., 2015). We use the MBT'_{5ME}-based Air Growing Season Temperature (Air GST, April to October) calibration (calibration D; Air GST = -3.82 + 22.71 *MBT'_{5ME} + 8.78 * IR) recently developed by de Jonge et al. 12 13 (2024) since it is the only calibration available that accounts for seasonal production bias by including soils frozen 14 during part of the year and corrects for the influence of pH on MBT'_{SME}. This calibration has a residual square mean error of 2.2°C. The branched and isoprenoid tetraether index (BIT; Hopmans et al., 2004) was calculated 15 16 following BIT = (Ia + IIa + IIIa + IIIa' + IIIa')/(Ia + IIa + IIIa + IIIa' + IIIa' + crenarchaeol), and the ratio of isoGDGTs 17 to brGDGTs (Ri/b; Xie et al., 2012) was calculated using Ri/b = Σ isoGDGTs/ Σ brGDGTs. For details about the

18 chemical structures and nomenclature of GDGTs, we refer to Kusch et al. (2019).

19 Terrestrial insect remains (mostly beetles) were studied (Table A1) in four samples from Bol'shoy Lyakhovsky 20 Island (L-11-B17, L-11-B19, L-12+30-B-18, R-22-B15, R-22-B16; Andreev et al., 2004, 2009; Kuzmina, 2015b) 21 and one sample from Oyogos Yar (Oya 5-1; Kienast et al., 2011). Sample preparation for terrestrial insect fossils 22 followed standard methods (Kuzmina, 2015b). The MCR method described above for plant macrofossils allows 23 reconstructing the MTWA and MTCO of the year by overlapping coexistence intervals of several species of insects 24 (or any other taxa) in single samples (Atkinson et al., 1987). The MCR method is widely used on fossil beetle 25 remains in Europe mainly because of the continuous research project and database BugsCEP (Buckland, 2007, 26 2014). The method has been adapted for North America (Elias, 2000, 2001) for the study of the late Quaternary 27 beetle fauna of East Beringia. To evaluate the LIG warming in the Dmitry Laptev Strait region, two sources of 28 thermal requirements are used, which are a West Beringian list (including phytophagous species; Alfimov et al., 29 2003) and a Transberingian list (excluding phytophagous species; Elias, 2000), both based on museum collections. 30 Chironomids were studied (Table A1) in profile R35 (Ilyashuk et al., 2006) on Bol'shoy Lyakhovsky Island and profile Oya 5-1 on Oyogos Yar (Kienast et al., 2011). Chironomid sample preparation followed standard methods 31 32 (Brooks et al., 2007). For the paleotemperature reconstruction from chironomid data, we inferred the T_{July} 33 (MWTA) by using a North Russian (NR) chironomid-based temperature inference model (WA-PLS, 2 component; r^2 boot = 0.81; RMSEP boot=1.43°C) based on a modern calibration data set of 193 lakes and 162 taxa from 34 35 northern Russia (spanning from 61 to 75°N, and 50 to 140 °E, T_{July} range 1.8 to 18.8 °C; Nazarova et al., 2015). 36 Water depths (WD) were reconstructed using a modern chironomid-based calibration dataset from East Siberia 37 that includes 147 lakes (WD range 0.1 to 17.1 m). The one-component WA-PLS model had the best performance: 38 r^2 boot = 0.62, RMSEP boot = 0.35 m for WD reconstructions (Nazarova et al., 2011). Both the T_{July} NR and the 39 WD East Siberia models were previously applied for paleoclimatic inferences in East Siberia and the Russian Far 40 East and demonstrated high reliability of the reconstructed parameters (Syrykh et al., 2017; Nazarova et al., 2017a, 2017b; Wetterich et al., 2018). Chironomid-based reconstructions were performed in C2 version 1.7.7 (Juggins, 41





- 1 2007). The data were square-rooted to stabilize species variance. Information on the ecology of chironomid taxa
- 2 was taken from Brooks et al. (2007), Moller Pilot (2009), and Nazarova et al. (2008, 2011, 2015, 2017a).
- 3 Cladocera were newly studied (Table A1) in profile L7-11 on Bol'shoy Lyakhovsky Island, in profiles Oya-3-11,
- 4 Oy7-01, Oy7-08, and in profile Oya 5-1 (Kienast et al., 2011) on Oyogos Yar. The cladocera sample preparation
 5 followed the standard methods (e.g., Kienast et al., 2011).
- 6 Mollusk fossil remains were obtained from samples BL-R-M1 (taken 1.8 m a.s.l. at profile R 41+50 m in 1999)
- and BL-R-M4 (taken at profile R32 in 1999) on Bol'shoy Lyakhovsky Island (E.E. Taldenkova, T.A. Yanina,
 unpublished data (Table A1), and from sample Oya 5-1 on Oyogos Yar (Kienast et al., 2011). The mollusk sample
- 9 preparation followed standard methods (e.g., Kienast et al., 2011).
- 10 Ostracod valves from Bol'shoy Lyakhovsky Island were studied in profiles R23+40, L11+40 (S. Wetterich,
- 11 unpublished, Table A1), L7-14 (Wetterich et al., 2009) and L7-11 (Schneider, 2010), and on Oyogos Yar in profiles
- 12 Oy7-08 (Wetterich et al., 2009), Oy7-01 (Schneider, 2010) and Oya 5-1 (Kienast et al., 2011). The ostracod sample
- 13 preparation followed standard methods (e.g., Wetterich et al., 2009).
- 14

15 **3.5** Clumped isotope analysis of biogenic carbonates and derivation of lake water δ^{18} O

16 An emerging method to derive quantitative paleotemperature estimates from ostracods is clumped isotope thermometry (Song et al., 2022). The advantage of this method is its independence of the temperature estimate 17 18 from the δ^{18} O signal of the water from which the ostracod and mollusk carbonate formed (Eiler, 2007). Two 19 ostracod species (Cytherissa lacustris, Candona candida) and a bivalve mollusk (Pisidium casertanum) were 20 selected from sample Oya 5-1 for clumped isotope analysis based on their relatively high abundance providing 21 sufficient sample material. Complete adult valves, with no visual evidence of dissolution or degradation, were 22 selected and cleaned. We manually removed sediment contamination under a binocular microscope with a 23 paintbrush and deionized water prior to the homogenization of the carbonate with a clean agate pestle and mortar. 24 Clumped isotope analysis was conducted in the NICEST laboratory at Northumbria University on a Nu Instruments 25 Perspective IRMS coupled with a NuCarb dual inlet prep system. Powdered samples of $325 \pm 25 \ \mu g$ were loaded into sample vials, evacuated, and reacted with concentrated orthophosphoric acid at 70 °C. Analyte gas was 26 27 dehydrated and cleaned following established methodologies (e.g., Bernasconi et al., 2018; Eiler and Schauble, 28 2004; Petersen et al., 2015). Briefly, CO2 was dehydrated at -80 °C in two liquid nitrogen-cooled coldfingers and 29 scrubbed of contaminants by passing through a static 1 cm cryotrap filled with PorapakTM Q absorbent (Waters 30 Corporation) cooled to -30 °C. The sample preparation system was baked out at 80 °C after each measurement to 31 avoid cross-contamination. A minimum of 17 replicate measurements was made of each sample, sufficient to 32 achieve standard errors ≤ 0.01 ‰ (i.e., 95% confidence interval < 0.02 ‰). Long-term instrument performance 33 was monitored with an internal standard, POL-2, giving a long-term Δ_{47} external standard deviation of 0.032 %. 34 Isotopic outliers (stable and clumped) and samples with elevated Δ_{48} values, indicative of sample contamination, 35 were discarded before final Δ_{47} values were calculated in the free software Easotope (www.easotope.org; John and Bowen, 2016) using the IUPAC parameters for ¹⁷O correction and calculation of isotopic ratios for VPDB and 36 37 VSMOW (Bernasconi et al., 2018; Brand et al., 2010; Daëron et al., 2016). Internal Δ_{47} values were projected onto 38 the carbon dioxide equilibrium space (ICDES-90) using standards ETH1, ETH2, and ETH3 (ETH Zurich, 39 Bernasconi et al., 2018), following the methods of Dennis et al. (2011), using ICDES Δ_{47} values (Bernasconi et 40 al., 2021). Clumped isotope-based carbonate precipitation temperatures ($T\Delta_{47}$) were calculated using the





1 composite calibration of Anderson et al. (2021), which has recently been shown to produce reliable temperature

- 2 estimates for ostracods (Marchegiano et al., 2024).
- 3 We determined the δ^{18} O of the water in which ostracod carbonates formed using T Δ_{47} values and the δ^{18} O values
- $4 \qquad of fossil ostracod and bivalve carbonate (measured during clumped isotope analysis). A constant \delta^{18}O \ vital offset$
- 5 +2.2 ‰ to Candona candida, +1.2 ‰ to Cytherissa lacustris, and +0.86 ‰ to Pisidium casertanum (von
- 6 Grafenstein et al., 1999) was applied before $\delta^{18}O$ of the formation waters were calculated using the calibration of
- 7 Coplen (2007) to describe the temperature-dependent water-calcite oxygen isotope fractionation.
- 8

9 3.6 Paleoclimate modeling

10 Within the framework of the 6th phase of the IPCC Climate Model Intercomparison Project (CMIP6), the 11 PaleoMIP intercomparison project was endorsed, leading to the identification of several past time periods for 12 paleo-climate simulations to focus on, following a standardized modeling protocol (Kagevama et al., 2018). One 13 of these time periods is the LIG, with a center on the time slice around 127,000 years ago, which lead to modeling 14 experiments summarized under the acronym lig127k. Monthly mean air temperature and precipitation are available 15 from 12 different global coupled climate models in the ligk127 experiment, providing between 100 and 700 years 16 of data for the LIG for the calculation of long-term averages (climatological means). In order to provide a reference for these simulations, all models also provided simulations of the pre-industrial period (PIcontrol). Commonly, 17 18 model results are presented as anomalies to this reference period to reduce the impact of systematic model biases 19 in the results (delta change method, e.g., Maraun and Widmann, 2018). The horizontal resolution of the models 20 varies between 100 km and 500 km (Table S8). Monthly mean temperatures of MTWA and MTCO were calculated 21 from each model on the model's native grid, first finding the maximum and minimum monthly values for each 22 year and then averaging over all years the model provided, both for the lig127k simulations and the pre-industrial 23 simulations. To obtain the anomalies, the resulting values were subtracted from each other (lig127k minus 24 PIcontrol). Mean annual precipitation (MAP) was calculated on each model's native grid, summing up monthly 25 precipitation values. Then, climatological means were calculated, averaging the years the model provided for both 26 the lig127 and the PIcontrol simulations. Anomalies were again obtained by subtracting both averages (lig127k 27 minus PIcontrol). Estimates and uncertainties for the sample sites Bol'shoy Lyakhovsky and Oyogos Yar, as well 28 as a generic reference point, were computed from the multi-model ensemble mean anomalies and of the grid cell 29 values the sites fall in, without spatial interpolation. To visualize temperature and precipitation patterns of the 30 Laptev Sea area, temporal averages of all models were regridded to a common 1° x 1° grid.

31 In order to compare the modeled anomalies with the absolute values determined from the proxies, it is necessary 32 to account for the discrepancy between the pre-industrial reference used for the model and the observed pre-33 industrial time values. For temperature, we used the gridded temperature anomalies from NOAA GlobTemp V6, 34 the most comprehensive gridded observational data record covering both present-day and pre-industrial climate 35 (Huang et al., 2024), to obtain anomalies for the observed pre-industrial time (1850-1900, Allen at al., 2018). For 36 the present-day reference time period in NOAA GlobTemp, the latest reanalysis product of the European Center 37 for Medium-Range Weather Forecast, ERA5, was used as a basis to calculate the absolute values (methods in 38 accordance with Allen et al. (2018) and Capron et al., (2014)). For pre-industrial precipitation, no equivalent data 39 set to NOAA GlobTemp exists. Therefore, it was not possible to obtain absolute values for MAP from the 40 PaleoMIP model anomalies. Instead, we use the multi-model ensemble mean. All models contributing to this





experiment use a present-day land-sea mask and sea level (Figure S3) that does not conform to the suggested land-1 2 sea mask of the area during the LIG. The warmest temperatures and mean annual precipitation are influenced by 3 a site's proximity to the coast. In the models, the horizontal resolution influences the position of the coastline and 4 its distance to the sample sites. The model grid layout also influences the partitioning between the water and land 5 of the grid cells in which the sample sites are located. To estimate the impact of the differences in coastlines among 6 the models as well as between the models and the conditions of the LIG, an additional reference point was chosen 7 for computation of MTWA, MTCO, and MAP that is situated within a land grid cell in every model and as close 8 to the sample sites as possible, referred to as LandPoint, situated at 71.2°N, 142°E (Figure S3). 9 As a reference for the present day, monthly mean air temperatures and precipitation ERA5 were used to calculate 10 MTWA, MTCO, and MAP. Values were calculated on the ERA5's native equal-area grid (nominal resolution 11 about 35 km) and then interpolated onto a regular grid for plotting maps. Climatological means are calculated over 12 the period 1990-2019 (WMO present-day climate reference period). Values for the sample sites and the reference

point were taken from respective grid cell values without spatial interpolation. Please note furthermore, that we use the modern calendar instead of an adjusted angular calendar that would account for shifts in solstice and the related seasons during the lig127 period caused by the high eccentricity of Earth's orbit around the sun. While studies like Shi et al. (2022) and Xu et al. (2024) demonstrate the profound impacts of using the classical calendar in particular in autumn, we expect the impacts on MTWA and MTCO calculations to be negligible because shifts in the position of a single month are small, especially winter and summer. We do not predefine which month of

19 the year is considered warmest or coldest; rather, we determine them for each year individually.

20 4 Results

21 4.1 Field observations

22 Ice-wedge pseudomorphs of 1-3 m thickness of the Krest-Yuryakh stratum are exposed between 0.5-10 m a.s.l. in 23 places along the southern coast of Bol'shoy Lyakhovsky Island (Figure 2a, Figure 3a). Such ice-wedge 24 pseudomorphs are filled with alternating beds of peaty brownish plant detritus layers, partly with twig and wood 25 fragments up to 5-8 cm in diameter and gray clayish silt layers. The thickness of individual layers varies from a 26 few millimeters to 1-2 cm. Ripple bedding (ripples 1-2 cm high, 2-5 cm distance), finely laminated layers (each 27 lamina 5-10 mm thick), and small-scale syn-sedimentary slumping structures are common (Figure 3b). Several 28 layers contain 5-10 mm large mussel fragments. Larger twig fragments and peat inclusions of 2-3 cm are present. 29 The cryostructure is dominantly massive, i.e., without visible ice structures. Only single thin ice veins (< 1 mm 30 thick) are observed in places parallel to the sedimentary bedding. Besides ice-wedge pseudomorphs, there are also 31 lacustrine deposits with horizontally alternating layers of well-laminated silty sand and peat.







1

- Figure 3. LIG (Krest-Yuryakh) deposits exposed at the southern coast of Bol'shoy Lyakhovsky Island (Figure 2a): (a)
 ice-wedge pseudomorph (profile L7-11) with well-bedded lacustrine deposits and (b) laminated lacustrine deposits
 (profile L7-14 A-C) with alternate bedding of peaty and silty sand layers, and a slumping structure (next to the hoe).
- 5 Ice wedge pseudomorphs like those on Bol'shoy Lyakhovsky Island have been studied at various locations along
- 6 the Oyogos Yar coast (Figure 4a). In addition, exposure of lacustrine gray silty fine sand (partly stratified) deposits
- 7 was studied over a length of about 110 m at 1–3 m a.s.l. with two-meter-thick deposits (profile Oy7-01; Figure
- 8 4b). About 50 m toward the east, the profile is characterized by alternating beds of grayish-brown silty material
- 9 and dark plant detritus, and mollusk shells.



10

Figure 4. LIG (Krest-Yuryakh) deposits at the Oyogos Yar coast (Figure 2b): (a) ice-wedge pseudomorph of alternately
 bedded peat and silty sand layers (ca. one meter high from the bottom to the grass cover); (b) stratified lacustrine
 deposits (profile Oy7-01) above the beach.

14

15 4.2 Luminescence dating

After preparation, two samples from stratified lacustrine Krest-Yuryakh deposits (profile L14-12) revealed sufficient material for IRSL dating of one sub-sample in the coarse silt fraction (40-63 μ m) and two sub-samples in the fine sand fraction (63-90 μ m). The obtained ages range from 127.3±6.1 ka to 117.6±6.0 ka (Table 1). The





- 1 three ages agree within errors, nevertheless the luminescence signal dispersion corresponding to the oldest age
- 2 shows a slightly higher skewness and hence, indicates a slight overestimation.
- 3

4 Table 1: IRSL sample characteristics, including paleodose and dose rate parameters.

Sample ID (Grain size fraction)		L14-12-OSL3 (63-90 µm)	L14-12-OSL1 (63-90 µm)	L14-12-OSL1 (40-63 µm)
Paleodose parameters				
n		25	20	20
Mean	[Gy]	295.1±1.2	287.5±2.7	271.9±0.6
Standard deviation	[%]	5.8	4,2	2,8
Skewness		0.2	0.8	0.4
Coefficient of variation	[%]	5.1	3.8	5.3
CAM	[Gy]	295.2±3.5	287.2±3.14	271.8±2.9
Dose rate parameters				
²³⁸ U-series	[Bq kg ⁻¹]	28.11±0.90	20.96±0.72	20.96±0.72
²³² Th-series	[Bq kg ⁻¹]	31.14±1.40	24.22±1.07	24.22±1.07
⁴⁰ K	[Bq kg ⁻¹]	475.32±1.82	481.98±1.66	481.98±1.66
Water content	[%]	35±5	35±5	35±5
Height	[m a.s.l.]	2.7	4.5	4.5
Cover thickness	[m]	30	28	28
Total dose rate	[Gy ka ⁻¹]	2.6±0.1	2.4±0.1	2.4±0.1
Age	[ka]	117.6±6.0	127.3±6.1	117.8±6.8

5

6 4.3 Sedimentology and biogeochemistry

7 Krest-Yuryakh deposits on Bol'shoy Lyakhovsky Island are characterized by low ice contents (20-33 wt%) and no 8 wedge ice at all. The magnetic susceptibility (MS) values vary between 22 and 55 10-8 m3kg⁻¹, differing from 9 outcrop to outcrop, while within single profiles, the differences are much smaller (Figure 5a). The TOC contents 10 range widely from 0.6 to 15.3 wt%. High TOC values (> 5 wt%) are related to plant detritus, peat, and woody 11 remains. The TOC/TN ratio reflecting the degree of organic matter decomposition is between 1.8 and 26.2. Low 12 TOC/TN ratios indicate high decomposition and view versa (Carter and Gregorich, 2008; White, 2005). The δ^{13} C 13 values range from -30.1 ‰ to -25.8 ‰. Differences of 3-4‰ occur within individual profiles. The carbonate contents derived from the TIC values range from 0.2 to 6.7 wt% (Figure 5a). High values are linked to the higher 14 15 presence of mollusk remains. The mean arithmetic grain size ranges between 15 and 78 µm, and the grain-size 16 distribution curves are characterized by a three-modal shape, with peaks in the fine silt, fine sand, and medium 17 sand fractions (Figure 5b).







Figure 5. Sediment data of LIG (Krest-Yuryakh) profiles on Bol'shoy Lyakhovsky Island: (a) absolute gravimetric ice
 content, mass-specific magnetic susceptibility (MS), TOC content, TOC/TN ratio, δ¹³C, carbonate content, arithmetic
 grain-size mean; (b) grain-size distribution curves and sand-silt-clay percentages.

5

1

6 The cryolithological characteristics of Krest-Yuryakh deposits from the Oyogos Yar coast are similar to those of 7 Bol'shoy Lyakhovsky Island (Figure 6a). The absolute ice contents range from 18 to 34 wt%. The MS varies 8 between 12 and 45 10^{-8} m³kg⁻¹. Within individual profiles, the differences are rather low, but there are stronger 9 differences in MS values between the profiles. The TOC contents range from 0.6 to 21.3 wt%. The TOC/TN ratio 10 is between 3.5 and 18.7. The δ¹³C values range from -30.8 ‰ to -26 ‰. The carbonate contents range from 1.4 11 to 22.4 wt%. The mean arithmetic grain sizes are between 15 and 59 µm, and the grain-size distribution curves are 12 three-modal (Figure 6b).







1 2 3

Figure 6. Sediment data of LIG (Krest-Yuryakh) profiles on Oyogos Yar: (a) absolute gravimetric ice content, massspecific magnetic susceptibility (MS), TOC content, TOC/TN ratio, δ¹³C, carbonate content, arithmetic grain-size mean; (b) grain-size distribution curves and sand-silt-clay percentages.

4 5

6 4.4 Pollen-spores-based vegetation and paleoclimate reconstructions

7 The pollen assemblages of the bottom sections of ice-wedge pseudomorphs of Krest-Yuryakh deposits on Bol'shoy 8 Lyakhovsky Island indicate that open steppe or tundra-steppe habitats with Poaceae and Artemisia dominated the 9 vegetation at the beginning of the LIG (Andreev et al., 2004; Ilyashuk et al., 2006). However, relatively high 10 abundances of Alnus fruticosa, Salix, and Betula sect. nana pollen indicate shrub presence in more protected places such as thermokarst basins and river valleys. The large amounts of coprophilous Sordariaceae fungal spores 11 12 indirectly point to the presence of grazing herds of the late Pleistocene mammoth fauna (Andreev et al., 2011). 13 The early to middle LIG pollen spectra are dominated by Poaceae, Cyperaceae, Betula, and Alnus (Andreev et al., 14 2004; Ilyashuk et al., 2006; Wetterich et al., 2009), reflecting a shrub-tundra vegetation. Relatively high 15 concentrations of herb pollen taxa (Artemisia, Brassicaceae, Caryophyllaceae, Asteraceae) indicate that open 16 habitats were also common. Relatively high amounts of Glomus fungal spores suggest that the local vegetation 17 was frequently disturbed, probably due to active erosion processes connected with melting ice wedges and the 18 formation of thermokarst lakes. 19 Pollen assemblages of the middle LIG from the Oyogos Yar coastal sections are dominated by Poaceae, 20 Cyperaceae, Larix, Alnus fruticosa, and Betula sect. nana and spores of Equisetum, dung-inhabiting Sordariaceae, 21 and Glomus (Wetterich et al., 2009; Andreev et al., 2011). Based on the relatively high percentage of Larix pollen,

22 we may infer that larch forest or forest-tundra with shrub alder and dwarf birch stands dominated the vegetation





- 1 in the Oyogos Yar area and document that the treeline was at least 270 km north of its current position during the
- 2 LIG optimum.
- Based on seven Krest Yuryakh profiles with 69 samples from Bol'shoy Lyakhovsky and one profile with 25
 samples from Oyogos Yar, the reconstructed mean MTWA was 9.0±3.0 °C for Bol'shoy Lyakhovsky (median
 9.7±3.1 °C) and 9.7±2.9 °C at Oyogos Yar (median 9.6±2.8 °C). The MAP was 271±56 mm (median 264±52 mm)
- 6 on Bol'shoy Lyakhovsky and 229±22 mm (median 230±23 mm) at Oyogos Yar, implying that the summer climate
- 7 conditions on Bol'shoy Lyakhovsky were a bit colder and moister than on Oyogos Yar.
- 8

9 4.5 Plant macrofossil-based vegetation and paleoclimate reconstructions

10 Plant macrofossil assemblages from Krest-Yuryakh deposits at both sides of the Dmitry Laptev Strait are 11 exceptionally well preserved and frequently allowed for identification at the species level, giving a detailed picture 12 of local vegetation and habitat conditions at the time of deposition (Table S2). On Bol'shoy Lyakhovsky Island, 13 assemblages are composed of remains of 100 vascular plant taxa, including aquatic macrophytes living in the 14 thermokarst lakes (Table A1). The detected species reflect a wide range of plant communities comprising open 15 subarctic shrub tundra with the tall shrubs Alnus alnobetula ssp. fruticosa and Betula fruticosa, as well as dwarf 16 shrubs like Betula nana s.l., Vaccinium vitis-idaea, Rhododendron tomentosum, and Empetrum nigrum 17 interspersed with patches of dry grasslands with Carex (formerly Kobresia) myosuroides, Potentilla spp., 18 Artemisia sp., Androsace septentrionalis, several steppe sedge species, and Ranunculus pedatifidus ssp. affinis 19 suggesting the existence of arid habitats during MIS 5e. Arid conditions are confirmed by the halophytes 20 (Puccinellia, Tripleurospermum hookeri, Stellaria crassifolia, Rumex maritimus) characteristic of salt marsh and 21 saline meadow vegetation near lake shores with fluctuating water levels. The salt accumulation in the upper soil 22 layer results from the capillary rise of solutes due to high evaporation under arid continental climates. The lakes 23 formed habitats of aquatic macrophytes like Callitriche hermaphroditica, Stuckenia vaginata, Myriophyllum 24 spicatum, Batrachium sp., Nitella sp., Hippuris vulgaris, Sparganium hyperboreum and S. minimum, species 25 absent in the study area today. Constantly wet habitats were occupied by littoral and tundra wetland vegetation 26 with Eriophorum spp., Carex aquatilis, C. sect. Phacocystis, Juncus biglumis, Chrysosplenium alternifolium, 27 Comarum palustre, Caltha palustris, Parnassia palustris, Ranunculus hyperboreus, R. lapponicus and 28 Gastrolychnis violascens. The estimated LIG MTWA on Bol'shoy Lyakhovsky Island is based on the MCR of 15 29 selected taxa (Table 2) and ranges from 10.3 °C to 12.9 °C. 30 The plant remains at the mainland coast of Oyogos Yar reflect a LIG vegetation similar to Bol'shoy Lyakhovsky

31 Island consisting of open shrub tundra and forest tundra interspersed with patches of steppe and meadow grassland. 32 In contrast to modern larch-dominated forest tundra, the LIG woodland was dominated by birches, as shown by 33 the abundance of birch remains from both trees and shrubs. In addition to tall and dwarf shrubs already recovered 34 from Bol'shoy Lyakhovsky Island, extralimital Ericaceae taxa (Arctostaphylos uva-ursi, Andromeda polifolia, 35 Chamaedaphne calyculata) and forbs (Moehringia laterifolia, Stellaria longifolia, Chamaenerion angustifolium) occurred at Oyogos Yar. Characteristic of the undergrowth of modern boreal forests, they likewise indicate a 36 37 relatively long and warm growing season during MIS 5e. 38 Analogous to Bol'shoy Lyakhovsky Island, the reconstructed wooded tundra at Oyogos Yar was rather open as

- 39 suggested by abundant remains of tundra-steppe plants like Carex myosuroides, Dryas octopetala s.l.,
- 40 Rhododendron sp., Potentilla stipularis, P. nivea, Ranunculus pedatifidus ssp. affinis and meadow steppe species,





- 1 such as Odontarrhena obovata, Allium sp., Artemisia sp., Carex duriuscula, C. supina s.l., Eritrichium sericeum,
- 2 Rumex acetosella s.l.. These meadow steppes merged into productive alkali grass meadows indicated by abundant
- 3 remains of Puccinellia. Puccinellia sp. and other halophilic taxa, like Chenopodium sp. and Spergularia salina,
- 4 have an affinity to brackish conditions, which suggests high evaporation and low lake levels in response to seasonal
- 5 aridity at Oyogos Yar during the LIG, similar to Bol'shoy Lyakhovsky Island.
- 6 The inventory of water plants at Oyogos Yar resembles that of the Bol'shoy Lyakhovsky assemblage and was
- 7 supplemented by abundant extralimital, i.e., thermophilous, aquatic macrophytes like Stuckenia filiformis and
- 8 Potamogeton perfoliatus. The estimated LIG MTWA at Oyogos Yar is based on the MCR of 17 selected taxa
- 9 (Table 2) and ranges from 12.7 °C to 15.3 °C.

Table 2: MTWA requirements and updated coexistence interval of selected vascular plant species that were identified
 II IIG (Krest-Yuryakh) deposits on Bol'shoy Lyakhovsky Island and the Oyogos Yar mainland coast. Determining
 values of the coexistence intervals are highlighted in bold.

Taxon	MTWA _{Min} [°C]	MTWA _{Max} [°C]	Bol'shoy Lyakhovsky Island	Oyogos Yar
Alnus hirsuta	12.7	18.4		Х
Alnus alnobetula subsp. fruticosa	7.5	18.4	Х	Х
Betula nana s.l.	5.2	18.0	Х	Х
Betula fruticosa	9.1	18.4	Х	Х
Potamogeton perfoliatus	10.3	18.4		Х
Myriophyllum spicatum / M. sibiricum	10.3	18.4	Х	Х
Larix gmelinii	8.0	18.4		Х
Betula divaricata	7.6	18.4		Х
Arctostaphylos uva-ursi	10.6	18.4		Х
Moehringia lateriflora	9.9	18.4	Х	Х
Callitriche hermaphroditica	8.1	18.4	Х	Х
Menyanthes trifoliata	5.2	18.1	Х	
Sparganium hyperboreum	8.1	18.1	Х	Х
Sparganium minimum	10.3	18	Х	Х
Cherleria arctica	3.3	13.3	Х	
Coptidium lapponicum	3.5	16.9	Х	Х
Silene involucrata	3.3	15.7	Х	Х
Ranunculus pedatifidus ssp. affinis	5.6	17.6	Х	Х
Sagina nivalis	2.6	12.9	Х	
Potentilla hyparctica	2.6	14.6	Х	
Ranunculus nivalis	1.6	15.3		Х
Coexistence interval MTWA [°C]			10.3 to 12.9	12.7 to 15.3

13

14 4.6 SedaDNA-based vegetation reconstruction

The Krest-Yuryakh deposits on Bol'shoy Lyakhovsky Island exhibit rich vegetation with *sed*aDNA derived from several woody taxa, including trees, shrubs, and sub-shrubs, suggesting interglacial, warmer-than-present conditions (Figure 7). The proportions of sequences assigned to woody taxa (trees < 1% and shrubs 6-87%), forbs (8-91%), and grasses (2-39%) were highest, while the proportions of sedges (< 1%), cryptogams (< 1%), and





1 aquatic forbs (up to 1.6%) were very low. Among woody taxa, we detected Larix, Picea, Populus, Alnus, Betula, 2 Ribes, Saliceae, and Cornus, as well as sub-shrubs such as arctic-alpine Dryas and Ericaceae, including Arctous, 3 Pyrola spp., Vaccinium uliginosum, and Vaccinium vitis-idaea (Zimmermann et al., 2017) which are typical 4 components of the understory in boreal forests but also of subarctic tundra habitats. The forbs contain mainly taxa 5 adapted to dry steppe conditions (Artemisia gmelinii, including halophilic Puccinellia), arctic-alpine tundra 6 (Braya, Draba, and Dryas), or pioneer plants (Papaver and Oxyria digyna). Other forbs such as Geum, Myosotis 7 alpestris, and Bistorta are typical components of forest margins or meadows. The Krest-Yuryakh deposits formed 8 in a shallow lake in which aquatic and riparian forbs included Menyanthes trifoliata, Stuckenia, Potamogenton,, 9 Hippuris, and Caltha palustris. Nevertheless, sedges in the lower part of the core L14-04 were composed of two 10 distinct Kobresia variants (same barcode shared between K. filifolia and K. simpliciuscula and between K. sibirica 11 and K.myosuroides (now Carex myosuroides) typical of dry to wet habitats while the upper section of the profile 12 also contained the sedges Carex and Eriophorum that are typical for wet habitats but also steppe. This shift between 13 8 and 12 m a.s.l. is accompanied by high proportions (up to 33%) of cryptogams and graminoids (Eriophorum, 14 Bryophytes), while woody taxa were only represented by Salix, overall suggesting a transition to cooler and more 15



16

Figure 7. Composition of plant functional groups in the *seda*DNA metabarcoding record of combined LIG (KrestYuryakh) samples from core L14-04 and profiles L14-04-B (indicated by B) and L14-04-C (indicated by C) from
Bol'shoy Lyakhovsky Island. Figure 7 was generated using ggplot2 v. 3.4.2 (Wickham, 2016) in R v. 4.1.3 (R Core Team,
2022).

22 4.7 Biomarker-based paleoclimate reconstruction





Samples from core L14-04 analyzed for GDGTs (Table S3) include those from the MIS 5e (Krest-Yuryakh stratum 1 2 (n = 3) as well as deposits from younger MIS 5d-a horizons (n = 6) and MIS 1 (active layer; n = 1). BrGDGT 3 distributions globally have a near-universal relationship with temperature irrespective of sample type (Raberg et 4 al., 2022), yet their producers are ubiquitous in nature. Since the Krest-Yuryakh stratum is composed of both 5 lacustrine deposits and peaty plant detritus layers, we tested the potential influence of in-situ production by benthic 6 bacteria in sediments using #ringstetra (Sinninghe Damsté, 2016). The #ringstetra values throughout core L14-04 7 range from 0.04 to 0.25, with values from 0.12 to 0.15 in the LIG deposits. These values indicate that brGDGTs 8 are not produced by benthic bacteria (#ringstetra >0.7), but instead mostly derive from soil/peat and, thus, record 9 Air Growing Season Temperature (GST). Reconstructed Air GST is 0.9 °C for the active layer, 2.8±0.3 °C for the 10 MIS 5e deposits and 1.3±0.9 °C for the MIS 5d-a deposits (Figure 8). 11 Although brGDGT distributional changes have been observed as a direct physiological response to temperature

12 (as well as pH and O₂ concentrations) in acidobacterial cultures (Halamka et al., 2021, 2023), various confounding 13 factors such as soil chemical properties (pH, cation availability) and bacterial community composition (e.g., 14 Halffman et al., 2021; de Jonge et al., 2024) can also affect brGDGT distributions. For example, the BIT and Ri/b 15 indices in soils show a relationship with mean annual precipitation/soil moisture. At lower soil moisture, BIT index decreases and the Ri/b increases (Xie et al., 2012; de Jonge et al., 2024). For core L14-04, Ri/b values are 16 17 substantially higher in the Krest-Yuryakh stratum (Figure 8), suggesting more arid conditions during MIS 5e compared to MIS 5d-a and MIS1. The (isoGDGT-1 + isoGDGT-3)/(isoGDGT-1 + crenarchaeol) values, which 18 19 seem to correlate with mean monthly precipitation (de Jonge et al., 2024) also follow this overall trend. Absolute 20 crenarchaeol concentrations do not correlate with Air GST (Pearson correlation coefficient r = 0.058, p = 0.87), 21 suggesting the observed trends are indeed controlled by soil moisture/precipitation rather than temperature. Yet, 22 no calibration exists that would allow us to calculate mean annual precipitation, thus we only use this information

23 qualitatively.



- Figure 8. BrGDGT-based proxies in core L14-04: (a) MBT'_{5ME}-based Air Growing Season Temperature (Air GST)
- 26 following de Jonge et al. (2024); (b) branched and isoprenoid tetraether index (BIT) and ratio of isoGDGTs to brGDGTs
- 27 (Ri/b); (c) ratio (isoGDGT-1 + isoGDGT-3)/(isoGDGT-1 + crenarchaeol).





1

2 4.8 Beetle-based faunal habitat and paleoclimate reconstructions

3 The fossil insect assemblages of the LIG on Bol'shoy Lyakhovsky Island and on Oyogos Yar are rich in species, 4 and the concentration of remains is very high in comparison to other stratigraphic units in the study area (Kuzmina, 5 2015a, 2015b, Table S4). Insect remains are well preserved. The fossil insect fauna shows a high amount of steppe 6 species (Table S5). The share of Morychus viridis reaches up to 15%. Several identified thermophilous steppe 7 species (Cymindis arctica, Chrysolina brunnicornis bermani, Stephanocleonus eruditus, S. fossulatus) are absent 8 in other Pleistocene samples. Arctic species (Chrysolina subsulcata, Ch. bungei) present only 3 %. The weevil 9 Dorytomus imbecillus indicates shrub vegetation. Several species prefer habitats in and on plant litter 10 (Cyrtodactylus irregularis, Eucnecosum tenue, Lathrobium sp., Philonthus sp., Quedius sp.). A number of riparian 11 and aquatic insects (Colymbetes dolabratus, Aegialia kamtschatica, Agonum impressum, Sericoda quadripunctata, 12 Scymnus sp., Notaris bimaculatus) identified in the Interglacial samples are not recorded on the island today. The 13 predaceous diving beetle Colymbetes dolabratus lives in the north of boreal forest and tundra zones up to Baffin 14 Island and Greenland. In Eurasia, the species is common in the north but is not found in the high Arctic. Other 15 species are nowadays distributed mostly in the forest zone, but their life cycle is not connected directly to the trees. 16 The ground beetle Sericoda quadripunctata is known as post forest-fire species but can also occur in any open 17 disturbed habitats. A brief comparison of representative insects from older and younger stratigraphic horizons are 18 summarized in a separate text as Text S1 and a possible periglacial landscape is presented in Figure S2. 19 To evaluate the LIG climate conditions in the Dmitry Laptev Strait region, two sources of thermal requirements 20 are used, which are a West Beringian list (including phytophagous species; Alfimov et al., 2003) and a 21 Transberingian list (excluding phytophagous species; Elias, 2000), both based on museum collections. In these 22 datasets, several species have slightly different temperature ranges in East and West Beringia (Table S6). The 23 overlap in coexistence intervals for West Beringian species is shown in Figure S1. Combined results are presented 24 in Table 3. Including phytophagous beetles provides important environmental information. The weevils 25 Stephanocleonus eruditus and S. fossulatus need high soil temperature (>12 °C) for the larvae to grow. Larvae of 26 these weevils are root eaters and live in the soil horizon. They are active in warm seasons only. Winter temperature 27 is not critical (Berman et al., 2011). The coexistence of thermophilous weevils and cold-adapted leaf beetles (MTWA range of Chrysolina subsulcata is 2 to 10 °C; Table S6) in one fossil assemblage highlights where the 28 29 coexistence intervals do not overlap (Alfimov et al., 2003) as also observed in samples R-22-B15 and L-11-B19 30 (Table 3). The thermal coexistence intervals of all considered beetle species, i.e., their MCR is 8 to 10.5 °C for MTWA and 31 32 -34 to -26 °C for MTCO on Bol'shoy Lyakhovsky, and 8 to 14 °C for MTWA and -38 to -26 °C for MTCO on

33 Oyogos Yar.

35 Table 3: MTWA and MTCO requirements and coexistence intervals of beetles from LIG (Krest-Yuryakh) samples 36 based on modern reference data in Alfimov et al. (2003) and Elias (2000) applying the MCR method. Determining values 37 of the coexistence intervals are highlighted in bold.

Sample ID	MTWA _{Min} [C°]	MTWA _{Max} [C°]	MTCO _{Min} [C°]	MTCO _{Max} [C°]					
Bol'shoy Lyakhovsky Island									
L-11-B17	8	13	-37	-26					
L-11-B19	4	10.5	-38	-24					





R-22-B15	4	18	-34	-26					
R-22-B16	8	14	-35	-26					
Oyogos Yar									
Oya 5-1	8	14	-38	-26					

1

2 4.9 Chironomid-based habitat and paleoclimate reconstructions

3 In profile R35 (Bol'shoy Lyakhovsky Island), 33 chironomid taxa were identified. The assemblage from the 4 lowermost sample (1.2 m a.s.l.) includes a relatively high share of semi-terrestrial taxa Metriocnemus-5 Thienemannia, Smittia, and Limnophyes-Paralimnophyes indicative of low and variable water level. Between 1.4 6 and 2.2 m a.s.l., we find a high relative abundance of the taxa typical of warm and more eutrophic conditions 7 (Chironomus plumosus-type, Cricotopus-Orthocladius, Procladius). Here, taxa characteristic for shallow water, 8 semi-terrestrial conditions, or temporary waters (Limnophyes-Paralimnophyes, Georthocladius, Hydrobaenus) 9 and taxa that can tolerate acidic conditions (Tanytarsus, Psectrocladius sordidellus-type) are less abundant. 10 Between 2.2 and 5.2 m a.s.l., a high share of eutrophic taxa (Chironomus plumosus-type, C. anthracinus-type, 11 Procladius) and those indicative of cooler and more acidic conditions (Sergentia coracina-type) are present. 12 The chironomid-inferred MTWA of R35 varies between 3.4 °C (at 1.2 m a.s.l.) and 15.3 °C (at 4.4 m a.s.l.) (Table 13 4). The median MTWA is 12.7 °C for the middle section (1.6-3.2 m a.s.l) and 13.9 °C for the upper section (3.6-14 5.2 m a.s.l.). The highest error of prediction (SE of \pm 4.8 °C) occurs in the lowermost sample (at 1.2 m a.s.l.). That 15 can be explained by the dominance of semi-terrestrial taxa, especially Metriocnemus, which is also often found in 16 lake sediments but has still debated ecological requirements (Moller Pillot, 2009 and reference therein). In the NR 17 dataset, Metriocnemus appears with a broad range of ecological conditions with a high-temperature tolerance of 18 9.3±4.6 °C (Nazarova et al., 2015), which leads to a high error in the temperature reconstruction. Therefore, these 19 data from the lowermost sample of profile R35 (at 1.2 m a.s.l.) are not considered in further paleoclimatic 20 interpretation. For all other samples, the errors of prediction remain at the average level of the transfer function 21 (1.4–1.5 °C; Nazarova et al., 2015). The inferred WD reflects a period of shallow water (WD of 1.7–2.4 m) during 22 deposition of the strata between 1.2 and 2 m a.s.l., rising water level (WD 4.5-5.6 m) between 2.4 and 3.2 m a.s.l., 23 and decreasing water level (mean WD of 3.8±0.5 m) between 3.6 and 5.2 m a.s.l. (Table 4). 24

Table 4: Mean air temperature of the warmest month of the year (MTWA) and water depth (WD) and the errors of prediction (SE) reconstructed from the chironomid communities of LIG (Krest-Yuryakh) deposits of Bol'shoy Lyakhovsky Island (profile R35; Ilyashuk et al., 2006) and Oyogos Yar (profile Oya 5-1; Kienast et al., 2011). Data in brackets are not considered for paleoclimatic interpretation.

Sampling height [m a.s.l.]	MTWA ± SE [°C]	WD ± SE [m]		
Bol`shoy Lyakhovsky	y Island, profile R35			
5.2	13.7 ± 1.4	3.3 ± 1.0		
4.8	13.2 ± 1.5	3.8 ± 1.0		
4.4	15.3 ± 1.5	4.1 ± 1.1		
4.0	13.9 ± 1.5	3.9 ± 1.1		





3.6	13.9 ± 1.4	2.7 ± 0.9						
3.2	12.7 ± 1.4	5.6 ± 1.0						
2.8	13.7 ± 1.5	4.5 ± 1.0						
2.4	9.4 ± 1.7	5.4 ± 1.0						
2.0	15.1 ± 1.5	1.7 ± 0.9						
1.6	10.3 ± 2.0	2.4 ± 1.0						
(1.2)	(3.4 ± 4.8)	(2.4 ± 1.2)						
Oyogos Yar, sample Oya5-1								
3.5	12.9 ± 0.9	2.2 ± 1.1						

1

The chironomid assemblage in sample Oya 5-1 is diverse and includes 16 taxa. The semi-terrestrial *Limnophyes*,
 Smittia, and the acidophilic *Psectrocladius sordidellus*-type dominate it. Phytophilic taxa indicative for temperate
 shallow lakes or littoral conditions are less abundant (*Cricotopus laricomalis*-type, *Tanytarsus pallidicornis*-type,
 Endochoronomus albipennis-type). The inferred MTWA from the chironomid community of the Oyogos Yar

6 sample (Oya 5-1) is 12.9±0.9 °C and WD 2.2±1.1 m (Table 4).

7

8 4.10 Cladocera-based habitat reconstruction

9 The fossil cladocera remains of LIG deposits on Bol'shoy Lyakhovsky Island and Oyogos Yar are exceptionally 10 well preserved. The overall cladocera record comprises 13 taxa, of which six were identified at the species level, 11 four to groups or taxa, and three at the genus level (Table S7). The most common species that occur in at least four 12 of the five profiles are *Chydorus* cf. *sphaericus*, *Bosmina* sp., and *Daphnia pulex* gr. The cladocera communities 13 are dominated by littoral shallow-water taxa, such as *Ch.* cf. *sphaericus* and *Alona guttata/Coronatella rectangula* 14 representing 79 % of the total number of individuals, while the proportion of planktic taxa (*Bosmina* sp., *D. pulex* 15 gr.) amounts to 21 %.

Profile L7-11 on Bol'shoy Lyakhovsky shows very low concentrations of 1-2 specimens per gram of dry sediment. In total, only 11 individuals of *Ch.* cf. *sphaericus*, *Bosmina* sp., and *D. pulex* gr. are found (Table S7). Of those, *Ch.* cf. *sphaericus* is the most common species that is a widely distributed, eurytopic, phytophilous pioneer species inhabiting the littoral (Bledzki and Rybak, 2016). This taxon is highly adaptive, resistant to adverse environmental conditions and low temperatures, and often migrates further north than other cladocera species (e.g. Frolova et al.,

21 2014; Luoto et al., 2011).

22 The cladoceran records on Oyogos Yar are more diverse and had much higher concentrations than those on

Bol'shoy Lyakhovsky. Exemplarily, the Oya 5-1 record (Kienast et al., 2011) revealed the most numerous record
 comprising >150 specimens per sample, representing a total of nine species, most of which belong to the family

25 Chydoridae (seven species). The assemblage is dominated by Ch. cf. spahericus (37%), A. guttata/C. rectangula

26 (29%), and *Bosmina* sp. (29%). Littoral species that inhabit macrophytes or detritus-rich silty lake margins, mainly

27 Ch. cf. sphaericus and A. guttata/C. rectangula, represent two-thirds of the assemblage, while one-third is

28 planktonic (mainly *Bosmina* sp. and *D. pulex* gr.) (Kienast et al., 2011).





Cladocera remains are also well represented in profile Oy7-08, where the high species richness (9 taxa in sample 1 2 Oy7-08-19) and the highest concentration of remains in sediments (39 specimens per gram of dry sediment in 3 Oy7-08-19) are noted (Table S7). Most remains belong to littoral phytophilous species associated with 4 macrophytes (Ch. cf. sphaericus, Acroperus harpae, Alonella excisa, Eurycercus sp., Sida crystallina). Besides 5 typical northern or Arctic species such as A. harpae, Ch. cf. sphaericus, and Alona affinis taxa indicative of higher 6 water temperatures are observed, such as Leydigia leidigi and S. crystallina that were not found in modern bottom 7 sediments of >30 water bodies on the coast of the Laptev Sea (L. Frolova, unpublished data). The cladoceran 8 assemblages of Oyogos Yar indicate habitats with a well-developed vegetated shallow littoral zone and pelagic 9 open-water zones.

10

11 4.11 Mollusk-based habitat reconstruction

LIG deposits on Bol'shoy Lyakhovsky Island contain *Sphaerium corneum* with ten complete valves and fragments,
 Valvata piscinalis with ten complete shells and fragments, *Lymnaea* cf. *peregra* with one shell, and *Pisidium* sp.
 with six valves (E.E. Taldenkova, T.A. Yanina, unpublished data).

15 At Oyogos Yar, mollusks were identified by A. Kossler. There, two freshwater gastropod taxa of the genera Radix 16 and Gyraulus are represented only by a few juvenile shell fragments impeding species identification and deduction of precise environmental implications (Kienast et al., 2011). The distribution of *Radix* further to the north than 17 18 today can be interpreted as an indication of warmer than present climate conditions. Additional identified shell 19 fragments include Valvata cf. piscinalis and Lymnea cf. stagnalis (E.E. Taldenkova, T.A. Yanina, unpublished 20 data). Furthermore, five bivalve species have been identified (Kienast et al., 2011): Pisidium casertanum, P. 21 subtruncatum, P. cf. lilljeborgii, P. obtusale f. lapponicum, and P. stewarti of which the most frequent (P. 22 casertanum and P. subtruncatum) are eurytopic and widely distributed, while the rare P. obtusale f. lapponicum 23 inhabits typically arctic and subarctic regions. The stenoecious species P. lilljeborgii indicates oxygen-rich, 24 oligotrophic, and stagnant water bodies. P. stewarti is only known from the Tibetan Plateau and the Siberian Irtysh 25 region (Kuiper, 1962, 1968). Additionally, the species Sphaerium cf. corneum has been found (E.E. Taldenkova, 26 T.A. Yanina, unpublished data).

27

28 4.12 Ostracod-based habitat reconstruction

29 The LIG ostracod record obtained at both shores of the Dmitry Laptev Strait comprises 23 taxa, of which 20 were 30 identified at the species level, two at the genus level, and one taxon comprises juvenile Candoninae (Table S8). 31 The most common species which have occurrences in at least four of the five studied profiles are Candona candida, 32 Fabaeformiscandona harmsworthi, F. levanderi, F. rawsoni, F. tricicatricosa, Eucypris dulcifons, Ilyocypris 33 lacustris, Cytherissa lacustris, and Limnocytherina sanctipatricii. Exemplarity, the Oya 5-1 record (Kienast et al., 34 2011) that revealed the most numerous record comprising >1000 specimens per sample belonging to a total of 11 35 species is dominated by C. candida (34 %), Cy. lacustris (26 %), and F. rawsoni (15 %). 36 The species Cy. lacustris, F. tricicatricosa, and L. sanctipatricii are adapted to cool water temperatures (Meisch, 2000), and T. cf. glacialis, F. rawsoni, and F. harmsworthi are cold-stenothermic (Wetterich et al., 2008a, 2008b). 37 38 Increased salinity in the water is tolerated by L. sanctipatricii (0.5-5 ‰), C. lacustris (up to 1.5 ‰) and F. levanderi

39 (up to 6 ‰; Meisch, 2000).





1 4.13 Clumped isotope temperature and thermokarst lake δ^{18} O reconstructions from ostracod and 2 bivalve calcite

- 3 Clumped isotope Δ_{47} values range between 0.641 and 0.658 ‰, with standard errors between 0.005 and 0.011 ‰
- 4 (95% confidence intervals between 0.01 and 0.022 ‰). Of the 54 sample replicates, three erroneous replicates
- 5 (with stable or clumped isotope values greater than $\overline{x} \pm 2\sigma$), and one contaminated replicate ($\Delta_{48} > 1$ ‰) were
- 6 removed from the final Δ_{47} calculations. The final values suggest carbonate precipitation temperatures (T Δ_{47})
- 7 between 5.3 and 10.3°C. The raw data is presented in Table S9 and results are summarized in Table 5.
- 8 Fossil carbonate δ^{18} O values range from -14.65 ± 0.02 ‰ to -14.12 ± 0.02 ‰ VPDB, resulting in reconstructed

9 water δ^{18} O estimates (δ^{18} O_W) between -18.9 ± 0.3 ‰ and -17.8 ± 0.6 ‰ VSMOW.

10

11 Table 5: Clumped isotope results from fossil biogenic carbonates from profile Oya 5-1. N = number of replicate 12 measurements used to calculate Δ_{47} with the number of rejected samples in parenthesis. Δ_{47} and $\delta^{18}O$ of carbonate 13 ($\delta^{18}O_{cc}$) uncertainties are given as external standard errors over multiple replicates. $\delta^{18}O_w$ is the estimated $\delta^{18}O$ of water 14 from which the carbonate formed, with uncertainty estimated through the propagation of temperature and isotope 15 uncertainties.

uncertainties.

Sample	Ν	Δ47 [‰ ICDES]	ΤΔ47 [°C]	δ ¹⁸ Occ measured [‰ VPDB]	δ ¹⁸ Ow [‰ VSMOW]
Candona candida	18 (1)	0.641 ± 0.011	10.2±3.2	-14.12 ± 0.02	-18.6 ± 0.7
Cytherissa lacustris	21 (1)	0.641±0.010	10.3±3.0	-14.31 ± 0.02	-17.8±0.6
Pisidium casertanum	15 (2)	0.658±0.005	5.3±1.5	-14.65 ± 0.02	-18.9±0.3

16

17 4.14 Paleoclimate modeling

18 Using the PaleoMIP lig127k model simulations (Otto-Bliesner et al., 2021; Kageyama et al., 2021, Table S10) 19 together with the NOAA GlobTempV6 ERA5 data, we derived maps of elimatological means of MTWA, MTCO, 20 and MAP for the Bol'shoy Lyakhovsky and Oyogos Yar region according to the methodology described above. 21 These maps cover the Laptev Sea to the west and north, the Eastern Siberian Sea to the east, and a small part of 22 continental Siberia to the south and provide regional patterns of these climate variables in addition to values for 23 the sample sites (Figure 9). Climate change signals for both warmest and coldest months as well as their ensemble 24 spreads are in agreement with the seasonal signals shown in Otto-Bliesner et al. (2021), where warmen winters 25 occur over the Arctic Ocean, albeit with a high inter-model spread, and warmer summers are evident dominantly 26 over the continents and less pronounced over the Arctic ocean, associated with low inter-model spread. Note that 27 due to the lack of a reference data set for pre-industrial precipitation, MAP values are PaleoMIP lig127k ensemble 28 means.

The MTCO for the LIG derived from modeled anomalies are between -40 and -26 °C, with a distinct north-south gradient and colder temperatures over grid cells that include land (Figure 9). The modern MTCO is higher than modeled temperatures for the LIG with larger differences over the sea than over land. The model agreement is highest over grid cells on the continent distal to the coastline, lower over the ocean, and lowest along the coastline, which indicates that a significant fraction of the uncertainty is related to the different land-sea masks in the different models. This is reflected in the values calculated for the sample sites and the generic LandPoint (see Table 6), with the highest MTCO for Bol'shoy Lyakhovsky and lowest MTCO for the generic LandPoint in both the PMIP multi-

36 model ensemble mean and ERA5, and a higher uncertainty for the sample points than for the generic land point.





1 LIG MTWA estimates from the PMIP multi-model ensemble mean range from 0°C over the sea to 18°C over the 2 south-western land area. Model temperatures are consistently higher than present-day temperatures from the ERA5 3 reanalysis. At the same time, the general spatial patterns are very similar (lowest temperatures over the northeastern sea corner of the plotted area, highest temperatures over the southwestern land area). The agreement between the 4 5 PaleoMIP models is higher than for the MTCO, with good agreement in all areas except the coastlines, again 6 indicating that higher uncertainties are related to the different land-sea masks in the different models. MTWA 7 values of the sample points and the generic land point reflect the north-south gradient shown in the map (Figure 8 9), with the lowest MTWA values for Bol'shoy Lyakhovsky and the highest MTWA for the LandPoint. Both the 9 LandPoint and Bol'shoy Lyakhovsky are located in grid cells that are considered land by most models, leading to 10 an uncertainty only half as high as for Oyogos Yar, which is situated in a grid cell with varying land content. 11 MAP from the PMIP multi-model ensemble mean is between 250 and 450 mm, showing lower values over the sea 12 and higher values over the continental land area. This general pattern is similar to that of the present-day reanalysis 13 results, where precipitation is lower than those modeled for the LIG. The PMIP models show the highest agreement 14 over the sea and the lowest agreement over the continental grid cells.

15



Figure 9. Climatological means of monthly mean temperature of the coldest (MTCO, top row) and the warmest month (MTWA, middle row) and of mean annual precipitation (MAP, bottom row) from the ERA5 reanalysis (left column), PaleoMIP multi-model anomaly added to observed PI values (Plobs+(lig127k-PI) for temperatures and PaleoMIP multi-model ensemble mean (lig127k ensemble mean) for precipitation, PaleoMIP ensemble mean anomaly with respect to modeled PI (lig127k-PI ensemble mean) and PMIP multi-model anomaly standard deviation (ensemble stdev). The plus signs denote the position of the sample sites, and the x signs denote the position of the generic LandPoint. Black lines mark today's coastlines, the white resp. gray lines mark the coastlines of the lig127 (after Alekseev et al., 1991b)



16





1

2 Table 6: Evaluation of MTWA and MTCO from the Plobs+(lig127k-Pl) multi-model ensemble mean and MAP from 3 the <u>PaloeMIP</u> lig127k multi-model ensemble mean. Values in <u>brackets</u> refer to the present-day reference from ERA5 4 (1900-2010)

4	(1990-201	9)

Site	MTWA <mark>[C°]</mark>	MTCO [C°]	MAP [mm]		
Bol'shoy Lyakhovsky Island	4.4±1.0 (2.7)	-31.1±1.4 (-32.7)	278±50 (262)		
Oyogos Yar	4.5±1.2 (7.5)	-31.6±1.4 (-34.1)	285±55 (243)		
LandPoint	13.6±0.9 (11.0)	-38.7±1.0 (-36.3)	328±70 (259)		

5 5 Discussion

6 5.1 Cryolithology of LIG thermokarst deposits

7 The cryolithological parameters of the LIG deposits are shown in Figure 10, each in comparison to the 8 stratigraphically younger Yedoma Ice Complex (mostly MIS 3) and Holocene (MIS 1) thermokarst deposits 9 according to Schirrmeister et al. (2011b) and Wetterich et al. (2009) respectively.

The absolute ice contents of the LIG deposits are very similar for Bol'shoy Lyakhovsky Island and the Oyogos Yar coast and up to half as low as those of the Yedoma Ice Complex and Holocene deposits at both sites. Thus, the freezing and thawing processes and moisture content of LIG thermokarst lake sediments are similar but clearly different from those of the younger horizons. The MS for the LIG deposits is similar at both sites, showing comparably high contents of magnetic minerals. These contents are up to twice as high as those of the Yedoma

15 Ice Complex and Holocene horizons. This could mean that the source material in the LIG was different.

16 The TOC contents show slight differences for both sites, with a mean of 2.4 wt% at Bol'shoy Lyakhovsky and 3.5

17 wt% at Oyogos Yar. In contrast, Yedoma Ice Complex and Holocene deposits show higher TOC values on 18 Bol'shoy Lyakhovsky with 3.2 and 7.8 wt%, respectively, if compared to Oyogos Yar with 2.7 and 6.2 wt%,

19 respectively. Different environmental conditions could play an important role and influence the preservation of

20 organic matter. Regardless, the Holocene deposits contain two to three times higher wt% of organic matter. The

21 TOC/TN ratio as an indicator for the source of/degree of decomposition of the organic matter in the LIG deposits

22 is very similar on Bol'shoy Lyakhovsky and on Oyogos Yar. The values for the younger deposits are in a similar

23 range (Figure 10), indicating a similar degree of decomposition of organic matter.

24 The mean carbonate content in LIG (2.3 wt%), Yedoma Ice Complex (0.5 wt%), and Holocene (1.6 wt%) deposits

25 on Bol'shoy Lyakhovsky Island is much lower if compared to the respective horizons on Oyogos Yar with 6.4,

26 3.9, and 3.5 wt%, respectively. This reflects a higher share of shells of mussels, gastropods, and ostracods in the

27 Oyogos Yar deposits. At each site, the Krest-Yuryakh deposits have the highest carbonate content.









Figure 10. Boxplots of sediment data from both study sites, including the LIG (Krest-Yuryakh) horizon and the stratigraphic younger late Pleistocene Yedoma Ice Complex (mostly MIS 3) and Holocene thermokarst (MIS 1) horizons. The boxplots show the standard deviation, the arithmetic mean, and the IQR (interquartile range). The numbers correspond to the respective number of samples included (Schirrmeister et al., 2011a, 2011b; Wetterich et al., 2009).

7

8 The mean δ^{13} C values of TOC for the LIG deposits are almost identical, with -27.3% on Bol'shoy Lyakhovsky 9 and -27.7% on Oyogos Yar. The respective values from Yedoma Ice Complex deposits are -26.5% and -27.6%, 10 and from Holocene thermokarst deposits are lower with -28.3% and -29.0%. The relationship between TOC/TN 11 and δ^{13} C indicates a mixture of organic matter derived from C3-type terrestrial plants and lacustrine algae. A large 12 number of data points plot along the mixing line between both endmembers (Figure S4). 13 The mean arithmetic grain size for the LIG deposits is 38.2 µm on Bol'shoy Lyakhovsky and 32.8 µm on Oyogos

Yar. The Yedoma deposits of Bol'shoy Lyakhovsky have a much smaller mean grain size of 18.2 μm, while the Holocene deposits are coarser, with a mean of 41.6 μm (Figure 10). The younger Yedoma and Holocene deposits of Oyogos Yar have a similar mean arithmetic grain size as the LIG sediments with 31.7 and 30.0 μm. This shows that the deposition conditions in the thermokarst lakes were similar in both areas during the LIG. On Bol'shoy Lyakhovsky, the deposition conditions and/or the sources of material in the stratigraphically younger units have

19 changed more than at Oyogos Yar.

20

21 5.2 Last Interglacial chronology and dating uncertainties

22 Different geochronological method results are available for the reconstruction of the timescale of Arctic permafrost 23 dynamic and corresponding investigations on feedbacks of periglacial landscapes and climate changes. Of core importance are radiocarbon dating (e.g. Wetterich et al., 2014), tephrachronology (e.g. Froese et al., 2009), 24 25 optically- and infrared-stimulated luminescence (OSL and IRSL; e.g., Murton et al., 2022), radioisotope disequilibria (²³⁰Th/²³⁴U) of frozen peat (e.g. Wetterich et al., 2016), uranium isotope (²³⁴U/²³⁸U) series (Ewing et 26 al., 2015), and ³⁶Cl/Cl radionuclide ratios of ground ice (e.g. Blinov et al., 2009). However, dating methods ranging 27 28 beyond radiocarbon maximum finite ages show specific challenges when applied to frozen material. Additionally, 29 when fusing the dating results into one single multi-method chronology, a careful interpretation is required because 30 individual methods use different components of permafrost deposits, including organic, mineral, or ice





- 1 components. Uncertainties also arise from unknown influences of freezing and thawing dynamics on chemical and
- 2 physical parameters, which are important to many age-determination techniques.
- 3 The chronostratigraphy of the LIG and its MIS 5 context relies on a few luminescence ages available from
- 4 Bol'shoy Lyakhovsky Island and the Oyogos Yar coast. The stratigraphic position at studied sites still outlines
- 5 challenges, especially from vertical discontinuities and hiatus. Currently, available age information of MIS 5-
- 6 related deposits is summarized in Figure 11. Sediments, which are stratigraphically older than Krest Yuryakh,
- 7 were found along the Laptev Strait coast as Buchchagy Ice Complex dated using 230Th/U to MIS 5e MIS 5b
- 8 $(126 + 16/-13 \text{ ka to } 89 \pm 5 \text{ ka}, \text{Wetterich et al., } 2019, \text{Opel at al., } 2017)$. The large variation of 230Th/U-ages
- 9 impedes highly resolved, millennial paleo-climate interpretations.
- Stadial conditions are recorded in floodplain sediments locally named as Kuchchugui stratum that has been cryostratigraphically aligned with the MIS 6 (Tumskoy and Kuznetsova, 2022),
- IRSL ages from Bol'shoy Lyakhovsky of 102±16 and 99±15 ka suggest its generation during MIS 5c, a period younger than the LIG. Nevertheless, corresponding deposits associated with the Kuchchugui stratum were dated by IRSL to slightly older ages (112.5 +9.6 -102.4±9.7 ka) at the mainland coast of Oyogos Yar (Opel et al., 2017). In this context, the newly IRSL-dated Krest Yuryakh thermokarst deposits provide, for the first time, robust age control for the LIG based on three consistent ages from two samples and two grain size fractions and with smaller age uncertainties compared to previous luminescence dating results., with ages of 127.3±6.1, 117.8±6.8, and 117.6±6.0 ka (Table 1; Figure 11).

19 The observed luminescence properties confirm a reliable luminescence - dose correlation for successful curve 20 fitting and age modeling. The coefficients of variation below 6 % testify suitable measurement conditions and 21 reproducible signals. The low standard deviation below 6 % and corresponding low skewness below 0.8 document 22 sufficient signal reset and call for the application of the central age model (CAM). The typical challenges in dating 23 permafrost samples related to sediment mixing are not indicated in our samples nor in the sampled sediment 24 section. The estimates of the paleo-water content were primarily based on the measured in-situ water content. 25 Although slight variations may have occurred over time, we assume that the sampled layers remained frozen and 26 hence, have kept the measured water content relatively constant. Nevertheless, uncertainties remain due to the fact 27 that the water was present not in its liquid but in its frozen form with potential effects on the penetration depth of 28 ionizing radiation. To account for the potential variations in the past plus uncertainties from radiation field 29 modeling based on water instead of ice, we included an overall water content uncertainty of 5 %. Site-specific 30 uncertainties may also arise from the unknown evolution (esp. with respect to timing) of the overburden and its 31 effects on the cosmogenic dose rate due to permafrost formation with sediment aggradation and permafrost 32 degradation with thaw subsidence. We evaluated the influence of an early reduction of overburden thickness by 33 comparing the full thickness of 35 m to 29 m, which would be more comparable to modern thickness assumptions. 34 As both overburden thicknesses are already strongly attenuating the incoming cosmic radiation, the effect on ages 35 is less than 1 %.







Figure 11. Age information obtained by IRSL (diamonds) and ²³⁰Th/U dating (circles) of cryostratigraphic units exposed at both coasts of the Dmitry Laptev Strait and aligned with MIS 5. White symbols refer to samples from the Oyogos Yar mainland coast, and filled symbols to those from the southern coast of Bol'shoy Lyakhovsky Island – compared to the LR04 benthic stack (Lisiecki and Raymo, 2005). Age determinations of Krest-Yuryakh lake deposits are from this study (highlighted in blue; Bol'shoy Lyakhovsky) and Opel et al. (2017; Oyogos Yar), Buchchagy Ice Complex from Wetterich et al. (2016; Bol'shoy Lyakhovsky) and Kuchchugui floodplain deposits from Opel et al. (2017; Oyogos Yar) and Andreev et al. (2004; Bol'shoy Lyakhovsky).

1

10 5.3 Proxy-based quantitative paleoclimate reconstructions compared to PMIP model simulations

When we compare the proxy-based and modeled climate and environmental parameters, regional differences 11 12 between Bol'shoy Lyakhovsky Island and the Oyogos Yar coast are obvious, as well as differences between 13 different proxy reconstructions at the same site (Table 7). The general pattern, however, is that all proxy-based 14 MTWA reconstructions indicate significantly warmer-than-today conditions. 15 For MTWA on Bol'shoy Lyakhovsky Island pollen, plant macrofossils, beetles, and chironomids overlap at 10.3-16 10.5 °C . The modeled temperatures (Plobs+(lig127k-Pl) are distinctly lower (Figure 12). BrGDGT-based AIR GST are lower (2.8±0.3 °C) but fit well with the MTWA estimates since they integrate the entire growing season 17 18 of bacteria. At Oyogos Yar, the MTWA of pollen, beetles, and chironomids overlaps at 12-12.6 °C, while plant 19 macrofossils indicate higher MTWA. The modeled temperatures for Oyogos Yar are again distinctly lower but are 20 similar to those of Bol'shoy Lyakhovsky. The mean temperatures of the coldest month (MTCO) show joint 21 overlaps between beetles and model data between -32.6 and -29.8 °C for Bol'shoy Lyakhovsky Island and -33.0 22 and -30.2 °C. For the mean annual precipitation (MAP), pollen and model data of PaleoMIP concur between 228-

- 23 327 mm for Bol'shoy Lyakhovsky Island (i.e., higher than at present, which is also implied by GDGTs) and 230-
- 24 251 mm for Oyogos Yar. The WD of thermokarst lakes, which were reconstructed using chironomids, overlap

26 10.2±3.0 and 10.3±3.2 °C near the surface and 5.3 °C at the bottom.

⁹

²⁵ between 1.7 and 3.3 m for both sites. The clumped-isotope-reconstructed water temperature of these lakes is





- 1 The generic LandPoint data of PaleoMIP overlap quite well for MTWA with most of the proxy data from Oyogos
- 2 Yar, with chironomid data, and a bit with plant macrofossil data from Bol'shoy Lyakhovsky (Figure 12). For
- 3 MTCO, a small overlap is visible with beetle data from Oyogos Yar. For MAP PaleoMIP reconstruction, the three
- 4 points and pollen data from Bol'shoy Lyakhovsky overlap between 258 and 327 mm.
- 5 The differences between different proxy reconstructions and between the two locations can have various causes.
- 6 For example, pollen, plant macrofossils, beetles, and chironomids may have reached their detectable stage in the
- 7 fossils at different times during the summer months. Thus, different conditions may have prevailed between early,
- 8 peak, and late summer during MIS 5e. On the other hand, MIS 5e lasted about 9 ka between 125 and 116 ka (van
- 9 Nieuwenhove et al., 2011). Unfortunately, the dating results available to us do not allow us to determine more
- 10 precisely whether our records relate to early, middle, or late MIS 5e. Therefore, differences may also have
- 11 stratigraphic and/or chronological causes.

12

13 Table 7: LIG proxy-based quantitative reconstructions and paleoclimate modeling results of Mean Air Temperature of

the Warmest Months (MTWA), Mean Temperature of the Coldest Month (MTCO), Growing Season Temperature (Air GST, April to October), Mean Annual Precipitation (MAP), and Water Depth (WD) and Water Temperature (Twater) of thermokarst lakes on Bol'shoy Lyakhovsly Island and the Oyogos Yar mainland coast. Values in brackets refer to

16 of thermokarst lakes on Bol'shoy Lyakhovsly Island and the Oyogos Yar mainland coast. Values in brackets refer 17 the present-day reference from ERA5 (1990-2019). n/a – not applicable.

Fossil proxy	MTWA	Air GST	МТСО	MAP	WD	Open Twater	Bottom			
Ę	[°C]	[°C]	[°C]	[mm]	[m]	[*C]	I water ['C]			
LandPoint										
PaleoMIP Modeling	n/a	n/a	n/a	328±70	n/a	n/a	n/a			
PIobs+(lig127k-PI)	13.6±0.9	n/a	-38.7±1.0	n/a	n/a	n/a	n/a			
(ERA5 reanalysis)	(11.0)	n/a	(-36.3)	(259)	n/a	n/a	n/a			
Oyogos Yar coast										
PaleoMIP Modeling	n/a	n/a	n/a	285±55	n/a	n/a	n/a			
PIobs+(lig127k-PI)	4.5±1.2	n/a	-31.6±1.4	n/a	n/a	n/a	n/a			
(ERA5 reanalysis)	(7.8)	n/a	(-34.4)	(243) n/a		n/a	n/a			
Clumped isotopes (Pisidium casertanum)	n/a	n/a	n/a	n/a	n/a	n/a	5.3±1.5			
Clumped isotopes (Cytherissa lacustris)	n/a	n/a	n/a	n/a	n/a	10.3±3.0	n/a			
Clumped isotopes (Candona candida)	n/a	n/a	n/a	n/a	n/a	10.2±3.2	n/a			
Chironomids	12.0 to 13.8	n/a	n/a	n/a	1.1 to 3.3	n/a	n/a			
Beetles	8 to 14.0	n/a	-38.0 to -26.0	n/a	n/a	n/a	n/a			
Plant macrofossils	12.7 to 15.3	n/a	n/a	n/a	n/a	n/a	n/a			
Pollen	9.7±2.9	n/a	n/a	229±22	n/a	n/a	n/a			
Bol'shoy Lyakhovsky Isl	and									
PaleoMIP Modeling	n/a	n/a	n/a	278±50	n/a	n/a	n/a			





PIobs+(lig127k-PI)	4.4±1.0	n/a	-31.2±1.4	n/a	n/a	n/a	n/a	
(ERA5 reanalysis)	(2.5)	n/a	(-33.1)	(262)	n/a	n/a	n/a	
Air GST (GDGTs)	Air GST (GDGTs) n/a		n/a	n/a	n/a	n/a	n/a	
Chironomids	9.4 to 15.3	n/a	n/a	n/a	1.7 to 5.6	n/a	n/a	
Beetles	8.0 to 10.5	n/a	-34 to -26	n/a	n/a	n/a	n/a	
Plant macrofossils	10.3 to 12.9	n/a	n/a	n/a	n/a	n/a	n/a	
Pollen	9.0±3.0	n/a	n/a	271±56	n/a	n/a	n/a	

1

2 Present-day ERA5 data has a severe bias over sea ice, especially during periods with cold temperatures;

3 temperatures are overestimated by up to 10°C when the air temperature is around -40°C (Wang et al., 2019, Batrak

4 & Müller, 2019). The differences between PaleoMIP model's land-sea mask and the actual coastline during the

5 LIG, concerning especially MAP and MTWA, might lead to underestimated MAP and MTWA. The MTWA for

6 the generic land point (13.6±0.9 °C, Table 6) is in the range of the reconstructed data sets between about 6 and 15

7 °C (Table 7). On the other hand, analog-based climate reconstruction methods applied to biotic proxies may

8 overestimate temperatures in northern Siberia (Klemm et al., 2013). The sites are presently located at the lower

9 temperature range of the training dataset, and as such, the taxa present in the observations are not covered with

10 their full occurrence range, which typically results in biases toward higher temperature values.

11



12

Figure 12. Boxplot of proxy-reconstructed and modeled climate and environmental data according to Table 7. BL – Bol'shoy Lyakhovsky, OY – Oyogos Yar, MTWA - mean temperature of the warmest month, MTCO – mean temperature of the coldest month, WD – water depth of thermokarst lakes, T open water – surface water temperature of lakes, T bottom water – bottom water temperature of lakes. Grey-shaded areas indicate overlap ranges; red triangles indicate the present-day reference.

18

19 5.4 Biogenic carbonate: Clumped and stable isotopes

20 All species analyzed (Candona candida, Cytherissa lacustris, Pisidia casertanum) require freshwater habitats and

thus depend on the presence of open water bodies, which are present solely in summer in modern times. Thus, the





- 1 derived temperatures are interpreted as reflecting the mean temperature of the warm season that integrates all ice-
- 2 free periods, i.e., the growth window of ostracods and bivalves.
- 3 Ostracod-derived clumped isotope temperatures (T Δ_{47}) are considerably warmer (10.2±3.2 and 10.3±3.0 °C) for
- 4 C. candida and Cy. lacustris, respectively) than those of P. casertanum (+5.3±1.5 °C) (Table 5). This difference
- 5 is attributed to differing habitation depths, with ostracods proliferating throughout the water column (Scharf, 1998;
- 6 Decrouy et al., 2012), and therefore recording surface and upper water column temperatures, and *P. casertanum*,
- 7 a benthic species that burrows continually into sediments (McMahon and Bogan, 2001) and thus records bottom
- 8 water temperature. Monitoring data in a polygon pond at Oyogos Yar during August 2007 shows that mean air
- 9 and surface water temperatures differed by only 0.3° C, while bottom water at 0.6 m WD and only about 0.2 m
- 10 above the permafrost table showed almost constant water temperature of 3.6 °C (Boike et al., 2008). Thus, we
- conclude that our reconstructed ostracod temperatures are likely similar to, or slightly below, warm season mean surface air paleotemperature. Our summer surface $T\Delta_{47}$ reconstructions of ca. 10 °C are considerably warmer (ca.
- surface an parotemperature. Our summer surface 124/ reconstructions of our 10° C are considerably warmer
- 13 +2 °C) than modern and in good agreement with other air temperatures derived in this study.
- 14 Our measured *Cy. lacustris* δ^{18} O values show good agreement with those previously recorded from the LIG at
- 15 Oyogos Yar in section Oy7-08 (-14.5 to -12.2 ‰, Wetterich et al., 2009). However, our *C. candida* values are ca.
- 16 2 to 3 ‰ more negative than those previously recorded in Oy7-08 (-12.6 to -11.3 ‰, Wetterich et al., 2009).
- 17 Wetterich et al. (2008a) showed that offsets in δ^{18} O between single species in neighboring polygon ponds of 2 to
- 18 3 ‰ are common and this likely could explain the discrepancies observed here.

19 Stable isotope compositions of ostracod calcite are driven by temperature and the isotopic composition of the 20 surrounding precipitation waters, making them effective proxies for paleoenvironmental conditions (Xia et al., 21 1997; von Grafenstein et al., 1999). For comparison with our paleorecord, modern C. candida δ^{18} O has been 22 measured at Samoylov Island (72.37°N, 126.48°E), in the Lena Delta, ranging between -17.7 and -10.4 ‰ 23 (Wetterich et al., 2008a), the Moma region (NE Yakutia, 66 °N, 143 °E) where values between -15.2 and -11.9 24 ‰ were recorded, and in Central Yakutia (62 °N, 129 °E) with values between -11.0 and -8.9 ‰ (Wetterich et al., 25 2008b). The more continental location of the latter two records, compared to the Samoylov record, induces higher temperature amplitudes, warmer summers, and higher evaporation and is reflected in more enriched (less negative) 26 27 modern carbonate δ^{18} O. The similarity of Oya 5-1 data to Samoylov Island, compared with the more continental 28 locations, suggests a precipitation and temperature regime closer to the former site in the modern day. Samoylov 29 Island is at a similar latitude as Oyogos Yar but records mean July air temperatures between 4 to 8 °C, 30 approximately 1 to 5 °C warmer due to its delta setting influenced by warm Lena River water (Boike et al., 2019). 31 Calculated δ^{18} O of carbonate precipitation waters between -18.5 and -16.6 ‰ are similar to modern summer 32 rainfall values, which range from -20.2 to -11.7 % (Opel et al., 2011). Small water bodies, such as those inhabited 33 by ostracods, have been shown to be predominantly fed by precipitation in northern Siberia (Wetterich et al., 34 2008a). Thus, their δ^{18} O will largely reflect that of precipitation with a small shift towards more positive values 35 (ca. +2 ‰), driven by evaporative processes (Wetterich et al., 2008b). The similarity of our reconstructed water δ^{18} O to modern precipitation would suggest a summer precipitation regime similar to the modern day. 36

37

38 5.5 Last Interglacial ecosystems

39 The paleobotanical and entomological data prove the presence of an open subarctic shrub tundra with restricted 40 steppe areas in the area of Bol'shoy Lyakhovsky Island and the existence of an open forest tundra at Oyogos Yar

41 during the LIG. The presence of the ant *Leptothorax acervorum* and the true bug *Sciocoris microphthalmos* in the





Oyogos Yar records is notable as both species at present inhabit forested areas, while tundra-steppe indicators are 1 2 rare and only represented by Morychus viridis and the meadow-steppe species Protapalochrus arcticus (former 3 Troglocollops arcticus). True steppe insects are not present in Oyogos Yar but two steppe weevils 4 (Stephanocleonus eruditus and S. fossulatus) were recorded in the Bol'shoy Lyakhovsky fauna. The presence of 5 tall boreal shrubs and even trees during the LIG in an area that is covered with arctic tundra today is noteworthy. 6 The only woody plants that are currently occurring at Oyogos Yar are the dwarf shrubs Dryas octopetala ssp. 7 punctata and Salix polaris, the latter forming thin prostrate stems piercing through and protected by the moss 8 cover. Ericaceae, Betulaceae, or other mainly boreal taxa do not occur in the study area today (Aleksandrova, 9 1980; Kienast et al., 2008) but were represented by many species during the LIG, e.g., Betula pendula, B. 10 divaricata, B. fruticosa, B. nana s.l., Arctostaphylos uva-ursi, Andromeda polifolia, Chamaedaphne calyculata, 11 Rhododendron tomentosum, and Vaccinium vitis-idaea. The majority of plant species recovered in LIG deposits 12 at both sides of the Dmitry Laptev Strait are extralimital, i.e., they do not occur in high arctic tundra today but 13 considerably further south. At Oyogos Yar, only ca. 80 km to the southeast of the Bol'shoy Lyakhovsky site, tree 14 species like Larix gmelinii, Betula pendula s.l., and Alnus hirsuta were already present during the LIG, indicating 15 that the treeline was shifted about 270 km further north than currently (Kienast et al., 2011). The nearest known 16 modern occurrence of grey alder is located at the Sobolokh Mayan River 910 km southwest of Oyogos Yar 17 (Krasnoborov and Malyschev, 2003; GBIF, 2023). 18 Numerous coprophilous Sordariaceae fungi spores found in our LIG deposits point to the presence of grazing herds

during this time. In West Beringia, forest-steppe-tundra provided grazing areas for large Pleistocene mammals sothey could survive the Pleistocene interglaciations (Kuzmina, 2015b).

Plant-derived *seda*DNA shows substantial overlap with the plant macrofossil record in recovering taxa that do not occur at Bol'shoy Lyakhovsky today, including *Betula*, several Ericaceae species, and *Potamogeton*. The taxonomic composition in profile L14-04 from Bol'shoy Lyakhovsky Island indicates that the interglacial vegetation was likely a mosaic of subarctic shrub-tundra and dry steppe communities with arctic-alpine and pioneer plants. The record shows many similarities in the sedaDNA plant record with the MIS 5e record from the Batagay megaslump (Courtin et al., 2022).

27 A major discrepancy to prior studies but also a highlight of our record is the detection of Larix, Picea, and Populus 28 in the interglacial strata, suggesting that the treeline reached indeed as far north as Bol'shoy Lyakhovsky Island 29 (73.3 °N). Larix-DNA was detected in several samples, all of which showed at least 2% Larix in the pollen 30 assemblage (Zimmermann et al., 2017). The pollen records of Larix are usually underrepresented because pollen 31 is produced in low quantities, and due to a high fall speed, the potential for long-distance dispersal is low (Sjögren 32 et al., 2008; Jørgensen et al., 2012; Niemeyer et al., 2015). Hence, single pollen grains have been accepted as 33 evidence for the local presence of Larix (Edwards et al., 2005). We verified the presence of Larix-DNA by re-34 amplification and re-sequencing with Larix-specific primer pairs, corroborating the authenticity of even low Larix 35 sequence counts in the metabarcoding record. Beetle remains and plant macrofossils derived from profile R35, 36 about a kilometer away from this site, indicate subarctic shrub tundra and the absence of trees at Bol'shoy 37 Lyakhovsky Island. Hence, we conclude that Larix was heterogeneously distributed in the landscape of Bol'shoy 38 Lyakhovsky Island, likely as individual trees or stands of trees within an open forest tundra, where trees were 39 growing in more protected sites with a favorable microclimate. Evidence of the presence of Larix trees as far north 40 as Kotelny Island during MIS 3 (van Geel et al., 2017) substantiates our assumptions.





In our LIG sedaDNA record, Larix was mostly accompanied by evergreen Picea and deciduous, broadleaved 1 2 Populus, yet the absence of macrofossil and pollen evidence requires a critical evaluation. The genetic marker 3 used in this study is located on the chloroplast genome, which in the genus Picea is inherited paternally via pollen 4 (Sutton et al., 1991). As such, Picea pollen, susceptible to long-distance transport, could be a source of DNA in 5 our record. Indeed, samples in which Picea-DNA was detected contained relatively high amounts of Picea pollen 6 grains. However, not all samples in which pollen proportions were relatively high also contained Picea-DNA, 7 rendering this explanation uncertain as well. Moreover, previous work implies that pollen may not be the source 8 of Picea sedaDNA (Sjögren et al., 2017; Niemeyer et al., 2017; Parducci et al., 2017) likely because the pollen 9 exine is very durable, making the pollen resistant to degradation but at the same time prevent the release of DNA 10 during our gentle DNA extraction procedure. A similar discussion about the authenticity of Picea abies in a 11 sedaDNA record from the Ural Mountains was led by Clarke et al. (2020), where findings of stomata were considered strong evidence for local occurrence. One of our samples indeed contained Picea cf. stomata, but 12 13 identifying the species-specific source of stomata was difficult, and they cannot be considered as strong evidence. 14 In contrast to Picea, the chloroplast genome of Populus is maternally inherited, and therefore, long-distance 15 transported pollen as a source of Populus-DNA can be excluded (Rajora and Dancik, 1992). Today, Populus 16 suaveolens populations occur relatively far north, with the northernmost documented individual in the Lena Delta 17 (73.2 °N, 128.6 °E; Seregin, 2023). As modern woody taxa penetrate the subarctic tundra belt along rivers 18 (Aleksandrova, 1980), it is possible that during the LIG, P. suaveolens could have progressed into our study area 19 at riversides and floodplains. The map "Late Pleistocene (Riss-Würm), 120 000 Years" of Alekseev et al. (1991b) 20 shows river valleys and temporary lakes on Bol'shoy Lyakhovsky Island and around Svyatoy Nos. In addition, 21 most of the area is labeled as relict alluvial and lacustrine plains.

Unless macrofossil evidence confirms the presence of *Picea* or *Populus* in the area, the question of whether these taxa were truly part of the interglacial vegetation cannot be answered fully. However, given that (1) absence of evidence is not evidence of absence, (2) *Populus* has been detected more often in the DNA than in the macrofossil record (Kjær et al., 2022) or the surrounding vegetation (Alsos et al., 2018), (3) the findings of extralimital species in interglacial strata (Kienast et al., 2008), and (4) the uncertainty about alternative DNA sources, the possibility remains that *Picea* and *Populus* were growing that far north during the LIG.

28 Aquatic macrophytes such as Potamogeton perfoliatus, Stuckenia filiformis, S. vaginata, Callitriche 29 hermaphroditica, and Batrachium sp. were abundant during the LIG but are completely absent today. These 30 findings are another indication of warmer than present-day conditions (Kienast et al., 2008, 2011; Stoof-31 Leichsenring et al., 2022). The aquatic freshwater LIG habitats are further characterized by fossil chironomid, 32 cladocera, ostracod, and mollusk communities. The presence of semi-terrestrial chironomid taxa at high 33 abundances and low abundances of cold-stenotherm taxa can indicate a transition from the preceding colder MIS 34 6 conditions to a warmer MIS 5e setting and probably correspond to the lower part of the R35 section on Bol'shoy 35 Lyakhovsky Island (Ilyashuk et al., 2006). Here, the subdominant taxa Chironomus anthracinus-type, Cricotopus 36 laricomalis-type, Tanytarsus pallidicornis-type, and Endochoronomus albipennis-type prefer relatively warm and 37 productive lakes (Nazarova et al., 2015, 2023), while Tanytarsus lugens-type and Parakiefferiella triquetra-type 38 taxa are in contrast cold stenotherm and characteristic for oligotrophic cold subarctic lakes. Limnophyes, 39 Metriocnemus eurynotus-type, and Parametriocnemus- Paraphaenocladius are typical for lake-level fluctuations 40 (Massaferro and Brooks, 2002). Smittia might indicate shore erosion processes or unstable lake-level conditions 41 (Brooks et al., 2008). The Oya 5-1 chironomid record from Oyogos Yar does not resolve lake development as R35





from Bol'shoy Lyakhovsky Island but instead aggregates different lake stages into one paleo-assemblage. The Oya5-1 cladoceran assemblages indicate habitats with a well-developed vegetated shallow littoral zone as well as pelagic open-water zones in the paleo-lake. The reconstructed WDs from chironomid data of 1.7±0.9 m to 5.6±1.0 m for Bol'shoy Lyakhovsky and 2.2±1.1 m for Oyogos Yar are within the range of measurements of modern thermokarst lakes of 1 to 6 m depth (e.g., Wilcox et al., 2022, Morgenstern et al., 2013, Kallistova et a., 2019 and references therein).

7 The LIG ostracod assemblages are characterized by species that tolerate considerable changes in temperature and 8 salinity regimes that are comparable to modern conditions in the periglacial landscapes of East Siberia, where 9 species such as Candona candida, Fabaeformiscandona rawsoni, and Limnocytherina sanctipatricii occur (Wetterich 10 et al., 2008a, 2008b). Single findings of the thermophilous species Cyclocypris ovum - not present in modern 11 environments of North Yakutia - indicate summer conditions distinctly warmer than today (Kienast et al., 2011). 12 The presence of benthic ostracods in lacustrine LIG deposits further indicates a sufficiently high oxygen content 13 in the water column of the host waters. Furthermore, the waters must have been ice-free for a certain period during 14 summer to facilitate the ostracod larvae development. As ostracods in high latitudes are apparently adapted to a 15 relatively short ice-free period, they conduct asexual reproduction (parthenogenesis), which explains relatively 16 high shares of adult females and only rare males in the fossil assemblages (Meisch, 2000). The high number of 17 juvenile shells indicates short summers in which the development of ostracods did not always reach its final stage. 18 The often-complete preservation of the fragile ostracod shells points to stillwater habitats and deposition, as well 19 as *in-situ* preservation. The shallow sublittoral zone of thermokarst lakes and ice-wedge casts formed by melting 20 wedge ice are the most probable habitats for the fossil ostracod assemblage (Wetterich et al., 2009; Kienast et al., 21 2011).

22 The discrepancy in the species inventories of the last and the current interglacials is certainly the result of climatic 23 differences, i.e., the recent phase - the late Holocene - is comparatively cold in comparison to earlier warm stages 24 in Northern Siberia. This is even true for the MIS 3 Interstadial when larch trees existed as far north as Kotel'ny 25 Island (van Geel et al., 2017). Larch and other woody plants probably spread northward during the LIG when 26 Kotel'ny Island was still part of the mainland. The connection of the New Siberian Archipelago with the mainland 27 during the LIG can be deduced from the highly continental climate character existing adjacent to today's Dmitry 28 Laptev Strait. The persistence of this potential feeding base for herbivores during preceding warm stages helps 29 explain why large cold-adapted grazers survived earlier interglacials in Beringian refugia, which became centers 30 of their dispersal during subsequent cold stages.

31

32 6 Conclusions

New IRSL ages confirm the LIG (MIS 5e) origin of the Krest Yuryakh ice-wedge pseudomorphs and lake sediments that are exposed at both coasts of the Dmitry Laptev Strait. The present study results are consistent with previous work interpreting the MIS 5e as a key warm period during which extensive permafrost thawing and thermokarst development occurred in north-eastern Siberia. The cryolithological features observed in the LIG deposits bear striking similarities to those of Lateglacial and early Holocene refrozen thermokarst deposits, suggesting comparable processes of deposition that were characterized by ground ice melting, surface subsidence, and thermokarst formation driven by climate warming.





Paleoclimate data synthesized from a variety of proxies - including plant macrofossils, aquatic and terrestrial 1 2 invertebrates, and lipid biomarkers - indicate that temperatures during the LIG were significantly warmer than 3 today. Mean temperatures of the warmest month (MTWA) reconstructed from proxies show a range of 6.0°C 4 (pollen data of Bol'shoy Lyakhovsky) and 15.3 °C (plant macrofossils of Bol'shoy Lyakhovsky and chironomid 5 of Oyogos Yar) and overlap of 10.3°C and 10.7°C for Bolshov Lyakhovsky) and 12.0 and 12.6 °C for Oyogos Yar, demonstrating the pronounced warming of this period. However, one of the critical challenges in predicting 6 7 future ecosystem responses lies in the fact that the land-ocean distribution during the LIG was markedly different 8 from today, affecting the degree of continentality, which played a major role in modulating climate and ecosystem 9 dynamics. 10 Paleoclimate models generally agree well with the mean temperature of the coldest month (MTCO) proxy data but

rateoclimate models generally agree wen with the mean temperature of the contest month (MTCO) proxy data but consistently underestimate the mean temperature of the warmest month (MTWA) across proxy records when using modern land-sea configurations. This mismatch is significantly reduced when models incorporate land-sea distributions that more closely reflect those of the LIG. This adjustment highlights the importance of considering past land-sea configurations in regional paleoclimate modeling when comparing proxy and model results, a critical step in refining our understanding of Arctic climate dynamics during MIS 5e.

The strong ecosystem response to the LIG warming, reflected in the high diversity of proxies, shows the sensitivity of permafrost regions to rising temperatures. In particular, the development of thermokarst landscapes created a mosaic of terrestrial, wetland, and aquatic habitats, fostering an increase in biodiversity. This biodiversity is evident in the rich variety of terrestrial insects, vegetation, and aquatic invertebrates preserved in these deposits. In addition, the tree line extended 270 km further north during the LIG than it does today, yet the cold-adapted mammoth fauna managed to persist in this region, probably finding refuge in the microclimates created by the thermokarst landscape.

While the LIG is often used as an analog for future climate warming in the Arctic, there are important differences. Most notably, the LIG warming was driven primarily by increased summer insolation, whereas current Arctic warming so far is most pronounced in winter due to anthropogenic forcing and climate system feedback mechanisms. This seasonal distinction is crucial because many of the environmental changes relevant today, particularly those related to ecosystem processes and permafrost dynamics, occur during the transitional seasons (spring and fall) - for which we currently lack proxy data from MIS 5e.

Ultimately, our results highlight the complexity of Arctic climate responses and emphasize the sensitivity to seasonal factors, which are important aspects of future climate scenarios. Nevertheless, the lessons learned from MIS 5e, particularly regarding thermokarst development and ecosystem adaptation to warming, provide valuable insights into the potential future trajectory of permafrost regions in the context of ongoing climate change. Further research is essential, particularly to fill gaps in proxy data for transitional seasons and to refine model-proxy comparisons to improve our predictions of Arctic climate dynamics.





1 7 Appendices

Table A1: Overview of sample collections for cryolithological and fossil proxy studies of Krest Yuryakh deposits
 exposed at both coasts of the Dmitry Laptev Strait.

4 8 Code availability

5 not applicable

6 9 Data availability

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- Clumped isotope sample and normalisation data will be uploaded to the EarthChem Library pending publication
 of this manuscript.
- 38

39 10 Executable research compendium (ERC)

- 40 not applicable
- 41 **11 Sample availability**





- 1 Original samples are available on request in the sample archives of the AWI Research Unit Potsdam.
- 2 12. Video supplement
- 3 not applicable
- 4 13 Supplement link
- 5 Supplement material_Figures
- 6
- 7 14 Team list
- 8 not applicable

9 15 Author contribution

10 LS designed the paper concept, compiled the various results, carried out the cryolithological studies and evaluations, organized the writing process, and wrote the first manuscript draft. LS, TO, FK, TK, SK, VT, GG, 11 12 VK, HaMe, GS, SB, SW, and MCF participated in one or more of the five expeditions to Bol'shoy Lyakhovsky 13 Island and the Oyogos Yar mainland coast between 1999 and 2014. MCF conducted the geochronological studies. 14 HaMe was responsible for isotope chemistry studies. A number of co-authors were responsible for certain 15 paleoproxies and environmental reconstructions based on them: AA - pollen, FK - plant macrofossils, mussels, AS - ostracods, plant macrofossils, LN - chironomids, LF - cladocerans, SK - insects, TK - mammals, UH, TB - pollen-16 based climate reconstructions, HHZ - sedaDNA, SB, SU, SM - clumped isotope analysis, SK - lipid biomarkers, 17 18 SW - ostracods. AP contributed with data on marine MIS 5e deposits. HeMa and GL carried out paleoclimate 19 modeling. All authors were involved in the data interpretation, took part in the scientific discussions and helped 20 with writing and editing the manuscript.

21 16 Competing interests

22 The authors declare that they have no conflict of interest.

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- 7

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Appendix A 2

- Table A1 Overview of sample collections for cryolithological and fossil proxy studies of Krest Yuryakh deposits exposed at both coasts of the Dmitry Laptev Strait 3
- 4





Profile	Location number in Table A1	Year	Coordinates °N, °E	Height [m asl]	Deposits type	cryo-lithology	Pollen,	SedalDNA	Plant macro-fossils	Chironomids	Additional bioindicators, clumped isotopes, and IRSL-dated samples	Ostracods	References
Bol'sh	oy Ly	akh	ovsky Island										
R22+ 60 (R22)	1	1999	73.339000 141.295100	1-4.8	pseudo- morph	x	R22+60 S-5, S-6, S-8, r2260s5_8 0, r220s54_2 00, r220s53_2 30		R22 OS- 53, OS- 54, OS-55		$\begin{array}{c} \text{beetles} \\ \text{and other} \\ \text{small} \\ \text{fossils,} \\ \text{R22 B15} \\ \text{h=}2.5\text{-}2.8 \\ \text{m (OS-}53, \text{OS-}54); \text{B16} \\ \text{h=}4 \\ \text{m (OS-}55); \\ \text{R22+}30 \\ \text{BL-R-} \\ \text{M2} \end{array}$		Schirrmeister et al. (2000); Andreev et al. (2004); Kienast et al. (2008); https://doi.pangaea. de/10.1594/PANGA EA.880948
R23+ 40	2	1999	73.339400 141.292500	1.8- 7.3	lake deposits	х	R23+40 S-1 to S-7				Pisidium sp. shell R23+40– 10	R23+ 40-S1, -4, -9	Schirrmeister et al. (2000); Andreev et al. (2009); https://doi.pangaea. de/10.1594/PANGA EA.880949
R32		1999	73.344863 141.265733		lake deposits						R 32 mollusks BL-R- M4		Schirrmeister et al. (2000)
R35	3	1999	73.345898 141.261696	1-5.2	pseudo- morph		R35 S-1 to S-11		R35 S-9	R35 S-1 to S-11			Schirrmeister et al. (2000); Ilyashuk et al. (2006); Kienast et al. (2008)
L11+ 40	4	1999	73.32330 141.38650	0.5-4.3	lake deposits	x	L11+40 S- 1 to S-10 OS-56, OS-57, OS-60		OS-56, OS-57, OS-60	OS- 56, OS-57	beetles and other small animals B-17 h=4-4.3 (OS-56, OS-57); B-19 h=7-7.3 (OS-60, OS-61)	L11- S-6	Schirrmeister et al. (2000); Kienast et al. (2008); Andreev et al. (2009); https://doi.pangaea. de/10.1594/PANGA EA.880935
L13+ 80	6	1999	73.322300 141.393200	5-6.3	lake deposits	x							Schirrmeister et al. (2000); https://doi.org/10.15 94/PANGAEA.880 936





L14	7	1999	73.322200 141.393800	3-5.4	pseudo- morph	x	L14 S-1, S-2						Schirrmeister et al. (2000); Andreev et al. (2004); https://doi.pangaea. de/10.1594/PANGA EA.880937
L7-11 A	8	2007	73.31672 141.42628	4-5.4	pseudo- morph	х			L7-11-07 to -12		Insects. daphnia, moss	L7- 11-07 to -12	Boike et al. (2008); Schneider (2010); https://doi.pangaea. de/10.1594/PANGA EA.727667
L7-14 B-C	9	2007	73.2877 141.69097	2.5-5	pseudo- morph	х	L7-14-04 to -15					L7- 14-04 to -15	Wetterich et al. (2009); Boike et al. (2008); https://doi.pangaea. de/10.1594/PANGA EA.727669
L7-16	10	2007	73.31385 141.4505	4.5-7	pseudo- morph	х							Boike et al. (2008); https://doi.pangaea. de/10.1594/PANGA EA.727669
L14- 04	11	2014	73.34100 141.28586	3.9-12 core	lake deposits	х	L14-03 6.73 to 12.87, L14.04 6.15 to 8.03	L14.0 4 6.15 to 8.03			GDGT		Zimmermann et al. (2017); https://doi.pangaea. de/10.1594/PANGA EA.868983 https://doi.pangaea. de/10.1594/PANGA EA.878884
L14- 04 B	11	2014	73.34100 141.28586	0.6- 5.0 outc rop	lake deposits	X		L14- 04B 2.45, 3.45			GDGT		Zimmermann et al. (2017)
L14- 04 C	11	2014	73.34100 141.28586	2.5- 7.5 outcro p	lake deposits	х	L14-04C 2.55 to 4.45	L14- 04C 2.55 to 4.45[LS3]			GDGT		Schwamborn and Wetterich (2015); Zimmermann et al. (2017)
L14- 12	12	2014	73.34055 141.28498	3-7	lake deposits						IR-OSL: L14-12- OSL3, L14-12- OSL1		Schwamborn and Wetterich (2015); this study
Oyogo	s Yar	coa	st										
Oya 3	13	2002	72.679317 143.551417	1-4	pseudo- morph	x							Grigoriev et al. (2003)
Oya 5-1	14	2002	72.68000 143.53000	3.5	pseudo- morph	х	Oya 5-1		Oya 5-1	Oya 5-1	beetles, cladocera ns, molluscs, clumped isotopes	Oya 5-1	Grigoriev et al. (2003); Kienast et al. (2011)
Oy7- 01 A- C	15	2007	72.67454 143.60981	1-2.5	lake deposits	х			Oy7-01- 01 to 13		Insects. Daphnia, moss, mollusks	Oy7- 01-01 to 13	Schneider (2010); https://doi.pangaea. de/10.1594/PANGA EA.727673





Оу7- 07 В	16	2007	72.67865 143.55718	5-6	lake deposits	х					Boike et al. (2008); https://doi.pangaea. de/10.1594/PANGA EA.727676
Oy7- 08 A- B	17	2007	72.68002 143.53181	2-6	pseudo- morph	х	Oy7-08- 02 to 24			Oy7- 08-02 to 24	Wetterich et al. (2009); Opel et al. (2017)

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