



Evidence of Ice Age humans in eastern Beringia suggests early migration to North America

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ABSTRACT

Our understanding of the timing and pathway of human arrival to the Americas remains an important and polarizing topic of debate in archaeology and anthropology. Traditional consensus, supported by archaeological and paleoenvironmental data, favors a 'swift peopling' of the Americas from Asia via the Bering Land Bridge during the last Glacial termination. More recent genetic data and archaeological finds have challenged this view, proposing the 'Beringian standstill hypothesis' (BSH), wherein a population of proto-Americans migrated from Asia during, or even prior to the Last Glacial Maximum (LGM) and lived in Beringia for thousands of years before their eventual spread across the American continents. Using a sediment archive from Lake E5 (68.641667° N, 149.457706° W), located on Alaska's North Slope, we present new data supporting the BSH and shedding new light on the environmental impact of these early American populations. Fecal biomarkers support human presence in the environs of the lake, and our data demonstrate elevated biomass burning in this region during the last Glacial. Elevated burning defies the expectation that natural fires would be less frequent in the Arctic during the last Glacial, thereby suggesting human ignition as the likely culprit. Our data shed new light on the pathway and timing of human migration to the Americas and demonstrate the possibility of the sustainable coexistence of humans and the Ice Age megafauna in Beringia prior to their extinction.

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1. Introduction

More than 1 billion people inhabit the Americas today, yet this land mass constitutes the final frontier of the global spread of *Homo sapiens* (Hoffecker et al., 2016). The timeline, pathway, and environmental impact of human arrival to these continents remain contentious even after decades of debate (Goebel et al., 2008; Hoffecker et al., 2014; Tamm et al., 2007). At the heart of these debates sits Beringia (Fig. 1), the corridor of human migration to the Americas (Goebel et al., 2008; Hoffecker et al., 2014). Due to lower sea levels, Beringia stretched from eastern Siberia to the western

edge of the Laurentide Ice Sheet during the last Ice Age or Glacial period.

Archaeological and genetic approaches offer complimentary yet inconsistent perspectives on the peopling of Beringia and the Americas (Fig. 2). Archaeological evidence suggests widespread human occupation of the Americas by the late Pleistocene (ca. 14 cal ka BP; Gilbert et al., 2008; Goebel et al., 2008), which could reflect a 'swift peopling' of the Americas by eastern Asian migrants crossing the Bering Land Bridge (West and West, 1996). Stone tools (Fig. 2; gray circles) at the Yana RHS (30 cal ka BP) and Ushki (13 cal ka BP) sites document human presence in western Beringia as do tools at the Swan Point (14 cal ka BP) and Nenana (13 cal ka BP) sites in eastern Beringia. There is no conclusive evidence for prolonged human presence in eastern Beringia prior to this (Fig. 2; Goebel et al., 2008). The timing of this inferred migration implies that the harsh climatic conditions of Glacial Arctic environments

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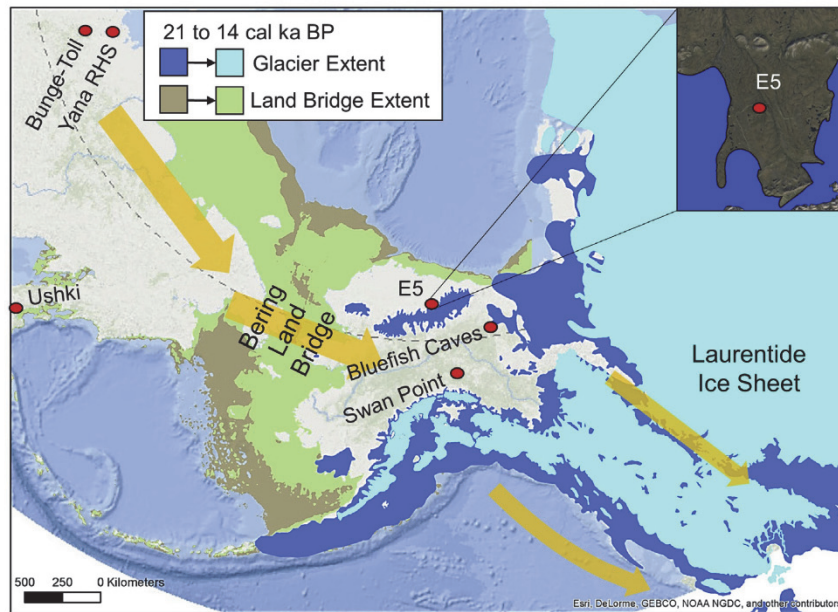


Fig. 1. Map of our study region, Beringia, with changes in the extent of the Laurentide Ice Sheet (shown in shades of blue) and the Bering Land Bridge (in green and brown) depicted from the Last Glacial Maximum (LGM; 21 cal ka BP) to 14 cal ka BP (Dyke et al., 2003; Manley, 2002). Our study site, E5, and recent archaeological finds are shown as red points. Suggested routes of human migration are shown with orange arrows. Inset shows E5's isolated location within inferred alpine glaciation boundaries at the LGM (21 cal ka BP). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

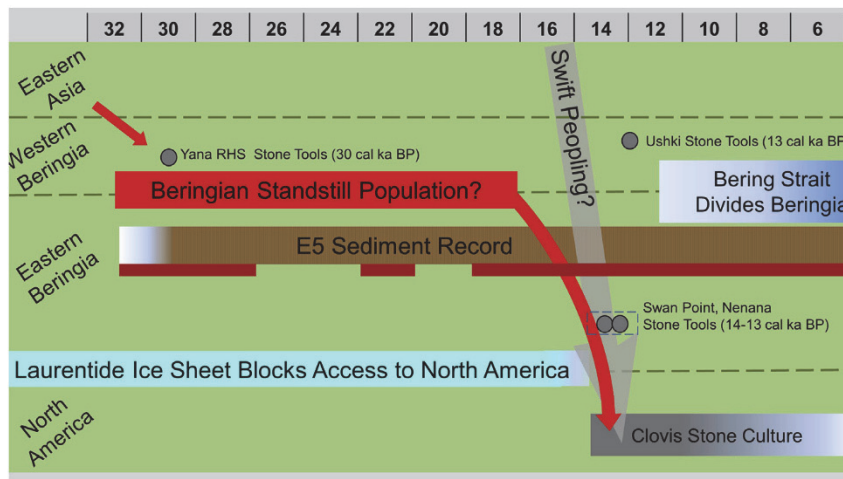


Fig. 2. Schematic of human migration to North America. Genetic (red arrows) and archaeological (gray) perspectives offer inconsistent hypotheses regarding the timing and pathway this human migration. The E5 sediment record reveals human presence in eastern Beringia throughout the last Glacial and Holocene (periods with contemporaneous fecal input and burning in maroon). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

inhibited human migration and climate amelioration during the last deglaciation paved the way for human migration around 14 cal ka BP. However, other paleoenvironmental data indicate that the southward migration of humans to the Americas was possible as early as 17 cal ka BP (Darvill et al., 2018; Lesnek et al., 2018), highlighting the uncertainty of the timing of Beringian habitability. Moreover, recent finds of cut bones, stone, and bone tools in eastern Siberia (western Beringia) dated to between 48 and 30 cal ka BP demonstrate that humans inhabited the western Arctic during the last Glacial (Pitulko et al., 2016, 2004), suggesting that the western Arctic was in fact habitable. Similarly, new genetic evidence suggests that humans settled in the North American Arctic prior to or during the height of the last Glacial (Goebel et al., 2008; Moreno-Mayar et al., 2018). Mitochondrial DNA evidence supports the

hypothesis of a migration of a proto-American population from eastern Asia to Beringia, contemporaneous with archaeological evidence in western Beringia (30 cal ka BP), but well before the southward migration across the Americas documented in archaeological data (Tamm et al., 2007).

The genetic evidence further indicates that the founder population paused, presumably in eastern Beringia, and genetically differentiated from east Asian populations for up to 15,000 years prior to populating the American subcontinents, the so-called “Beringian Standstill Hypothesis” (hereafter BSH; Hoffecker et al., 2016; Tamm et al., 2007). In contrast, full genome analyses of modern and ancient DNA indicate that ancestral Native American populations diverged from their Asian ancestors no more than ca. 23 cal ka BP (Raghavan et al., 2015), leaving little time for the

genetic isolation intrinsic to the BSH. However, recent analyses of ancient DNA suggest divergence occurred ca. 36 cal ka BP, with final separation between 25 and 20 cal ka BP, potentially indicating geographic separation of populations well before the BSH suggests (Moreno-Mayar et al., 2018). These genetic data suffer from the uncertainties inherent to molecular clocks (e.g. constant mutation rate estimates, varying genetic indicators; Kumar, 2005; Scally and Durbin, 2012), and although archaeological finds of cut bones in the Canadian Arctic as old as 23.7 cal ka BP document human presence in eastern Beringia (Bourgeon et al., 2017), their singular occurrence and lack of contemporaneously deposited stone tools or hearths call into question whether these sites record continuous human occupation. Thus, the most persistent obstacle to determining the timing and manner of human migration to the Americas is the lack of direct physical evidence for human occupation of eastern Beringia to test the predictions of the molecular genetic data.

This study presents new analyses of a sediment core from Lake E5 (68.642° N, 149.458° W), located in the northern foothills of the Brooks Range of northern Alaska (Fig. 1). We combine traditional paleoecological methods (charcoal and pollen) with novel organic geochemical biomarkers (polycyclic aromatic hydrocarbons and sterols) to reconstruct ecosystem changes and human presence in eastern Beringia over the last 32,000 years. Additionally, we use transient climate model simulations to contextualize our findings and ecological interpretations. We present direct evidence of both human fecal presence and sustained burning of Arctic Alaskan landscapes as early as 32,000 years ago.

2. Regional setting

Lake E5 (68.641667° N, 149.457706° W) is a small (surface area = 0.1 km²) lake in the northern foothills of Alaska's Brooks Range (Fig. 1). In the Quaternary, the Brooks Range hosted several alpine glacial complexes which contributed to the geomorphology of Alaska's North Slope (Badding et al., 2013; Ellis and Calkin, 1984; Hamilton, 2003). Lake E5 is located on an older glacial landscape (>125 ka BP), referred to as the Sagavanirktok, that escaped glaciation during the last Glacial maximum (LGM), allowing it to archive environmental changes during the last Glacial (Fig. 1, inset; Hamilton, 2003). E5 is one of the few lakes in northeastern Beringia to have persisted through the cold, arid conditions of the last Glacial (Abbott et al., 2010), and thus provides a rare opportunity to examine the region's environmental history.

3. Materials and methods

3.1. Sediment core and chronology

We obtained overlapping sediment cores using a MUCK corer (for the upper sediments) and a modified square-rod Livingstone piston corer (for deeper sections). Using these cores, we constructed a composite stratigraphic sequence for which we calculated an age-depth model using ¹⁴C and ²¹⁰Pb chronostratigraphic techniques and the CLAM age modelling software (Binford, 1990; Blaauw, 2010). We used ultra-microscale ¹⁴C analysis (Shah Walter et al., 2015) to graphitize and date small (10–100 µg) terrestrial plant macrofossils and insect parts, which afforded a relatively high number of age control points. We were unable to determine if insects were of terrestrial or aquatic origin. Materials for radiocarbon dating were obtained by wet sieving ~5 cm³ sediment samples at 500 and 150 µm, respectively, followed by characterization and identification of materials under a dissecting microscope. Radiocarbon ages were calibrated to years before CE 1950 and sediment ages are reported in thousands of calibrated calendar years (e.g. 0 cal ka BP = CE 1950) (Reimer et al., 2013). Our core was

stratigraphically aligned to that of Eisner and Colinvaux (1992) using profiles of sedimentary organic matter, distinct lithological/color changes, and pollen abundance transitions. This allowed us to align the Eisner and Colinvaux (1992) pollen data to our core and results (see Supplementary Material).

3.2. Charcoal analyses

Charcoal analysis was performed following standard procedures (Chipman et al., 2015; Higuera et al., 2009). Volumetrically measured (0.5–1.5 cm³), contiguous (resolution = 0.5–1.0 cm) sediment samples were taken from the core for charcoal analyses. Subsamples were immersed in a 10 mL solution of 50% bleach (10%) and 50% hexametaphosphate (10%) for 24 h before wet sieving (>150 µm, Endecotts brass test sieve, 3 inches) with deionized water. Particles were identified and counted under a binocular dissection microscope (4–40x magnification). Charcoal accumulation rate (CHAR), fire events and the frequency of those events were calculated using the CharAnalysis MATLAB suite (Higuera, 2009). Fire events were calculated from CHAR anomalies exceeding the 90th percentile of the noise distribution fit to the CHAR value distribution.

3.3. Organic geochemical analyses

Subsamples were taken from the core, freeze-dried, and their total lipids extracted (TLE) into dichloromethane:methanol (9:1 by volume) using an Accelerated Solvent Extraction (ASE) system. TLE was dried and weighed before separation into acid (4% acetic acid in ether) and neutral (dichloromethane:isopropanol; 2:1) fractions using aminopropylsilyl gel columns. The neutral fraction was further separated by polarity into N1 (hexane), N2 (dichloromethane), and N3 (methanol) fractions using silica gel chromatography. The N3 fraction was further separated into NAI1 (hexane:dichloromethane; 1:1) and NAI2 (dichloromethane:methanol; 1:1) fractions using an alumina column. PAHs and stanols were isolated in the N2 and NAI2 fractions, respectively. The NAI2 fraction was silylated with N,O-bis(trimethylsilyl)trifluoroacetamide (BSTFA) prior to quantification. Compound abundances in the N2 and NAI2 fractions were measured on an Agilent 6890N gas chromatograph coupled with a 5973N mass spectrometer (GC-MS) and equipped with an Agilent VF-200 ms 60 m capillary column (0.1 × 250 µm). The initial oven temperature was 40 °C and increased by 7 °C/min to a maximum temperature of 320 °C. Flow rate was 1.3 mL/min. Compounds were identified using external standards, characteristic mass fragments, and published literature. Compounds were quantified using an internal standard (hexamethylbenzene) and by the proportional relation of the peak areas of the chromatographs of the characteristic ions of each biomarker of interest. Fecal biomarker ratios were computed following D'Anjou et al. (2012).

3.4. Transient climate model simulations

To assess whether natural ignition sources (lightning) increased during the Glacial, we extracted and calculated regional (latitude from 68 to 70°N and longitude from 165 to 145° W) convective cloud fraction (CCF) from the fully coupled global climate model, FAMOUS (Smith, 2012). FAMOUS is a fast-physics (100 year time step), reduced-complexity general circulation model, which facilitates relatively inexpensive simulations extending back 400 ka BP (which would be prohibitively expensive for a state-of-the-art coupled general circulation model, for example). Indeed, FAMOUS is the only publicly available climate model with a simulation overlapping the time period evaluated in this study. Although

convective cloud-top height would be the best parameterization of lightning probability, these simulations do not resolve sub-grid scale convective processes related to thunderstorm activity, and so CCF offers the best available estimate of convective potential energy for thunderstorm initiation and subsequent lightning strikes (Price et al., 1994; Price and Rind, 1992). We additionally extracted regional temperature, precipitation, and evaporation, and also calculated water balance changes (P-E; precipitation minus evaporation) to fully evaluate changes in climate relevant to fire.

4. Results

4.1. Sediment composition and chronology

The Lake E5 sediments consist of interbedded silts and clays (Fig. 3; right). The core contains several slump/turbidite sequences that we identified based on their clear visual appearance (cm-scale normally graded sequences), as well as radiocarbon analysis of various sediment constituents and lithology. These intervals were removed from the stratigraphy and from all analyses.

Our age-depth model is constrained by seven ^{210}Pb and sixteen ^{14}C age control points (Fig. 3; Table 1; Daniels, 2017; Longo, 2017). We rejected three dates that were much older than surrounding sediments (209.5 and 213.5 cm; Table 1 and Fig. 3); we infer that these macrofossils were stored for thousands of years in soils prior to their transport into the lake, a process common in Arctic landscapes (Oswald et al., 2005). We also rejected a radiocarbon date at 364.5 cm in the core as too young because the accuracy and precision of this measurement was likely compromised by its minuscule size. Our confidence in its measurement was very low as the sample produced only $6\text{ }\mu\text{g}$ of CO_2 , which is the reliability limit for ultra-microscale ^{14}C analysis (Shah Walter et al., 2015). Laboratory standards run along with the samples dated for this study indicate that the measurement blank strongly affects samples representing $<12\text{ }\mu\text{g}$ CO_2 . The date at 364.5 is the only sample in our age model $<12\text{ }\mu\text{g}$ CO_2 . Further, acceptance of that date would result in

unrealistically high sedimentation rates (e.g. nearly instantaneous deposition of 80 cm of sediment) that are incongruous with the stratigraphy of the core.

4.2. Proxy data

Fire proxies in the E5 sediment core indicate there was increased burning during the last Glacial relative to the deglaciation and Holocene. The increase in charcoal is coincident with the greatest fluxes of coprostanol and stigmastanol in the sediment record (Fig. 4). The accumulation rates of charcoal particles (CHARs) were greatest from 32 to 19 cal ka BP (0.0–2.8, mean = $0.26\text{ }\#/\text{cm}^2/\text{yr}$) and lower from 19 cal ka BP to present (0.0–0.1, mean = $0.0\text{ }\#/\text{cm}^2/\text{yr}$). The only statistically supported fire events detected in our record occurred between 32 and 19 cal ka BP and the frequency of those events was greatest from 32 to 30 and 29 to 27 cal ka BP. Similarly, the fluxes of total PAHs were greatest from 32 to 19 cal ka BP (0.0–24.2 $\text{ng}/\text{cm}^2/\text{yr}$, mean = $4.4\text{ ng}/\text{cm}^2/\text{yr}$) and were low from 19 cal ka BP to present (0.0–2.1 $\text{ng}/\text{cm}^2/\text{yr}$, mean = $0.2\text{ ng}/\text{cm}^2/\text{yr}$). The last Glacial (32–19 cal ka BP) also exhibited the greatest fluxes of coprostanol (0.0–3.1 $\text{ng}/\text{cm}^2/\text{yr}$, mean = $0.6\text{ ng}/\text{cm}^2/\text{yr}$) and stigmastanol (0.0–48.8 $\text{ng}/\text{cm}^2/\text{yr}$, mean = $8.0\text{ ng}/\text{cm}^2/\text{yr}$) whereas the fluxes of these compounds were generally lower from 19 cal ka BP to present (0.0–0.76 and 0.0–3.7 $\text{ng}/\text{cm}^2/\text{yr}$ for coprostanol and stigmastanol, respectively). The ratio of coprostanol:stigmastanol, an indicator of human fecal presence (see Discussion and Fig. 5), exceeded 0.18, at several points prior to 19 cal ka BP (31, 29, 28, 25 and 22 cal ka BP), as well as consistently from 19 cal ka BP to present.

4.3. Transient climate model simulations

The FAMOUS climate model simulation displays important differences in atmospheric conditions between the Glacial (32–19 cal ka BP) and deglaciation and Holocene (19 cal ka BP to present). The sum of the convective cloud fraction in the atmospheric column in our study region was low from 32 cal ka BP to 19 cal ka BP (0.013–0.025, mean = 0.018), and higher from 19 cal ka BP to present (0.019–0.035, mean = 0.030; Fig. 4). Similarly, modelled temperature, evaporation, and precipitation were all low from 32 to 19 cal ka BP (mean differences from pre-Industrial = $-5.7\text{ }^\circ\text{C}$, $-4.9 \times 10^{-7}\text{ kg}/\text{m}^2/\text{s}$, and $-3.4 \times 10^{-6}\text{ kg}/\text{m}^2/\text{s}$, respectively; Fig. 5). Taken together, low CCF (which should closely track thunderstorm and thus lightning activity) coupled with low temperatures and evaporation rates would imply that there is little evidence for changes in fire incidence due to changes in background climate.

5. Discussion

5.1. Fecal sterols support human presence in eastern Beringia

Fecal biomarkers strongly support human presence in the Lake E5 watershed during the last Glacial. Fecal stanols distinguish carnivore, omnivore, and herbivore feces as a result of differences in diet and gut processing (Leeming et al., 1996). Fecal sterols preserved in lake sediments have been used to infer and corroborate human presence in several recent studies (Argiriadis et al., 2018; Battistel et al., 2017; D'Anjou et al., 2012), but their reliable interpretation requires consideration of faunal assemblages contributing to sedimentary sterol assemblages. Fluxes of both coprostanol and stigmastanol are greatest during the Glacial at Lake E5, coincident with elevated fire activity. Elevated fluxes of coprostanol have been interpreted to directly reflect human presence (Argiriadis et al., 2018; D'Anjou et al., 2012), as coprostanol in

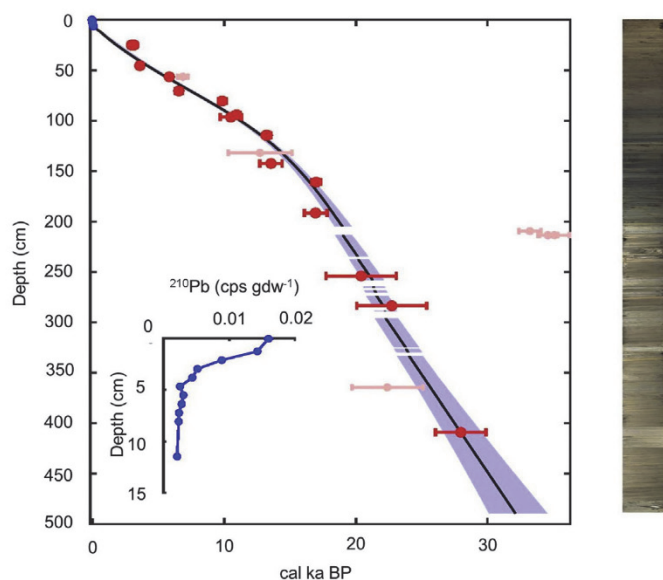


Fig. 3. Age-depth model of the Lake E5 sediment core. Error bars denote 2σ age bounds of calibrated ^{14}C dates (red = accepted, pink = rejected). Blue shading depicts 95% confidence interval and black line denotes best fit age-depth model. Inset: Down core ^{210}Pb activity (cps gdw^{-1} ; counts per second per gram of dry sediment) of uppermost sediments. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

Table 1
Radiocarbon ages informing the E5 age-depth model.

Sample Depth (cm)	Material Dated	Laboratory ID	^{14}C Age	^{14}C Age Error	Calibrated Age ^a
Accepted					
25	Plant Parts	OS-118632	2760	100	2738–3156
25	Insect Eggs	OS-118642	2960	55	2961–3326
45.5	Plant and Insect Parts	OS-123775	3360	50	3461–3707
56.5	Insect Eggs	OS-123776	5090	65	5662–5982
70.5	Plant and Insect Parts	OS-118631	5740	120	6301–6789
80.5	Plant and Insect Parts	OS-123771	8760	70	9549–10133
94.2	Plant Parts	OS-112452	9600	100	10681–11205
96.5	Unidentified Leaf	OS-118634	9320	290	9703–11283
114.5	Insect Eggs	OS-123768	11300	85	13022–13316
114.5	Ephippia and Insect Eggs	OS-123779	11400	150	13003–13549
142.5	Plant Parts	OS-113019	11550	370	12706–14393
161	Plant Parts	OS-117775	1400	90	16650–17328
191.5	Insect Parts	OS-123780	13950	330	16071–17793
254	Plant Parts	OS-118250	16550	1200	17736–23080
283.5	Plant Parts	OS-115834	18550	1200	20071–25404
409	Plant Parts	OS-118653	23600	980	26074–29891
Rejected					
56.5	Plant Parts	OS-118633	5980	170	6467–7247
132	Plant Parts	OS-118260	10750	920	10296–15122
209.5	Plant and Insect Parts	OS-123767	29200	740	31615–34601
213.5	Wood	OS-123774	31300	1000	33779–37913
213.5	Plant Parts	OS-123773	30600	800	33399–36311
364.5	Plant and Insect Parts	OS-123781	18250	1200	19691–25091

^a Calibrated with Intcal13 (Reimer et al., 2013). Range represents 95% confidence interval (2σ range) of the ranked and summed probabilities of calendar years determined by radiocarbon calibration.

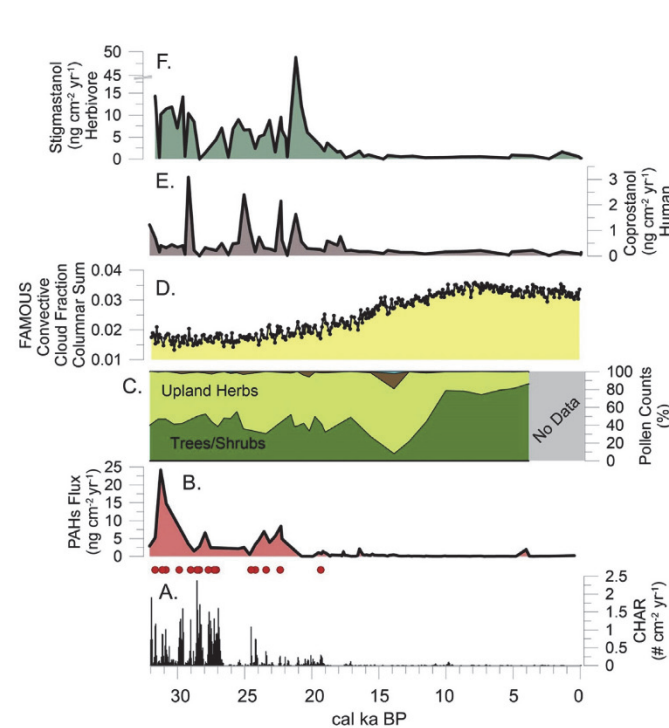


Fig. 4. Paleolimnological data from Lake E5. Charcoal accumulation rate (A; CHAR, black bars), CHAR-derived fire events (red points; see Fig. 5), and total PAH concentrations (B; black line, red shading) indicate there was elevated biomass burning during the Glacial period. Pollen assemblage data (C; divided into upland herb (lime green), shrub (green), terrestrial vascular cryptogam (brown), and aquatic and moss species (blue)) indicate that vegetation did not co-vary with fire history considerably. Regional total column convective cloud fraction (CCF) (D; FAMOUS simulation; black with yellow shading) indicates low lightning ignition potential during the Glacial, coincident with elevated fluxes of the human (E; coprostanol; brown shading) and herbivore (F; stigmasterol; green shading) fecal biomarkers. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

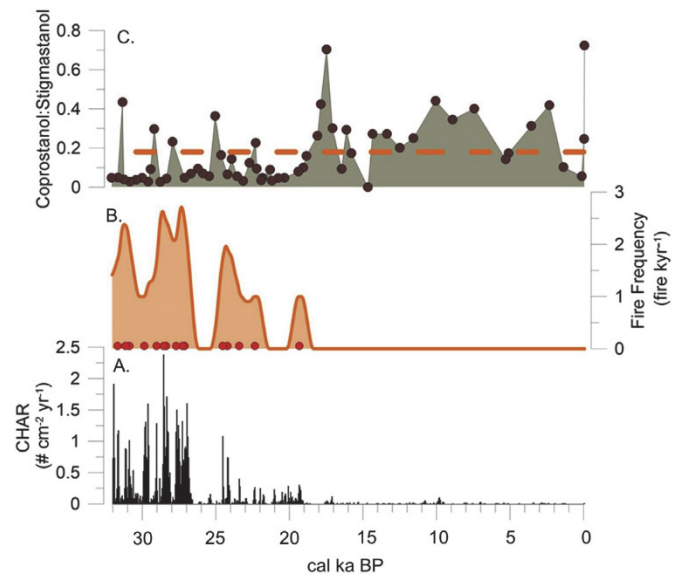


Fig. 5. Paleolimnological data from Lake E5. CHAR (A; black) used to calculate fire events (90th percentile, red points) and fire frequency (B; orange). Coprostanol:stigmasterol ratios (C; brown points) with the coprostanol:stigmasterol ratio of mammoth feces (dotted orange line; van Geel et al., 2011). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

human feces is at least an order of magnitude more concentrated than in those of herbivores (D'Anjou et al., 2012). The coprostanol:stigmasterol ratio has been previously used to distinguish human and ruminant herbivore fecal inputs to lake sediments in Norway (D'Anjou et al., 2012). We observe elevated ratios of coprostanol:stigmasterol at several periods within the last Glacial, as well as consistently after 19 ka. Mammoth dung dating to the LGM has a coprostanol:stigmasterol ratio of 0.18 (van Geel et al., 2008). Animal biomass of northern Alaska during the Glacial was 49%

mammoth, 23% horse, and 22% bison (Mann et al., 2013). No comparable Glacial coprolite sterol compositions have been published for horses or bison, so we utilize the mammoth value of 0.18 to distinguish human from non-human fecal input. This is a conservative estimate because modern horse feces have a coprostanol:stigmastanol ratio of 0.11, as do Heck cattle, a close ruminant herbivore analog to bison, which do not have published sterol data (Prost et al., 2017). Human feces has a coprostanol:stigmastanol ratio of 2.22–5.5 (Bull et al., 2002; Prost et al., 2017), at least an order of magnitude higher than that of woolly mammoth, so this ratio is particularly sensitive to human fecal input.

Importantly, the biomarkers we measured reflect a composite mixture of all fecal inputs to the lake sediment. Though our coprostanol:stigmastanol ratios are all <1, we do not expect values equivalent to the sterol composition of human feces as this would insinuate the only fecal input to the lake was derived from humans. Since 94% of animal biomass (mammoth, horse, and bison) in the paleontological record of pre-Holocene Arctic Alaska would provide fecal inputs with coprostanol:stigmastanol ratios <0.18 (see above), deviations of sedimentary assemblages above this ratio likely indicate a human fecal contribution. Omnivores could feasibly contribute coprostanol to the sterol assemblages (Leeming et al., 1996), but their biomass would have been negligible relative to the megafauna of the mammoth steppe (Mann et al., 2013), so they would not likely have altered the coprostanol:stigmastanol ratios. Thus, we can conclude that values exceeding the 0.18 value of mammoth dung most likely reflect human fecal input (Fig. 5).

Sediment coprostanol:stigmastanol values greatly exceed herbivore compositions at several points coincident with increased stanol fluxes (e.g. 29 and 26 cal ka BP), suggesting human presence as early as 31 cal ka BP. These data indicate human fecal deposition in Lake E5 throughout the Glacial, contemporaneous with evidence of increased burning. Diagenesis of sterols has been shown to decrease sterol preservation and concentrations but not to affect the relative distributions of sterols in older sediments (Gaskell and Eglinton, 1976; Meyers et al., 1995). Further, in this study we consider only stanols, sterols containing no double bonds, which are more resistant to diagenesis than sterols containing double bonds. The limited role of diagenesis therefore reinforces the reliability of the coprostanol:stigmastanol values and renders the high sterol fluxes in the Glacial even more impressive (Fig. 4). Notably, coprostanol:stigmastanol values consistently exceed the 0.18 threshold after ca. 18 cal ka BP. We suggest that this shift in the record represents more permanent settlement and/or declines in the herbivore population relative to humans.

We analyzed two modern (ca. 2010 and 1980 CE) sediment samples from E5 and found that coprostanol:stigmastanol values are comparable to those of the fecal input observed in the Holocene and occasional Glacial samples, despite lower modern fluxes of coprostanol and stigmastanol relative to the Glacial (Fig. 4). While there is not modern human settlement in the watershed of the lake, there is frequent visitation to the lake by scientists from the nearby Toolik Field Station and seasonal caribou hunters. The greater herbivore biomass of the mammoth steppe would have driven the coprostanol:stigmastanol values down, requiring a larger overall human presence during the Glacial to produce comparable coprostanol:stigmastanol ratios. The comparable coprostanol:stigmastanol values between the modern and Glacial samples thus suggest that human presence relative to other herbivores in the Ice Age was on par with that of the modern but that overall human presence in the Glacial was more pronounced than at modern. This offers insight into the taphonomy of fecal sterols; humans need not settle within the watershed of a lake to be recorded in its sediments, they only need to visit and defecate regularly.

5.2. Fire in eastern Beringia during the last Glacial

Multiple lines of proxy data suggest elevated biomass burning during the last Glacial. Fire frequency inferred from CHARs was greatest from 32 to 19 cal ka BP, similar to the elevated biomass burning inferred from PAHs between 32 and 19 cal ka BP (Fig. 4), together indicating that fire was more frequent during the Glacial period. Importantly, fire events interpreted from CHAR likely reflect relatively local (within a few kilometers of the watershed) fires (Hu et al., 2010; Peters and Higuera, 2007; Whitlock and Larsen, 2002). PAHs can reflect changes in local fire occurrence (Denis et al., 2012), but can also be airborne for long distances (Halsall et al., 2001) and thus the high concentrations preserved in the E5 record likely represent both local and regional inputs (Miller et al., 2017). Previous work farther west in Arctic Alaska also identified greater CHAR in Glacial sediments (Eisner and Colinvaux, 1990), indicating that fire was much more frequent across much of the Alaskan Arctic during the cooler Glacial period relative to the deglaciation and Holocene. This result is surprising because we would expect burning to decrease with cooler temperatures (Hu et al., 2015, 2010; Young et al., 2017). This Glacial burning was originally interpreted as an indicator of aridity (Eisner and Colinvaux, 1990). However, at the time of that publication it was assumed that humans could not survive Glacial climate conditions of the Arctic, in contrast to current genetic evidence and the Beringian Standstill Hypothesis (Moreno-Mayar et al., 2018; Mulligan and Szathmáry, 2017; Tamm et al., 2007). Thus, human populations were not considered as a potential ignition source to trigger Arctic fires.

Two variables may account for increased burning in eastern Beringia during the Glacial: increased fuel quality and/or more frequent ignitions. We consider fuel quality to be comprised of fuel loading and moisture content, which are determined by vegetation and climate. Pollen data from our site indicate that Glacial vegetation was characterized by a diverse mix of grass and upland herb species known as the “mammoth steppe,” with decreased percentages of shrubs relative to the modern and Holocene shrub tundra (Fig. 4; Eisner and Colinvaux, 1992; Zimov et al., 2012). Paleoenvironmental evidence suggests that the mammoth steppe was relatively lush and supported herbivore-dominated faunal communities (Fox-Dobbs et al., 2008; Guthrie, 2001; Mann et al., 2015, 2013; Zimov et al., 2012, 1995). Published pollen records indicate that vegetation in Beringia was spatially heterogeneous with a mosaic of communities but climates were generally colder and drier (Matthews, 1982). Although these grasslands would provide a finer, potentially more flammable fuel load, their spatial discontinuity might also reduce landscape-scale burning (Higuera et al., 2009). Further, no clear relationship exists between periods of increased herbaceous taxa (fuel quality) and fire activity during the Glacial period in our record (Fig. 4). This lack of a relationship suggests that fire activity was not modulated by vegetation changes during the Glacial. However, there is a clear relationship between fire activity and vegetation on multi-millennial timescales (i.e. between the Glacial, deglaciation, and Holocene). This contrast suggests that the mammoth steppe may have been particularly susceptible to burning relative to other vegetation assemblages that have existed in Beringia.

Lightning strikes are the principal source of non-anthropogenic fire ignitions, but are quite rare in our study region today (Veraverbeke et al., 2017; Wein, 1976). The probability of a lightning-based wildfire depends on the frequency of lightning occurrence and the likelihood of ignition with each strike. Tundra fires can be relatively frequent in lower latitude ecoregions of Alaska, but the North Slope Foothills and Coastal Plain hosted only 11% ($n = 107$) of the total number of observed (74 years) Alaskan tundra fires (French et al., 2015). Further, existing records

document charcoal-based mean fire return intervals for the North Slope Foothills during the Holocene of 4730 and 6045 years for Perch and Upper Capsule lakes, respectively (Chipman et al., 2015). The rarity of fires north of the Brooks Range is a function of ignition limitation (Pfeiffer et al., 2013; Reap, 1991), as lighting frequencies are among the lowest observed on Earth (Christian et al., 2003). For example, within 10 km of Lake E5, only 211 lightning flashes were recorded from CE 1986–2012 and none produced observed fire ignitions (data available for download from the Alaska Interagency Coordination Center at <http://fire.ak.blm.gov/predsvcs/maps.php>). Only 20 and 85% of negative and positive lightning flashes, respectively, have long-continuing currents capable of igniting fires (Latham and Williams, 2001). Further, modern grasslands in the western United States, reasonable analog for the Beringian steppe, exhibit the lowest lightning ignition efficiency (<0.005 fires/flash) of fuel types (Latham and Williams, 2001). For peat moss, which has been suggested as an appropriate fuel analog for grasses, the ignition probabilities are $0.839e^{-0.058*mc}$ and $0.715e^{-0.072*mc}$ for negative and positive flashes, respectively, where mc is moisture content (Latham and Schlieter, 1989). A fuel moisture content decrease from 30 to 10% would result in an ignition probability increase from 0.082 to 0.348 and 0.147 to 0.470 for positive and negative flashes, respectively. The arid conditions of the last Glacial may have increased the likelihood of ignition, but this was balanced by decreased lightning frequency. Thus, ignition probability may have increased with finer, drier fuels, however, cooler Glacial climates may have had limited lightning frequency requisite to light natural fires.

There is no direct proxy for lightning frequency in the past; however, the convective cloud fraction (CCF) simulated by global climate models is directly related to the convective potential energy available for thunderstorm initiation and natural ignition frequency (Liu et al., 2009). Colder temperatures should in theory decrease lightning frequency, and indeed simulated CCF values were lowest during the last Glacial, suggesting that the probability of lightning strikes was lower (Fig. 3). This stands in contrast to evidence for frequent fires during the last Glacial in our sediment core. We therefore conclude that natural ignition frequency did not increase during the Glacial, and therefore cannot account for the increased burning we observe.

Other factors also influence fuel loading and moisture content. Grazing in shrub steppe can increase herbaceous fuel moisture by as much as 2.2 times, and significantly decrease herbaceous cover and continuity (Davies et al., 2017). The net effect of grazing in lower latitude shrub- and grass-dominated rangelands is to promote fuel moisture and limit fire spread (Davies et al., 2016, 2015; Diamond et al., 2010). The Beringian mammoth steppe supported a diverse array of herbivores (Mann et al., 2015, 2013; Yurtsev, 2001), so grazing may have been a key control of vegetation continuity and fuel moisture content (Zhu et al., 2018). Indeed, fluxes of stigmastanol, a herbivore biomarker (Fig. 4), are highest in the Glacial so it is possible that increased ungulate herbivory may have decreased fuel loading and increased fuel moisture content.

Climate certainly influenced Glacial fire regimes and aridity may have promoted fuel quality (increased loading and decreased moisture content), but there is little data to indicate that aridity could be the sole driver of fire regimes in this region. Rather, temperature and temperature-driven moisture balance changes are the primary climatic drivers of modern tundra fire regimes (Hu et al., 2010; Jones et al., 2009; Young et al., 2017). FAMOUS climate model output for northern Alaska suggests that temperature, precipitation, and evaporation were lower during the Glacial, relative to mean pre-Industrial values (AD 850–1850), suggesting climatic conditions would have inhibited tundra fires (Fig. 6). Thus, colder Glacial temperatures in Beringia, in combination with

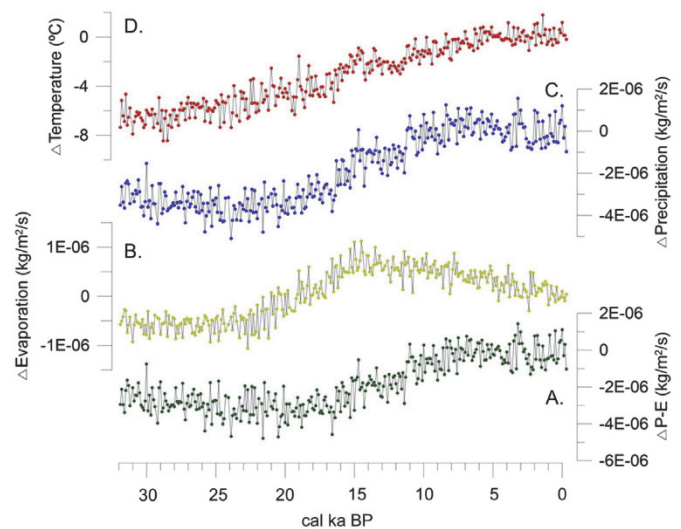


Fig. 6. FAMOUS modelled precipitation minus evaporation (A; green) anomalies, calculated from evaporation (B; yellow) and precipitation (C; blue) anomalies. FAMOUS modelled temperatures are also plotted (D; red). Anomalies are calculated relative to mean pre-Industrial values (AD 850–1850). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

decreased lightning frequency (as inferred from CCF) should have lowered fire frequency.

We cannot conclusively disprove the Glacial fires were natural. However, there is little evidence to support such elevated activity, especially if we consider that ignition frequency (lightning), which today severely limits fires, was almost certainly suppressed by Glacial cooling. Thus, we conclude that human ignitions provide the best explanation for increased fire activity in northeastern Beringia during the last Glacial. Increased burning is commonly observed during periods of human immigration and occupancy in other ignition-limited or previously unpeopled ecosystems (Argiriadis et al., 2018; Mann et al., 2008). Further, the greatest fluxes of coprostanol, a human fecal biomarker, are contemporaneous with the increased burning. The Lake E5 watershed may have been particularly suitable for temporary or sustained human occupancy because of its relatively isolated location (Fig. 1; inset), and the reality that in such an arid environment (Abbott et al., 2010; Gaglioti et al., 2018), Lake E5 was likely one of the few lakes and sources of freshwater in the region.

We speculate that humans may have burned landscapes as part of hunting practices. Megafauna of the mammoth steppe subsisted upon grasses, sedges, and herbaceous plants (Fox-Dobbs et al., 2008), so human-induced burning could have facilitated fresh food growth attracting animals to isolated areas for hunting. Similarly, fires could have been used to drive animals (Roos et al., 2018). Though the sparse archaeological records cannot support these speculations, similar anthropogenic burning of landscapes has been demonstrated in LGM Europe (Kaplan et al., 2016). Notably, the decrease in fire activity evident after 20 cal ka BP coincides with decreased fluxes of coprostanol and stigmastanol but increased coprostanol:stigmastanol values, which could indicate that shrinking megafauna populations were accompanied by smaller human populations with lesser impacts on the landscape.

5.3. Archaeological and ecological implications

Our data provide new constraints for the timing of human arrival to eastern Beringia. Archaeological evidence places east Asian ancestor populations in western Beringia between 48 and

30 cal ka BP (Pitulko et al., 2016, 2004). The Bluefish Caves demonstrate human presence in eastern Beringia (Bourgeon et al., 2017), but do not archive sustained human occupation similar to the Yana RHS site in western Beringia. Our data document human presence for thousands of years during the last Glacial. Although our data cannot distinguish permanent human occupation of eastern Beringia, in lieu of archaeological artifacts our data potentially represent the only means of inferring human presence in eastern Beringia during the Glacial. Importantly, our data confirm that founder populations were present in the American Arctic well before human expansion across the Americas, consistent with the Beringian Standstill Hypothesis (Tamm et al., 2007). Moreover, our data indicate humans were present in eastern Beringia well before the timing of their genetic isolation from their Asian ancestors. This could reflect uncertainty in molecular clock estimates, or continued exchange between eastern and western Beringian populations after initial colonization of the Americas, until a final isolation event occurred at ~23 cal ka BP (Moreno-Mayar et al., 2018; Raghavan et al., 2015).

These biomarker and paleoecological data offer novel insight and perspective into the community ecology of the mammoth steppe and megafauna extinctions in Arctic Alaska. In particular, the relative roles of humans, hunting, and climate change in latest Pleistocene megafauna extinction remain debated (Gill et al., 2009). Further, data constraining archaeological landscape burning is rare (Scherjon et al., 2015). Our data suggest prolonged co-occurrence of megafauna and humans in Beringia since at least 32 cal ka BP, yet the paleontological record shows that megafaunal extinctions in the northern foothills of the Brooks Range did not begin until ca. 13 cal ka BP (Mann et al., 2015). Thus, sustainable subsistence hunting of megafauna by humans was possible and indeed occurred in Beringia for nearly 20,000 years during the Pleistocene. Climatic and subsequent environmental shifts (Finkenbinder et al., 2015) contemporaneous with the end-Pleistocene extinctions suggest that in eastern Arctic Beringia, climate change likely played a dominant role in the megafauna extinctions (Mann et al., 2015, 2013), though it is difficult to discount the role of humans and their long-term occupancy.

6. Conclusions

These data provide a new perspective regarding the timing of human arrival in eastern Beringia. Archaeological finds place east Asian ancestor populations in western Beringia between 48 and 30 cal ka BP (Pitulko et al., 2016, 2004). These data indicate that humans occupied eastern Beringia at the same time they inhabited Siberia, and that they affected Arctic landscapes during the height of the last Ice Age. Our novel, multiproxy evidence demonstrates human presence in eastern Beringian by 32 cal ka BP, nearly contemporaneous with western Beringian populations. These findings confirm that founder populations were present in the American Arctic well before human expansion across the Americas, and indicate that eastern Beringia was occupied both prior to and during the period of genetic isolation from their Asian ancestors beginning ca. 23 cal ka BP. This finding fundamentally alters our understanding of the timing, extent, and duration of the migration of humans into the Americas and offers insights into the modes of life and environmental impact of these early Americans. Further research is needed to fully disentangle the relative influences of climate, vegetation, and human activities in driving the Glacial burning evident in the Lake E5 sediment record.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.quascirev.2018.12.003>.

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