| 1 | A GCM Comparison of Plio-Pleistocene SuperInterglacial Periods in |
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| 2 | Relation to Lake El'gygytgyn, NE Arctic Russia |
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| 11 | Abstract |
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| 13 | Until now, the lack of time-continuous, terrestrial paleoenvironmental data |
| 14 | from the Pleistocene Arctic has made model simulations of past interglacials |
| 15 | difficult to assess. Here, we compare climate simulations of four warm interglacials |
| 16 | at Marine Isotope Stage (MIS) 1 (9ka), 5e (127 ka), 11c (409 ka), and 31 (1072 ka) |
| 17 | with new proxy climate data recovered from Lake El'gygytgyn, NE Russia. Climate |
| 18 | reconstructions of the Mean Temperature of the Warmest Month (MTWM) indicate |
| 19 | conditions up to 0.4, 2.1, 0.5 and 3.1 °C warmer than today during MIS-1, 5e, 11c, |
| 20 | and 31, respectively. While the climate model captures much of the observed |
| 21 | warming during each interglacial, largely in response to boreal summer orbital |
| 22 | forcing, the extraordinary warmth of MIS-11c relative to the other interglacials in |
| 23 | the Lake El'gygytgyn temperature proxy reconstructions remains difficult to |
| 24 | explain. To deconvolve the contribution of multiple influences on interglacial |
| 25 | warming at Lake El'gygytgyn, we isolated the influence of vegetation, sea ice, and |
| 26 | circum-Arctic land ice feedbacks on the modeled climate of the Beringian interior. |
| 27 | Simulations accounting for climate-vegetation-land surface feedbacks during all |
| 28 | four interglacials show expanding boreal forest cover with increasing summer |
| 29 | insolation intensity. A deglaciated Greenland is shown to have a minimal effect on |
| 30 | Northeast Asian temperature during the warmth of stage 11c and 31 (Melles et al., |
| 31 | 2012). A prescribed enhancement of oceanic heat transport into the Arctic Ocean |

does have some effect on Lake El'gygytgyn regional climate, but the exceptional
warmth of MIS-l1c remains enigmatic relative to the modest orbital and greenhouse
gas forcing during that interglacial.

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- 37 1. Introduction
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Knowledge of Pleistocene climate history has increased dramatically over the past three decades, however existing records remain strongly biased toward an oceanic viewpoint, due to the lack of long terrestrial archives. In the context of future warming, it is clearly important to understand the effects of warming on the terrestrial Arctic, the strength of polar amplification, and systemic teleconnections to and from other latitudes. Past warm periods known as Interglacials, over the past 2.8 million years, provide a means of studying climates warmer than today.

In 2009, a multinational team drilled a sediment core from a 25 km wide impact 46 crater lake named "Lake El'gygytgyn" (alternatively, Lake "E"), in northeast Siberia 47 (Brigham-Grette et al., 2013; Melles et al., 2012). The core contains the longest Arctic 48 terrestrial record ever recovered, extending back ~3.5 million years, and provides 49 50 evidence for periods of exceptional warmth during Pleistocene interglacials as defined by marine benthic δ^{18} O records (Lisiecki and Raymo, 2005) (Figure 5A&B). It has been 51 52 shown that Marine Isotope Stage(s) 1, 5e, 11c and 31 were among the warmest interglacials in the Pleistocene Arctic (Melles et al., 2012). 53

54 To explore the sensitivity of northwestern Beringia to interglacial forcing and the mechanisms responsible for the observed climate changes, we use a Global Climate 55 Model coupled to an interactive vegetation model to simulate the terrestrial Arctic's 56 response to the greenhouse gas and astronomical forcing associated with specific 57 interglacial (e.g., Yin and Berger, 2011). A range of sensitivity tests were performed and 58 59 a range of changes in boundary conditions are imposed to test the response of the region to changes in circum-Arctic ice sheets and possible changes of ocean heat transport into 60 the Arctic Ocean. The results are then compared to the Lake E multi-proxy 61 reconstructions. 62

63 2. Model and experimental design

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65 All global climate simulations discussed herein were performed using the current version of the Global ENvironmental and Ecological Simulation of Interactive Systems 66 (GENESIS) Global Climate Model (GCM) version 3.0 (Alder et al., 2011; Thompson and 67 68 Pollard, 1997). GENESIS is an atmosphere, land-surface, ocean, snow, sea ice, ice sheet and vegetation coupled model. As used here, spectral resolution of the atmosphere GCM 69 is T31 resolution (approximately 3.75° resolution) with 18 vertical levels (Thompson and 70 Pollard, 1997). The AGCM is coupled to 2°x2° soil, snow, vegetation, ocean, and sea ice 71 72 model components. The GCM is interactively coupled to the BIOME4 (Kaplan, 2003) vegetation model that predicts equilibrium vegetation distribution, structure and 73 biogeochemistry using monthly mean climatologies of precipitation, temperature and 74 75 clouds simulated by the GCM. Vegetation distributions take the form of 27 plant biomes 76 including 12 plant functional types (PFTs) that represent broad, physiologically distinct 77 classes (Kaplan, 2003). GENESIS includes options for coupling to an Ocean General 78 Circulation Model (Alder et al., 2011) or a non-dynamical, slab ocean model that incorporates heat transfer, calculations of sea-surface temperatures (SST) and feedbacks 79 80 operating between ocean surface and sea ice. The slab mixed layer ocean model is used here to allow multiple simulations to be performed with and without imposed 81 82 perturbations of surface ocean conditions. This version of the GCM has a sensitivity of 2.9 °C, without GHG, vegetation or ice sheet feedbacks. Greenhouse gasses and orbital 83 84 parameters for each interglacial simulation were prescribed according to ice core records (Loulergue et al., 2008; Lüthi et al., 2008; Schilt et al., 2010) and standard astronomical 85 86 solutions (Berger, 1978).

The strategy adopted here was to target Marine Isotope Stage (MIS) 1 (11 ka), 5e (127 ka), 11c (409 ka) and 31 (1072 ka), corresponding to the timing of peak summer warmth observed at Lake E and identified as "super-interglacials" by Melles et al., (2012). Equilibrium simulations were performed at the time of peak boreal summer insolation at 67.5°N (Laskar et al., 2004) assuming the real climate system equilibrated within a half-precession cycle. Model temperature and precipitation values were calculated from 20-year averages taken from the 60 to 80-year equilibrated simulations.

94 Preliminary analysis of pollen assemblages in the Lake E core is assumed to provide a 95 record of peak summer temperatures, so our data-model comparisons focus on warmest 96 monthly mean climate (July). A simulation of pre-industrial climate (280 ppmv pCO_2) 97 was run as a control experiment to evaluate the model's representation of Beringian climate and to provide a baseline for comparing super-interglacial simulations. A modern 98 99 Greenland Ice Sheet (GIS) is prescribed unless otherwise noted. In simulations without a 100 GIS, the ice sheet is replaced with ice-free, isostatically equilibrated land surface 101 elevations.

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- 103 **2.1 MIS 1, 9 ka**
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MIS-1 represents the last 11,000 years and its onset roughly coincides with the 105 end of the Younger-Dryas (~11,500 ka). Peak boreal summer insolation occurs ~9 ka, 106 when summer insolation was \sim 510 Wm⁻² at 65 °N, relative to 446 Wm⁻² today. Proxy 107 indicators suggest conditions were warmer than present (+1.6 °C over western Arctic and 108 +2 to 4°C in circum-Arctic) with lush birch and alder shrubs (Melles et al., 2012) 109 dominating the vegetation around the lake. This period, known as the Holocene Climate 110 111 Optimum (HCO), was spatially variable, with most warming in the high latitudes, and 112 minimal warming in the mid-latitudes and tropics (Kitoh and Murakami, 2002).

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- 114 **2.2** MIS-5e, 127 ka

115 MIS-5e, also known as the Last InterGlaciation (LIG), is one of the warmest interglacials of the Pleistocene and lasted roughly \sim 12-10 kyr (130 to 116 ka). High 116 obliquity, eccentricity and the timing of perihelion (precession) combined to produce 117 high intensity boreal summer insolation at around 127 ka. Greenland ice core records 118 119 (Dahl-Jensen and NEEM community members, 2013) suggest summer warming up to 8±4 °C over northeast Greenland, but only a modest reduction in the size of the 120 Greenland Ice Sheet (GIS). Studies involving Sr - Nd - Pb isotope ratios of silt-sized 121 122 sediment discharged from southern Greenland suggest that no single southern Greenland 123 geologic terrain was completely deglaciated during the LIG, however, some southern GIS 124 retreat was evident (Colville et al., 2011). A previous model study of MIS-5e by (Yin and 125 Berger, 2011) involved running a model of intermediate complexity to test relative 126 contributions of Greenhouse Gas (GHG) and insolation forcing on LIG warmth. They 127 found that GHGs play a dominant role on the variations of the annual mean temperature of both the globe and the southern high latitudes, whereas, insolation plays a dominant 128 129 role on precipitation, northern high latitude temperatures, and sea ice extent (Yin and 130 Berger, 2011). Similarly, model simulations have shown that insolation anomalies during MIS-5e likely caused significant summer (JJA) warming throughout the Arctic (Bakker 131 et al., 2013; Lunt et al., 2013; Otto-Bliesner et al., 2006). 132

The LIG simulation shown here is used to compare paleoenvironmental conditions in western Beringia, including, temperature, vegetation and precipitation, to Lake E pollen proxy analysis. Orbital parameters and greenhouse gas concentrations are set at their 127 ka values to represent peak boreal warmth during MIS-5e.

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138 2.3 MIS-11c, 409 kyr

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140 MIS-11c is another exceptionally warm interglacial (Howard, 1997) that lasted from 428 to 383 ka (~45 ka). Sediment records from the Arctic containing information on 141 142 MIS-11 are generally lacking (Miller et al., 2010b). Unlike the other interglacials, MIS-11c was remarkably long, with two boreal insolation maxima at ~409 ka and 423 ka, 143 144 creating extensive warmth throughout the Arctic (Melles et al., 2012). Unlike MIS-5e, there is evidence that the GIS may have been much reduced in size (Raymo and 145 146 Mitrovica, 2012; Willerslev et al., 2007), with lush boreal forest covering most of 147 southern Greenland (de Vernal and Hillaire-Marcel, 2008). Particularly warm conditions 148 are also suggested by pollen records analyzed from Lake Biwa (Tarasov et al., 2011) 149 located in Shiga Prefecture, Japan. Likewise, a study from Lake Baikal also indicates 150 warmer than modern temperatures with a "conifer optimum" suggesting warmer conditions and less aridity, perhaps influenced by higher sea levels and reduced 151 152 continentality (Prokopenko et al., 2010).

Three different simulations (Table 1, 2) were run to test the sensitivity of the lake region to MIS-11c forcing. The first simulation uses default boundary conditions, including a modern GIS (MIS11GIS). The second simulation tests the sensitivity of the

Lake E region to an ice-free Greenland (MIS11NG). In this simulation, the entire GIS 156 157 was removed and topography of Greenland was corrected for glacial isostatic adjustment. 158 The final sensitivity experiment includes an increase in sub-sea ice surface heat flux from 2 Wm² in our modern control, to 10 Wm² (additional +8 Wm²) to test the Beringian 159 160 sensitivity to a mostly ice-free Arctic Ocean. The increased heat flux assumes an extreme ~3 Sverdrup (Sv) increase in Bering Strait through flow and a 4 °C temperature contrast 161 162 between North Pacific and North Polar surface water (Melles et al., 2012, supplemental). The additional heat flux convergence is used to crudely mimic the influence of a wider 163 and deeper Bering Strait during times of higher sea level. Using the predictive BIOME4 164 interactive vegetation model, direct comparisons of observed and modeled Arctic 165 vegetation within the Lake E region can be made. Furthermore, simulations using 166 prescribed distributions of biome flora can be used to quantify the local effect of 167 changing vegetation cover around the region. 168

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- 170 2.4
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MIS-31, 1072 ka

MIS-31 (~1062-1082 ka) (Lisiecki and Raymo, 2005) has only been identified in 172 a few Arctic records prior to Lake E. The Interglacial represents one of the last 41-kyr 173 174 glacial cycles and is best known for extreme warmth in circum-Antarctica ocean waters 175 induced by a deterioration of the Polar Front (Scherer et al., 2008) and the collapse of the 176 marine based West Antarctic Ice Sheet (WAIS) (DeConto et al., 2012; Pollard & 177 DeConto, 2009), by intrusion of warm surface waters onto Antarctic continental shelves. On Ellesmere Island, Fosheim Dome includes terrestrial deposits that date to ~1.1 Ma, 178 179 which contains fossil beetle assemblages dated within MIS-31, suggesting temperatures of 8 to 14 °C above modern values (Elias and Matthews Jr., 2002). It is speculated, like 180 MIS-11c, that the Arctic may have been too warm to support a GIS which may have been 181 substantially reduced in size, or possibly nonexistent (Melles et al., 2012; Raymo and 182 183 Mitrovica, 2012). Therefore, simulations of MIS-31 are run both with and without a GIS 184 (Table 1, 2).

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187 **3. Results**

188 **3.1 Control Simulations**

- 189 **3.1.1 Pre-Industrial**
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Simulations of preindustrial 2-m mean annual temperature (MAAT) and MTWM 191 at Lake E are -12 and 10.3 °C respectively, -3 °C and -1.7 °C lower than the modern 192 simulations. Preindustrial summer temperatures (8 °C) are -2.2 °C lower than modern. 193 GHG radiative forcing from a combination of CO₂, CH₄, and N₂O atmospheric mixing 194 ratios implies a 1.8 Wm⁻² reduction relative to modern, accounting for most of the cooling 195 in the preindustrial simulation. Generally, mean annual precipitation (PANN) values in 196 197 the cooler, preindustrial simulation are slightly lower than modern precipitation. At Lake E, preindustrial annual precipitation was 438 mm year⁻¹, substantially wetter than 198 observations (+122 mm year⁻¹). Winter (DJF) precipitation in the preindustrial simulation 199 was ~ 24 mm month⁻¹, while mean summer (JJA) precipitation was 43 mm month⁻¹. 200

Simulated pre-industrial vegetation distributions are assumed to be in equilibrium (Fig. 3A). In the preindustrial simulation, shrub tundra dominates the Lake E region, with evergreen taiga and deciduous forests maintained in interior Siberia and Yukon. Simulated Siberian biome distributions are similar to modern day vegetation described by Kolosova (1980) and Viereck & Little Jr (1975). Shrub tundra in the preindustrial simulation can be attributed to cool and dry Arctic conditions in the preindustrial run.

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- 208 **3.2** Paleoclimate simulations

209 3.2.1 MIS-1 (9 ka); Holocene Thermal Maximum

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July temperatures at Lake E in the MIS-1 simulation (12.4 °C) are ~2.1 °C warmer than preindustrial (10.3 °C) and summer (JJA) temperatures are 1.6 °C warmer (Fig. 2A). Overall, the Siberian interior warms > 5 °C in July, relative to preindustrial. Simulated MTWM exceed > 2 °C around Lake E.

215 Simulated MIS-1 PANN values at the lake (~438 mm year⁻¹) are close to 216 preindustrial values, although somewhat drier conditions dominate further inland, 217 possibly as a result attributed increased proximity away from a moisture source. Simulated vegetation around Lake E is close to the transition between dominant shrubtundra to the east and deciduous forest to the west (Fig. 3B).

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- 221 **3.2.2** MIS-5e (127 ka)
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Overall warming of the Beringian interior in the MIS-5e simulation is > 2 °C 223 224 relative to preindustrial temperatures (Fig. 2B). Most of this warming can be attributed to the direct effects of the MIS-5e orbit (Groll et al., 2005; Langebroek and Nisancioglu, 225 2014), which produces an Arctic summer insolation anomaly of >50 Wm⁻² at the top of 226 the atmosphere, relative to a pre-industrial (modern) orbit (Fig. 1B). According to ice 227 core records, carbon dioxide (CO₂) concentrations during this period were about 287 228 ppmv, contributing 0.132 Wm^{-2} more surface radiative forcing than preindustrial, but the 229 combination of CO₂, CH₄, and N₂O attributes just -0.0035 Wm⁻² forcing relative to 230 preindustrial GHG mixing ratios. 231

Comparing MIS-5e with respect to the preindustrial control simulation at Lake E 232 shows differences in summer (JJA) and MTWM temperatures of +2.5 and +4.2 °C, 233 respectively (Fig. 2B). Summer warming over the GIS is +5 °C relative to preindustrial, 234 235 which is comparable to the LIG warming reported in a recent Greenland ice core study 236 (Dahl-Jensen and NEEM community members, 2013). Mean annual precipitation at Lake E (~401 mm year⁻¹), is 37 mm year⁻¹ less than pre-industrial levels, and the difference is 237 statistically significant at the 95% confidence level with a p-value of 0.029. Overall, 238 239 similar precipitation patterns are seen at Lake E, relative to MIS-5e and the pre-industrial control scenario, which reflects both the overall wet bias in the GCM and the similar 240 241 continental/ice sheet boundary conditions, in both simulations.

A less moist, but warm high latitude environment produces deciduous taiga and evergreen taiga biome distributions around Lake E (Fig. 3C), with evergreen taiga being the most dominant in eastern Beringia and deciduous taiga being more dominant around the Lake E region and most of western Beringia.

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247 **3.2.3** MIS-11c (409 ka)

Due to an eccentricity minimum, MIS-11c is a longer interglacial than the other interglacials in this study (Howard, 1997). We assume an ice-free Greenland in our MIS-11c simulations, with the ice sheet removed and replaced with isostatically equilibrated (ice-free) land elevations. Additional experiments including an imposed increase in subsea ice heat flux in the Arctic Ocean basin will also be discussed.

Model simulations show summer insolation anomalies (relative to preindustrial) during MIS-11c ranging from +45 - 55 Wm⁻² (Fig. 1C) allowing temperatures over the Lake E region during July (month of maximum insolation) to increase 2.2 °C relative to preindustrial. Overall, mean annual summer temperatures (JJA) over the circum-Arctic and Lake E are 2 to 4 °C warmer than pre-industrial temperatures, with the Siberian interior warming the most (Table 2).

In MIS-11c simulations performed with (MIS11GIS) and without a GIS (MIS11NG), the effect on temperature at the Lake E is shown to be small (~0.3 °C). Geopotential height anomalies at 500hPa (+4 – 10 meters) indicate upper-level warming east of Lake E, and cooling west of Lake E, but the net effect of ice sheet loss on surface air temperatures is mostly limited to Greenland itself and the proximal ocean, with little effect at the distance of Lake E, as shown in other modeling studies (Koenig et al., 2012; Otto-Bliesner et al., 2006).

The warmer MIS-11c climate and possible reductions of Greenland and West 267 268 Antarctic ice sheet sheets are thought to have contributed to sea levels as much as >11 meters (Raymo and Mitrovica, 2012) higher than today. Arctic sea ice was also possibly 269 270 reduced (Cronin et al., 2013; Polyak et al., 2010). In order to test the influence of high sea levels and a mostly ice-free Arctic Ocean on Lake E climate, heat flux convergence 271 under sea ice was increased from 2 Wm⁻² to 10 Wm⁻² in the slab ocean/dynamic sea ice 272 model. The resulting reductions in sea ice extent and warmer (~0.2 - 1.0 °C) (Fig. 4A) 273 Arctic SST's produced negligible warming around Lake E (< 0.7 °C), suggesting the 274 275 Lake E region was relatively insensitive to Arctic Ocean conditions.

Precipitation amounts at Lake E during MIS11GIS are close to modern values of 475 mm year⁻¹. Also, MIS11NG exhibits the same precipitation amounts as our preindustrial control run (~438 mm year⁻¹) (Table 2). Simulated precipitation conditions in the Arctic Ocean basin are fairly dry, ~200 mm year⁻¹, comparable to reanalysis data sets (Serreze and Hurst, 2000). On the contrary, simulations of MIS11NG show reduced
precipitation amounts by -37 mm year⁻¹ relative to MIS11GIS. Runs with increased subice oceanic heat flux reduced the drying seen in the MIS11NG simulation and produced
values matching rainfall rates of modern control values (~475 mm year⁻¹).

A warmer and wetter MIS-11c places Lake E on the border of evergreen taiga and shrub tundra biomes (Fig. 3D). Vegetation limits, such as tree lines, are slightly changed during our simulations with increased heat flux and a warmer, open Arctic Ocean. Evergreen forests around the Lake E region extend poleward to the coast and slightly eastward.

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- 290 **3.2.4 MIS-31 (1072 ka)**
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292 An extreme warm orbit with high obliquity, high eccentricity and precession aligning perihelion with boreal summer allows insolation anomalies to be $> 50 \text{ Wm}^{-2}$ at 293 the surface and + 60 - 80 W m⁻² (Fig. 1D) at the top of the atmosphere at the latitude of 294 Lake E. Average summer temperatures around the lake are about +3.6 °C warmer than 295 preindustrial (Fig. 2D; Table 2). While MIS-31 is beyond the temporal range of ice core 296 greenhouse gas records, proxy geochemical records imply MIS-31 has the highest pCO_2 297 (~325 ppmv) of the mid-Pleistocene (Hönisch et al., 2009), contributing ~+0.80 Wm⁻² 298 299 relative to pre-industrial values. As a result, modeled July temperatures at Lake E are >5 °C warmer than pre-industrial temperatures. 300

301 Simulated precipitation at Lake E during MIS-31 is ~438 mm year⁻¹ (Table 2), 302 similar to that in MIS-11c simulations Vegetation distribution is similar to the other 303 interglacials described here (Fig. 3E). The Lake E region is dominated by evergreen 304 taiga.

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306 4. Discussion

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The warm periods of Marine Isotope Stage(s) 1, 5e, 11c and 31 show similar changes around Lake E. Temperature reconstructions during the Holocene Thermal Maximum (9 kyr) indicate +1.6 (± 0.8) °C warming in the western Arctic (Kaufman and 311 Brigham-Grette, 1993) with an overall warming of 1.7 (±0.8) °C in the circum-Arctic 312 (Miller et al., 2010a), relative to modern temperatures. Though our model does not fully 313 account for all the warming during this period, it does produce the warming in the 314 western Arctic as documented by Kaufman and Brigham-Grette (1993). With the decrease in Arctic moisture and low CO₂, deciduous and evergreen forests dominate the 315 316 Arctic in the model, matching the dominant vegetation such as *Alnus*, *Betula* (nut bearing trees and fruits), Poaceae (grasses) and some birch and alder seen in the Lake E record 317 (Melles et al., 2012). 318

Marine Isotope Stage 5e produced the greatest summer warming among the four 319 interglacials simulated here. Comparisons with a preindustrial control run show that 320 differences in MTWM at Lake E during MIS-1 and 5e (+2.1 and +4.2 °C) are similar to 321 322 the changes seen in MIS11NG and 31(+2.2 and +3.5 °C) (Table 2). Similar warming has 323 been seen in other modeling studies showing that a high obliquity and high eccentricity 324 with precession aligning perihelion with boreal summer will yield the warmest boreal summer temperatures (Koenig et al., 2011; Lunt et al., 2013; Otto-Bliesner et al., 2006; 325 326 Yin and Berger, 2011). Strong insolation forcing at these latitudes cause July maximum temperatures to exceed pre-industrial temperatures by >2 °C. The 2–4 °C simulated MIS-327 328 5e warming in Siberia and Lake E has also been seen in proxy data compilations (CAPE, 329 2006; Lozhkin and Anderson (1995); Lozhkin et al. (2006)) and in simulations using a 330 GCM without vegetation feedbacks. Most of the warming has been linked to the summer 331 insolation anomaly associated with the MIS-5e orbit (Otto-Bliesner et al., 2006). The 332 exceptional summer warmth of MIS-5e compared to other interglacials was previously 333 thought to have caused a substantial reduction in the GIS, however, more recent work 334 suggests the GIS contributed only ~1.4 to 4.3 m of equivalent eustatic sea level rise 335 during the LIG (Colville et al., 2011; Quiquet et al., 2013; Robinson et al., 2011; Stocker et al., 2013; Stone et al., 2013), and remained mostly intact (Dahl-Jensen and NEEM 336 337 community members, 2013). This suggests that our simulations of MIS-5e with a modern 338 GIS are a good approximation for this period. Colder and fresher sea surface conditions 339 in the North Atlantic, Labrador and Norwegian Seas have been found in marine sediments records possibly indicating freshwater input (perhaps from parts of Greenland) 340 341 which may have led to early LIG warming attributed to stronger ocean overturning

(Govin et al., 2012). In the model, Arctic warming during MIS-5e allows almost a full 342 replacement of shrub tundra with deciduous forest in and around the Lake E region. 343 344 Pollen analysis during this period shows tree species of birch, alder, pine and spruce (Melles et al., 2012). However, multiproxy studies of MIS-5e show a change in MTWM 345 of only +2 °C compared to modern temperatures (Melles et al., 2012) (Table 2). It can be 346 concluded that the warm boreal summer orbit at MIS-5e can account for much of the 347 warmth in Beringia, and the cirum-Arctic, but the particularly muted response in the Lake 348 E proxy record to summer insolation forcing cannot be fully explained. 349

Simulations of MIS-11c exhibit another very warm interglacial at Lake E, with 350 MTWM maxima approaching +2.2 °C warmer than pre-industrial temperatures (Table 2). 351 Similarly to MIS-5e and 1, peak warmth coincides with perihelion during boreal summer, 352 353 however low eccentricity and obliquity attenuates the effects of precession relative to 5e and 1, making summer insolation less intense. A combination of eccentricity, obliquity 354 and precession elevates summer insolation for ~45k years, a much longer (but less 355 356 intense) interval of elevated summer insolation than during the other interglacials studied 357 here. The overall warmth of MIS-11 is, in part, an outcome of reduced snow and ice cover. 358

359 Another possible mechanism contributing to Lake E warmth at MIS-11 might be related to elevated sea level at this time (Raymo and Mitrovica, 2012), possibly 360 361 contributing to increased Bering Strait throughflow. Today, the Bering Strait is limited to \sim 50 m in depth with a net northward transport of \sim 0.8 Sv (Woodgate et al., 2010). 362 363 Oceanic heat transport into the Arctic basin might have been elevated during high sea level, providing a source of warm water intrusion into the Arctic Ocean basin from the 364 365 North Pacific. As a simple test of the potential for a warmer Arctic Ocean with less sea ice to affect temperatures over terrestrial Beringia, heat flux convergence under sea ice in 366 the Arctic Ocean was increased from 2 to 10 W m⁻². Summer sea ice fraction was 367 reduced by 25 - 50 % and summer ocean temperatures warmed by 0.2 - 1.0 °C (Fig. 368 4A,B). The warmer Arctic Ocean warmed the Lake E region, but only slightly (+0.7 °C), 369 370 and does not account for the exceptional warmth observed during MIS-11c relative to MIS-5e. 371

372 The influence of MIS-11c temperatures on terrestrial biome distributions is 373 supported by a poleward advance of evergreen needle-leaf forest around the lake, which 374 is in good agreement with palynological analysis (Melles et al., 2012) showing forest-375 tundra and northern larch-taiga dominated by spruce, pine, birch, alder and larch (Melles et al., 2012). Surface warming as a result of albedo feedbacks associated with needle-leaf 376 377 forests during snow-covered months accounts for some of the warming during this period, however increased evergreen, terrestrial forest and enhanced evapotranspiration 378 provides a slight net cooling during the summers. 379

A deglaciated Greenland has been shown to have regional effects on SSTs and 380 sea-ice conditions, however warming of the circum-Arctic has been shown to be minimal 381 (Koenig et al., 2012; Otto-Bliesner et al., 2006). This is also demonstrated in our 382 simulations, whereby the loss of the GIS warms summer annual temperatures around 383 Lake E by only 0.3 °C (Table 2). An analysis of 500 hPa geopotential height anomalies 384 show ridging (positive height anomalies of > 10 m) to the east and troughing (negative 385 height anomalies) to the west of Lake E, indicating a slight change in the large-scale 386 387 planetary wave patterns over Beringia. Over Lake E, positive height anomalies are also present, indicating slightly warmer conditions and a slight eastward shift of an 388 389 atmospheric ridge that may have been set up further west of Lake E. The ridging in these 390 simulations may also be related to a decrease in precipitation at Lake E when the GIS is 391 removed in GCM. Extended high pressure over Beringia associated with ridging would 392 create somewhat drier conditions for the region. If the exceptional warmth of MIS-11c is 393 indeed related to the melting of the GIS, freshwater input may have been a mechanism to 394 strengthen North Atlantic overturning creating the warmth missing in our simulations 395 (Govin et al., 2012). Furthermore, it is not clear why the GIS would have survived MIS-396 5e warmth, and not MIS-11c. In sum, the exceptional Arctic warmth of MIS-11c remains 397 difficult to explain and is not a straightforward result of greenhouse gases, orbital forcing, 398 vegetation feedbacks, or Arctic Ocean warming.

Elevated GHG concentrations and a very warm summer orbit can explain much of the warmth during MIS-31, assuming atmospheric CO_2 was higher than MIS-5e and MIS-11 (Hönisch et al., 2009). In the model, the combination of elevated greenhouse gases and strong summer insolation forcing at 1072 ka allow dense needle-leaf and 403 deciduous forests to grow around the Lake. Simulated summer temperatures are about 12 °C (Table 2), +2 °C warmer than modern summer temperatures around Lake E. Biome 404 405 simulations derived from pollen analysis of the Lake E core show a maxima of trees and shrubs during peak northern hemisphere insolation of MIS-31 at 1072 ka. Our model 406 simulations show similar results around Lake E, with increased boreal forest and less 407 tundra and small dwarf shrubs. The snow-albedo effect combined with low-albedo forest 408 409 cover allows temperatures to increase in the Arctic during MIS-31. Peak precipitation rates derived from proxy analysis indicate about 600 mm year⁻¹, or about 125 mm year⁻¹ 410 more precipitation than in our modern model simulation (Melles et al., 2012). GCM 411 results at MIS-31 indicate annual precipitation of ~490 mm year⁻¹ (Table 2), the most 412 annual precipitation among the four interglacials simulated here. While the GCM does 413 not fully capture the enhanced precipitation indicated in the proxy record, a relative 414 415 increase in precipitation is evident. Extraordinary warmth during MIS-31 correlates well with a diminished WAIS (Pollard and DeConto, 2009) implying strong inter-hemispheric 416 coupling that has been related to possible reductions in Antarctic Bottom Water (AABW) 417 418 formation during times of ice-shelf retreat and increased fresh water input into the Southern Ocean (Foldvik, 2004). WAIS collapse could also be linked with the Beringian 419 420 and Lake E warmth during MIS-11c and MIS-5e, but definitive evidence of WAIS retreat 421 during these later Pleistocene interglacials is currently lacking (McKay et al., 2012).

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| 424 5 | . Conclusion |
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426 Lake E provides a high-resolution terrestrial proxy record of climate variability in 427 the Arctic. A linked climate modeling study described here shows that Arctic summers were significantly warmer during several Pleistocene interglacials by as much as + 2 °C 428 during MIS-1 and 11c, and by as much as + 4 °C during MIS-5e and 31 relative to pre-429 430 industrial. It can be inferred that most of the warming in the interglacial simulations can be attributed to a combination of elevated GHGs and astronomical forcing, although, 431 astronomical forcing (at times producing high-intensity summer insolation >50 Wm⁻² 432 higher than today) was the dominant warming mechanism. Greenhouse gas levels during 433

MIS-31 remain poorly known, and the extreme warmth of this particular interglacial 434 could have been substantially augmented by GHG forcing. MIS-1 had relatively low CO₂ 435 around the time of peak Holocene warmth, producing 0.44 Wm⁻² less radiative forcing 436 relative to pre-industrial levels (Melles et al., 2012), but the combination of orbital 437 forcing and perhaps other factors such as changes in Antarctic Bottom Water (AABW) 438 production and reduced Arctic sea-ice may have contributed to exceptional Arctic 439 440 warmth at this time. Thorough testing of these ideas will require additional simulations with coupled atmosphere-ocean models, changes in circum-arctic ice sheets, eustatic sea-441 levels, continentality, changes in sea-ice distributions and the addition of melt-water 442 inputs into northern and southern hemisphere oceans. 443

Extreme interglacial warmth shifted Lake E vegetation from mostly tundra with 444 445 small shrubs as we see the Arctic today to thick, lush evergreen and boreal forest. Due to the extreme warmth, wetter conditions prevailed during the super-interglacials, allowing 446 forest biomes to thrive and increase their maximum extent poleward. While simulated 447 warming at Lake E is broadly similar during each interglacial, the vegetation response in 448 449 each simulation is unique, reflecting differences in seasonal temperatures and hydroclimate. The GIS was significantly reduced during some interglacials (Stone et al., 450 2013), allowing summer temperatures to increase to almost 16 °C warmer than present 451 over Greenland, but with limited impact on temperatures around Lake E. The observed 452 453 response of Beringia's climate and terrestrial vegetation to super-interglacial forcing is still not fully understood and creates a challenge for climate modeling and for quantifying 454 455 the strength of Arctic amplification. Among the interglacials studied here, MIS-11c is the warmest interglacial in the Lake E record, yet MIS-5e is the warmest simulated by the 456 457 model. The model produces overall drier conditions in the earlier interglacials (11c and 31) than suggested by pollen analysis. If the proxy interpretations were correct, this 458 would suggest that the model is missing some important regional processes. The timing 459 of significant warming in the circum-Arctic can be linked to major deglaciation events in 460 461 Antarctica, demonstrating possible inter-hemispheric linkages between the Arctic and 462 Antarctic climate on glacial-interglacial timescales, which have yet to be explained.

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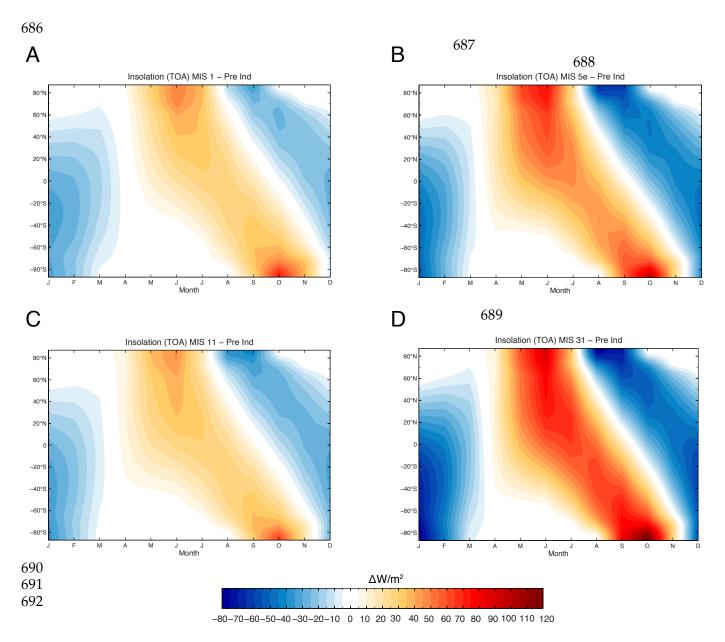


Figure 1: Monthly insolation anomalies at the top of the atmosphere for the interglacial intervals modeled here $[W/m^2]$. A MIS-1 anomalies with respect to modern orbit, B MIS-5e anomalies with respect to modern orbit, C MIS-11c anomalies with respect to modern orbit and D MIS-31 anomalies with respect to modern orbit.

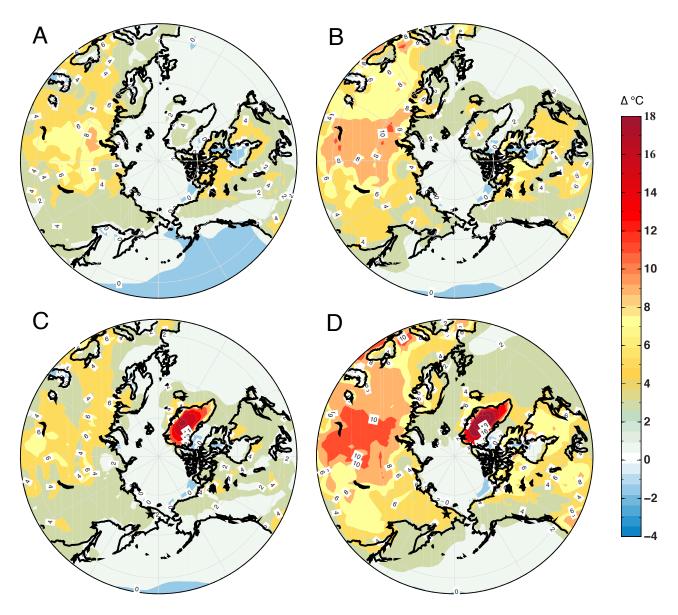


Figure 2: Simulated interglacial anomalies (2-meter annual air temperature in °C) relative to preindustrial temperatures. A MIS-1 (9 ka orbit and GHGs), B MIS-5e (127 ka orbit and GHGs), C MIS-11c (409 ka orbit and GHGs, and no Greenland Ice Sheet), D MIS-31 (1072 ka orbit and GHGs, and no Greenland Ice Sheet). The location of Lake El'gygytgyn (black star) is shown near the bottom of each panel. Areas of no shading (white) roughly correspond to no change that is statistically significant at the 95% confidence interval.



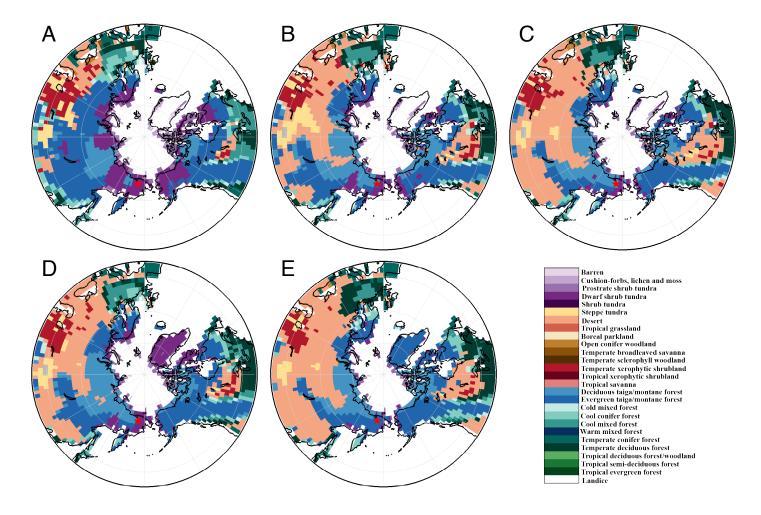
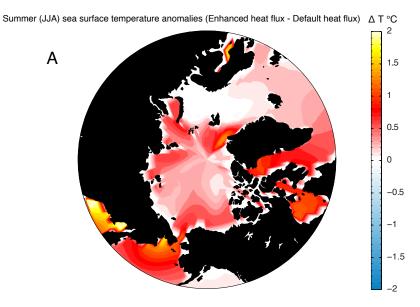


Figure 3: Distribution of interglacial vegetation simulated by the BIOME4 interactive vegetation model coupled to the GCM. A Pre-Industrial vegetation corresponding to modern summer anomalies, **B** MIS-1 (9 ka), **C** MIS-5e vegetation, **D** MIS11NG vegetation and **E** MIS-31 (no GIS) vegetation. The location of Lake E is shown near the bottom of each figure with a red star. Note the poleward advancement of evergreen and needle-leaf trees around the lake during each interglacial and the replacement of shrub tundra to taiga forest.





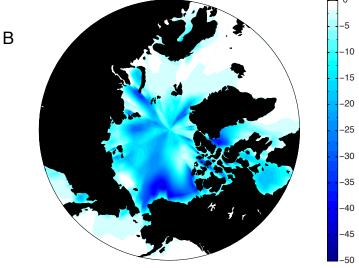


Figure 4: Model simulated (MIS11NG) Summer sea surface temperature and sea ice anomalies caused by enhanced oceanic heat flux (+8 W/m²) at 409 ka. A Summer (JJA) sea surface temperature change with respect to default heat flux simulation (T °C) and B Summer (JJA) sea ice fraction anomalies (%) with respect to default heat flux simulation. With +8 W/m² of sub-sea ice heat flux convergence, Arctic Ocean SSTs rise > 0.5 °C and sea ice fraction decreases 25-50% in most areas.

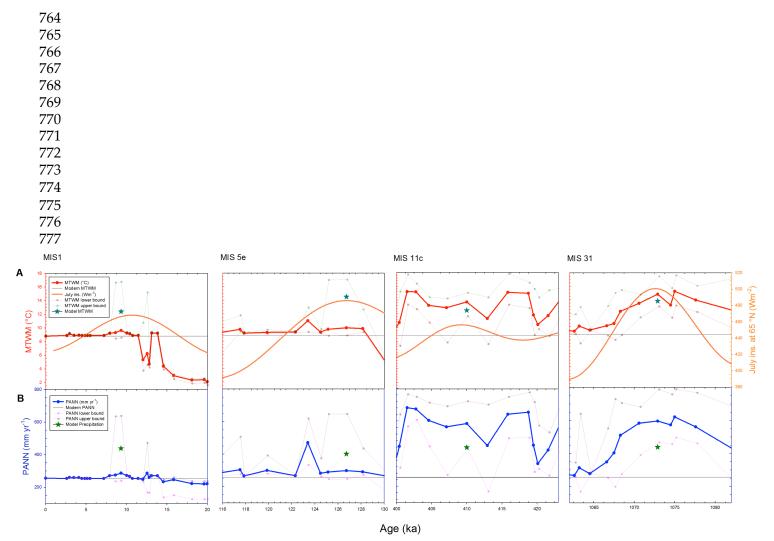


Figure 5: (**A** and **B**) **A** Reconstructed MTWM and **B** PANN from *Melles et al., 2012*. Transparent data above and below the **bolded** lines are upper and lower limits of each data point calculated from a best modern analogue technique (MAT) function. The dark cyan (**A**) and dark green (**B**) stars denote results from the GCM simulations with respect to MTWM and PANN.

Table 1: Overview of interglacial simulations performed during this study. Orbital configurations (Berger, 1978) and greenhouse gas (GHG) concentrations (Honisch et al., 2009; Loulergue et al., 2008; Lüthi et al., 2008; Schilt et al., 2010). Modern GHG concentrations are taken from 1950 AD; obliquity is given in degrees and precession is Ω in degrees.

| Age | Run description | CO ₂ (ppmv) | CH ₄ (ppbv) | N ₂ O (ppbv) | Eccentricity | Obliquity (°) | Precession (Ω, °) |
|---------|---|------------------------|------------------------|-------------------------|--------------|---------------|-------------------|
| 1850 AD | pre-industrial simulation with pre- industrial GHG concentrations | 280 | 801 | 289 | 0.01671 | 23.438 | 101.37 |
| 9 ka | MIS 1 - with (modern) GIS | ~260 | ~611 | ~263 | 0.01920 | 24.229 | 310.32 |
| 127 ka | MIS 5e - with (modern) GIS | 287 | 724 | 262 | 0.03938 | 24.040 | 272.92 |
| 409 ka | MIS 11c - with (modern) GIS | 285 | 713 | 285 | 0.01932 | 23.781 | 265.34 |
| 409 ka | MIS 11c - no GIS | 285 | 713 | 285 | 0.01932 | 23.781 | 265.34 |
| 409 ka | MIS 11c - no GIS + 10 Wm ⁻² increase of heat flux under sea ice | 285 | 713 | 285 | 0.01932 | 23.781 | 265.34 |
| 1072 ka | MIS 31 - with no GIS | 325 | 800 | 288 | 0.05597 | 23.898 | 289.79 |

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Table 2: List of GCM simulations with corresponding variables at the grid cell location of Lake E.

| Run | Pre-industrial | MIS 1-with GIS | MIS 5e-with GIS | MIS 11c-with GIS | MIS 11c-no GIS | MIS 11c-noGIS-10Wm ⁻² | MIS 31-without GIS |
|-----------------------------|----------------|----------------|-----------------|------------------|----------------|----------------------------------|--------------------|
| Lake-E | | | | | | | |
| MAAT (°C) | -12 | -12 | -12.4 | -11.5 | -12.5 | -10.5 | -10.4 |
| Summer Temp (JJA; °C) | 8 | 9.6 | 10.5 | 10 | 10.2 | 10.5 | 11.8 |
| MTWM (July,°C) | 10.3 | 12.4 | 14.5 | 12.2 | 12.5 | 13.2 | 13.8 |
| PANN (mm yr ⁻¹) | 438 | 438 | 401 | 475 | 438 | 475 | 438 |
| 833 | | | | | | | |

835