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Sedimentary biomarkers reaffirm human impacts on northern Beringian ecosystems during the Last Glacial period

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Our understanding of the timing of human arrival to the Americas remains fragmented, despite decades of active research and debate. Genetic research has recently led to the 'Beringian standstill hypothesis' (BSH), which suggests an isolated group of humans lived somewhere in Beringia for millennia during the Last Glacial, before a subgroup migrated southward into the American continents about 14 ka. Recently published organic geochemical data suggest human presence around Lake E5 on the Alaskan North Slope during the Last Glacial; however, these biomarker proxies, namely faecal sterols and polycyclic aromatic hydrocarbons (PAHs), are relatively novel and require replication to bolster their support of the BSH. We present new analyses of these biomarkers in the sediment archive of Burial Lake (latitude 68°26′N, longitude 159°10′W m a.s.l.) in northwestern Alaska. Our analyses corroborate that humans were present in Beringia during the Last Glacial and that they likely promoted fire activity. Our data also suggest that humans coexisted with Ice Age megafauna for millennia prior to their eventual extinction at the end of the Last Glacial. Lastly, we identify fire as an overlooked ecological component of the mammoth steppe ecosystem.

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Human arrival to the American continents remains one of the most debated topics in our understanding the global dispersal and proliferation of *Homo sapiens* (Goebel *et al.* 2008; Waters 2019). Most researchers agree that Beringia, the landmass that spanned northeastern Asia and northwest North America during the Last Glacial period (herein referring to Marine Isotope Stages 2 and 3), was the initial entryway of this migration to the Americas (West 1996; Hoffecker *et al.* 2014, 2016), but genetic data and archaeological artifacts provide a fragmented history of human populations in the region. Despite assumptions that human populations could not survive the cold climate of the Glacial Arctic, cut-marked bones found at the Bunge Toll site (Pitulko *et al.* 2016), and stone tools found at the Yana site complex (Pitulko *et al.* 2017), in Siberia place humans in western Beringia *c.* 48 thousand calibrated years before present (cal. ka BP) and 32 cal. ka BP (Pitulko *et al.* 2016), respectively. In contrast, the earliest unequivocal archaeological evidence in eastern Beringia dates to 14 cal. ka BP (Swan Point; Potter *et al.* 2013), roughly contemporaneous with the earliest finds in the American continents. This coincidence of timing supports the hypothesis of a 'swift peopling' of eastern Beringia and the American continents *c.* 14 000 years ago (Goebel *et al.* 2008). However, cut-marks on animal bones found in the Bluefish Caves equivocally support human presence in eastern Beringia during the Last Glacial (Morlan & Cinq-Mars 1982; Cinq-Mars 1990; Cinq-Mars & Morlan 1999; Morlan 2003), but have been controversial for decades. More recently, stone artifacts in the Bluefish Caves that had remained overlooked for decades were reexamined and found to indicate human presence during the Last Glacial (Bourgeon *et al.* 2017; Waters 2019). These findings, combined with genetic data, stimulated the proposal of the 'Beringian standstill' hypothesis (BSH), which suggests a small group diverged from East Asians *c.* 36 000 years ago, moving to isolation in Beringia before eventually moving south into the continent (Tamm *et al.* 2007; Skoglund & Reich 2016; Mulligan & Szathmáry 2017; Moreno-Mayar *et al.* 2018; Waters 2019). Importantly, the BSH is built upon earlier genetic analyses that detected differences between Native Americans north and south of the Laurentide Ice Sheet (Szathmary 1993; Bonatto & Salzano 1997) and anthropological inferences from linguistic analyses (Nichols 1990, 2008). It has also been bolstered by dental analyses (Scott *et al.* 2018) and further genetic analyses of ancient DNA and whole genomes (Moreno-Mayar *et al.* 2018; Sikora *et al.* 2019). Though the inferences drawn from linguistic and dental analyses support early divergence of the Native American founder group from its Asian ancestors, these analyses do not place humans in Beringia during the Last Glacial. At present, the Bluefish Caves provide the only archaeological site supporting a human population in eastern Beringia during the Last Glacial, although lack of more estab-

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lished forms of archaeological evidence, such as stone tools and fire pits, still cast uncertainties on the attribution of cut-marks on bones to humans.

The BSH also has important implications for our understanding of Beringian ecosystem dynamics in the Last Glacial and the role of humans in the extinction of Pleistocene megafauna. During the Last Glacial, Beringia was home to the mammoth steppe ecosystem, a productive, diverse grassland that supported and was in turn enhanced by megafauna herbivores including mammoths, bison, horses, caribou, woolly rhinoceros, saiga and muskoxen (Guthrie 2001; Mann *et al.* 2013). The ecosystem dynamics and demise of the Beringian mammoth steppe and its megafauna are debated (Guthrie 2001; Yurtsev 2001; Zimov *et al.* 2012; Mann *et al.* 2013, 2015; Sandom *et al.* 2014). To date, little research has characterized the role that a Standstill population of humans might have had in the demise of this ecosystem without modern counterparts.

Recent palaeolimnological analyses from Lake E5, located in northern Alaska, provide additional biogeochemical evidence supporting the presence of humans in Beringia during the Last Glacial (Vachula *et al.* 2019). Measurements of charcoal and polycyclic aromatic hydrocarbons (PAHs) in the E5 sediment record indicate increased fire activity from 32 to 19 cal. ka BP, despite natural lightning ignitions being suppressed by a cold glacial climate (Vachula *et al.* 2019). In many ignition-limited regions, evidence of increased burning has been observed to coincide with human arrival (Mann *et al.* 2008; Pinter *et al.* 2011; Argiriadis *et al.* 2018). Similarly, the arrival of humans to Australia was accompanied by increased fire activity (Rule *et al.* 2019). This circumstantial evidence for human presence is further supported by faecal sterol data suggesting human faecal contamination at E5. Thus, the Lake E5 record provides evidence of a sustained human presence in eastern Beringia during the Last Glacial (Vachula *et al.* 2019). The Lake E5 analyses support the BSH but require replication to ensure their validity and to reinforce the determination of human presence prior to the preservation of archaeological artifacts. These biomarkers (PAHs, faecal sterols) are relatively novel, so their reliability must be scrutinized before a consensus can be reached regarding the BSH.

Here, we present new analyses of biomarkers preserved in a lake sediment core from the Brooks Range in northwestern Alaska. We seek to replicate the analyses undertaken on the Lake E5 sediments and determine whether palaeolimnological data can reliably identify human presence in the absence of archaeological artifacts. Though fire was a hallmark of human presence, its ecological role in the glacial ecosystems of Beringia has not been explored (Bliss & Richards 1982; Guthrie 1982, 2001). We therefore also assess the role of humans and fire in the mammoth steppe biome that spanned Beringia during the Last Glacial.

Study site

Burial Lake (68°26′N, 159°10′W; 460 m a.s.l.; Fig. 1) is located in the Noatak River Basin in the Brooks Range in northwestern Alaska (Kurek *et al.* 2009; Abbott *et al.* 2010; Dorfman *et al.* 2015; Finkenbinder *et al.* 2015). The lake is deep (21.5 m) and small (0.8 km^2), with a relatively small watershed (3.3 km^2), one outlet stream, and several seasonally ephemeral inlets (Finkenbinder *et al.* 2015). Like Lake E5 in north-central Alaska (Vachula *et al.* 2019), Burial Lake is one of a small number of lakes that persisted during the cold and arid Last Glacial period (Finkenbinder *et al.* 2015). As such, sediments from E5 and Burial are valuable environmental archives.

Material and methods

Sediment core and chronology

Sediment cores were collected from several water depths in Burial Lake (5.0, 7.9, 13.2 and 21.5 m), but sedimentary hiatuses associated with the drier glacial period interrupt all of these archives with the exception of the core from the deepest water (Abbott *et al.* 2010; Finkenbinder *et al.* 2015). The sediments preserved in this core span the last 37 000 years. The age-depth chronology of this core was established by Finkenbinder *et al.* (2015, 2018) using the CLAM age modelling package (Blaauw 2010). The chronology is informed by 15 radiocarbon-dated terrestrial macrofossils (Fig. 2). In this paper, we refer to sedimentological ages as thousands of calibrated years before present (1950 CE = 0 cal. ka BP).

Organic geochemical analyses

Following Vachula *et al.* (2019), we quantified polycyclic aromatic hydrocarbons (PAHs) and faecal sterols in the Burial Lake sediment record. Briefly, an accelerated solvent extraction system (ASE) was used to extract lipid biomarkers from sediments with dichloromethane (DCM):methanol (MeOH) (9:1 by volume). The total lipid extracts were chromatographically separated into acid (4% acetic acid in ether) and neutral (DCM: isopropanol; 2:1 by volume) fractions with aminopropyl gel columns. The neutral fraction was further divided into hexane, DCM (containing PAHs) and MeOH fractions with silica gel columns. The MeOH fractions (containing sterols) were further purified with alumina columns using hexane:dichloromethane (1:1) and dichloromethane: methanol (1:1) as eluents. Sterol fractions were derivatized with N,O-bis(trimethylsilyl)trifluoroacetamide (BSTFA) for 2 h at 80 °C before quantification. Analytes were identified and quantified with an Agilent 6890N gas chromatograph (Agilent VF-200 ms 60 m capillary col-

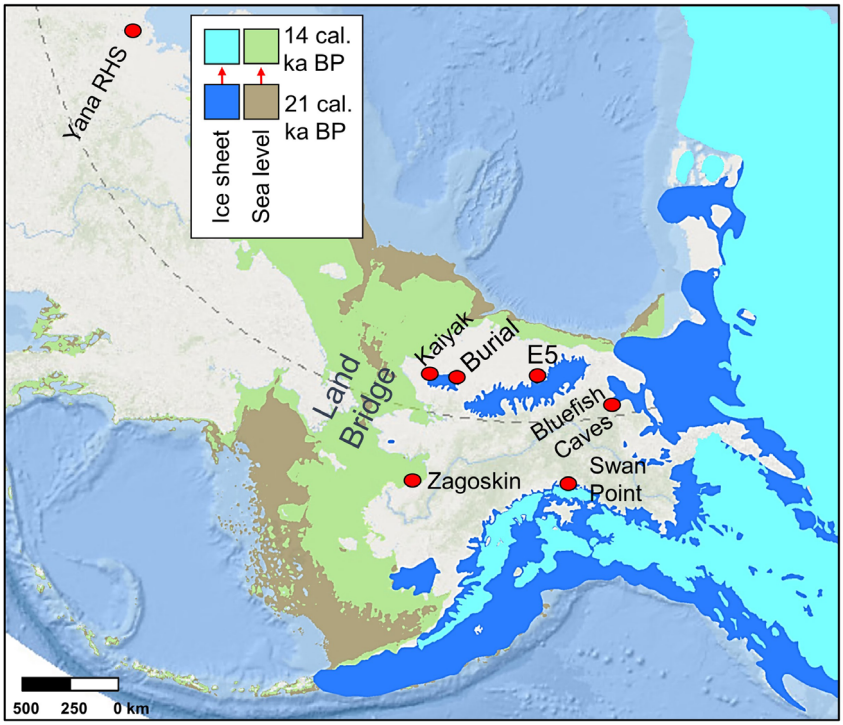


Fig. 1. Map of Beringia showing exposed areas of the Bering Land Bridge at 21 cal. ka BP (brown) and 14 cal. ka BP (green), and Laurentide Ice Sheet (dark blue, 21 cal. ka BP; light blue, 14 cal. ka BP; Manley 2002; Dyke *et al.* 2003). Red points show our study site, Burial Lake, as well as the locations of archaeological finds and other palaeoecological records referred to in the text.

umn (0.1×250 μm)) paired with a 5973N mass spectrometer (GC-MS). The oven temperature initialized at 40 °C, increasing by 7 °C per min to a maximum of 320 °C. PAH and faecal sterol fluxes were calculated by normalizing measured sedimentary concentrations (ng per g of dry sediment) of biomarkers by dry bulk density (g cm^{-3}) and accumulation rate (cm a^{-1}). Samples were taken from 3-cm-thick sediment intervals, except in cases where sediments were not available (mean sample thickness = 2.6 cm). The dry masses of these samples ranged from 1.0 to 4.9 g (mean = 2.5 g). Following Vachula *et al.* (2019), we measured stigmastanol, a herbivore biomarker, and coprostanol, a human faecal biomarker. We used coprostanol:stigmastanol ratios to identify human faecal contamination in the Burial Lake sediments (D'Anjou *et al.* 2012; Vachula *et al.* 2019). We interpret coprostanol:stigmastanol values exceeding 0.18 to indicate human faecal contamination in the mammoth steppe, as this value represents the likely maximum background coprostanol:stigmastanol input to the lake, based on estimated megafauna abundances and faecal sterol assemblages (Bull *et al.* 2002; van Geel *et al.* 2008; D'Anjou *et al.* 2012; Prost *et al.* 2017; Vachula *et al.* 2019).

Published palaeoecological data

We compare our organic geochemical analyses with previously published palaeoecological and palaeoclimate data from Burial Lake and the region. Sedimentary pollen data from nearby lakes, including Feniak (Eisner & Colinvaux 1992) and Niliq (Anderson 1988), as well as from Burial itself (Abbott *et al.* 2010) have been published but have important caveats (discontinuities, uncertainties). Thus, we compare our record with the pollen data from nearby Kaiyak Lake (Fig. 1; Anderson 1985) as it is the only pollen record that fully chronologically overlaps with our analyses. Informed by the originally published radiocarbon data (six bulk sediment samples) of Anderson (1985), we remodelled the age-depth chronology of the Kaiyak Lake core using the CLAM age modelling package (Blaauw 2010). Although the reservoir effect makes bulk sediment a less ideal material than terrestrial macrofossils for reliable dating of Arctic sedimentary records (Oswald *et al.* 2005), Kaiyak Lake generally offers an accurate depiction of vegetation during the Burial hiatus. We discuss these data and their relationships with characterizations of mammoth steppe vegetation using ancient DNA and nematode assemblages (Willerslev 2014). We also compare our data with published chironomid-based palaeotemperature records from Burial and Zagoskin Lakes (Fig. 1; Kurek *et al.* 2009). The chironomid-based palaeotemperature record from Burial Lake was updated to the age-depth model presented in Finkenbinder *et al.* (2018), which is used in this study.

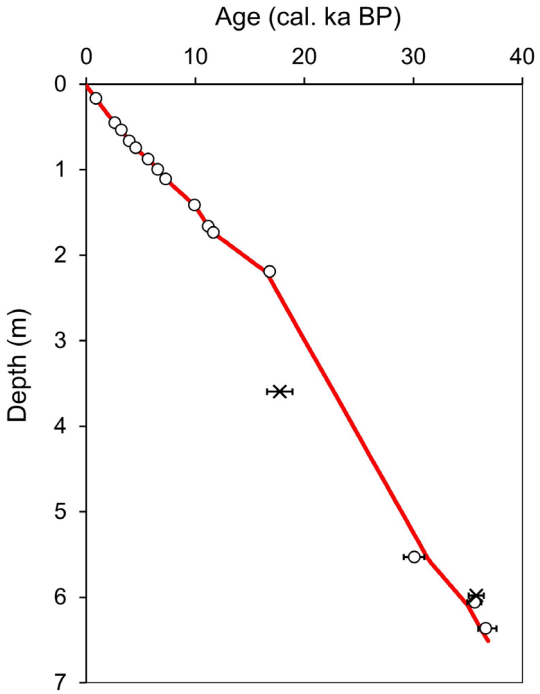


Fig. 2. The age-depth model of the Burial Lake sediment core, with white circles showing accepted radiocarbon dates and crosses depicting rejected dates (Finkenbinder *et al.* 2015, 2018).

Results

Fluxes of PAHs and coprostanol in the Burial Lake sediment core document increased burning and more pronounced human presence during the Last Glacial compared to the deglaciation and Holocene (Fig. 3). The fluxes of PAHs were greatest from 34 to 16 cal. ka BP (0.0–2.6, mean = 1.2 ng cm^{-2} a^{-1}) and lowest from 16 to 0 cal. ka BP (0.1–1.4, mean = 0.6 ng cm^{-2} a^{-1}), as were those of coprostanol (34 to 16 cal. ka BP: 0.0–0.5, mean = 0.1 ng cm^{-2} a^{-1}; 16 to 0 cal. ka BP: 0–0.2, mean = 0.1 ng cm^{-2} a^{-1}). In contrast, fluxes of a herbivore biomarker, stigmastanol, were relatively stable throughout the last 34 000 years, although there are notably low values during the Last Glacial Maximum (*c.* 24 to 20 cal. ka BP; Fig. 3). The ratio of coprostanol:stigmastanol, an indicator of human faecal presence in the Beringian mammoth steppe (Vachula *et al.* 2019), was consistently greater than the background input ratio (0.18) from 34 to 12 cal. ka BP (Fig. 4).

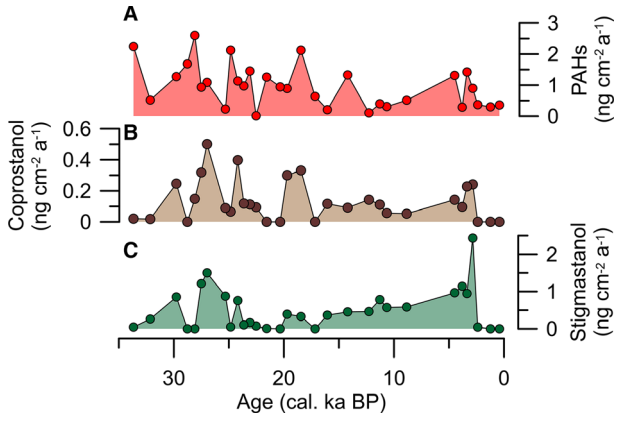


Fig. 3. Fluxes of PAHs (A) and coprostanol (B) from Burial Lake. These proxies indicate there was elevated biomass burning and more pronounced human presence during the Last Glacial. Fluxes of herbivore fecal sterols, stigmastanol (C), suggest herbivore populations were relatively stable during the last 34 000 years.

Discussion

Evidence supporting human presence in eastern Beringia during the Last Glacial

Organic geochemical analyses of Burial Lake sediments demonstrate the presence of humans in eastern Beringia during the Last Glacial, supporting the Beringian standstill hypothesis (BSH) and previous palaeoecological records from Lake E5. Increased fluxes of PAHs from 34 to 16 cal. ka BP indicate increased fire activity in eastern Beringian landscapes during the Last Glacial (Fig. 3). Although climate was more arid during the Last Glacial, as evidenced by Burial Lake PAH levels (Fig. 5; Abbott *et al.* 2010), natural lightning ignitions were likely less frequent in eastern Beringia during the Last Glacial due to decreased convective energy available in the atmosphere (Vachula *et al.* 2019). Decreased natural ignitions during the Last Glacial are difficult to reconcile with evidence of increased burning. Though increased aridity and more readily flammable vegetation assemblages (i.e. mammoth steppe) might have promoted burning, human ignitions offer an alternative explanation for the magnitude of elevated fire activity. Indeed, during the same period of elevated fire activity (34 to 16 cal. ka BP), the fluxes of coprostanol, a human faecal biomarker, are greatest, and coprostanol:stigmastanol values consistently exceed the 0.18 threshold value indicative of human faecal contamination (Vachula *et al.* 2019). Taken together, these data suggest that humans played an integral role in fire regimes near Burial Lake. The timing of this inferred human presence agrees with genetically-inferred timing of the initial divergence of Ancient Beringians from East Asians (Tamm *et al.* 2007; Skoglund & Reich 2016; Mulligan & Szathmáry 2017; Moreno-Mayar *et al.* 2018; Waters 2019). As such, our data and those of Vachula *et al.* (2019) provide physical evidence supporting the BSH. To conclusively support the BSH, further research is needed to confirm that the humans evident in the Burial Lake sediment record are indeed the ancestors of Native Americans.

Our interpretation of faecal sterol ratios as indicative of human presence in eastern Beringia is grounded by current understanding of the typical sterol assemblages in the faeces of different animals and the abundance of

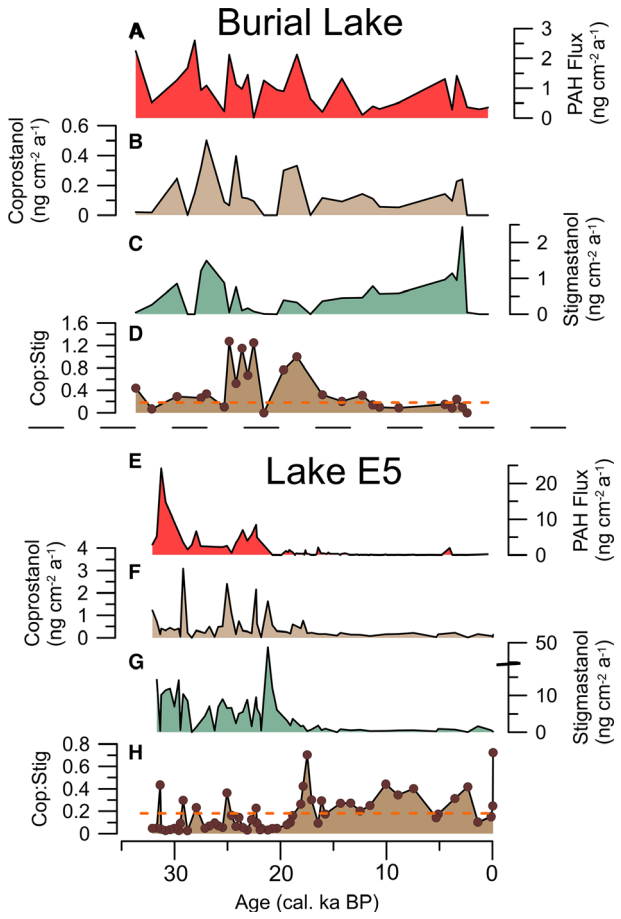


Fig. 4. Comparison of palaeolimnological data from Burial Lake (top) and Lake E5 (bottom). PAH fluxes in both lakes (A and E) indicate elevated biomass burning during the Last Glacial period, coincident with increased fluxes of the human fecal biomarker, coprostanol (B and F). Stigmastanol fluxes in the Burial Lake record (C) are consistent throughout the last 34 000 years, relative to those in Lake E5 (G). Coprostanol:stigmastanol ratios (D and H) consistently exceed the 0.18 threshold value (orange dashed line) in both lakes during the Glacial period, indicating prolonged human fecal contamination. Overall, the consistency of these results from two disparate lakes in northern Beringia suggests humans were present in Beringia during the Last Glacial and promoted biomass burning.

different animals in the mammoth steppe ecosystem of eastern Beringia. Following Vachula *et al.* (2019), we assume that coprostanol:stigmastanol values exceeding a background input ratio of 0.18 indicate human faecal contamination of the sediment. This threshold value was determined by estimating the likely 'natural' faecal sterol assemblage of sediments that would result from faecal inputs of fauna present in eastern Beringia during the Last Glacial. Namely, 94% of faunal biomass in this region consisted of large herbivores including mammoths (49%), horses (23%) and bison (22%; Mann *et al.* 2013). Whereas human faeces has coprostanol:stigmastanol values of 2.22 to 5.5 (Bull *et al.* 2002; Prost *et al.* 2017), the values expected in the faeces of mammoths, horses and bison are 0.18, 0.11 and 0.11, respectively (van Geel *et al.* 2008; Prost *et al.* 2017; Vachula *et al.* 2019). These values are derived from measurements of coprolites and modern faecal samples and could have varied in the past and with changes in diet or gut physiology. Nonetheless, human faeces have coprostanol:stigmastanol values that are at least an order of magnitude greater than those of the herbivores dominating faunal assemblages of the mammoth steppe, justifying our interpretation of coprostanol:stigmastanol values exceeding 0.18 to indicate human faecal contamination. Other omnivores (e.g. pigs, opossums) could also contribute coprostanol to the sedimentary coprostanol:stigmastanol values (Leeming *et al.* 1996), which would confound the identification of human faecal contamination. However, palaeontological data indicate that omnivore biomass was quite limited in the mammoth steppe (Mann *et al.* 2013). Overall, it is unlikely that sedimentary coprostanol:stigmastanol ratios could have exceeded 0.18 during the Last Glacial without human faecal input.

Although we interpret our faecal sterol data to indicate human presence in eastern Beringia during the Last Glacial, we concede that there are alternative explanations for our interpretation of human impacts on fire. Namely, the elevated fire activity from 34 to 16 cal. ka BP, as inferred from increased fluxes of PAHs (Fig. 3), could result from natural climatic forcing. Climate was significantly more arid during the Last Glacial in eastern Beringia (Finkenbinder *et al.* 2015), suggesting that elevated fire activity could have resulted from climate rather than human activity. Colder glacial temperatures, however, ought to decrease biomass burning (Hu *et al.* 2010; Young *et al.* 2017), thereby bolstering the case for anthropogenic fire activity. Biomass burning proxies cannot distinguish anthropogenic and natural fire activity, complicating the conclusive interpretation of our data. However, our faecal sterol data, in conjunction with the growing body of interdisciplinary research supporting the BSH (Nichols 1990, 2008; Bonatto & Salzano 1997; Tamm *et al.* 2007; Skoglund & Reich 2016; Mulligan & Szathmáry 2017; Moreno-Mayar *et al.* 2018; Sikora *et al.* 2019; Waters 2019), provide compelling support for human presence in eastern Beringia during the Last Glacial, and it is certainly possible that their activity promoted more widespread fire activity. However, this anthropogenic burning may be superimposed upon naturally elevated fire activity. In this way, further research is needed to more thoroughly dissect the fire dynamics of the mammoth steppe in eastern Beringia.

Though key differences exist between Burial Lake and Lake E5, our proxy results from the Burial Lake sediment core generally agree with those from Lake E5 and support human presence in eastern Beringia during the Last Glacial. Vachula *et al.* (2019) found elevated charcoal accumulation rates and PAH fluxes from 32 to

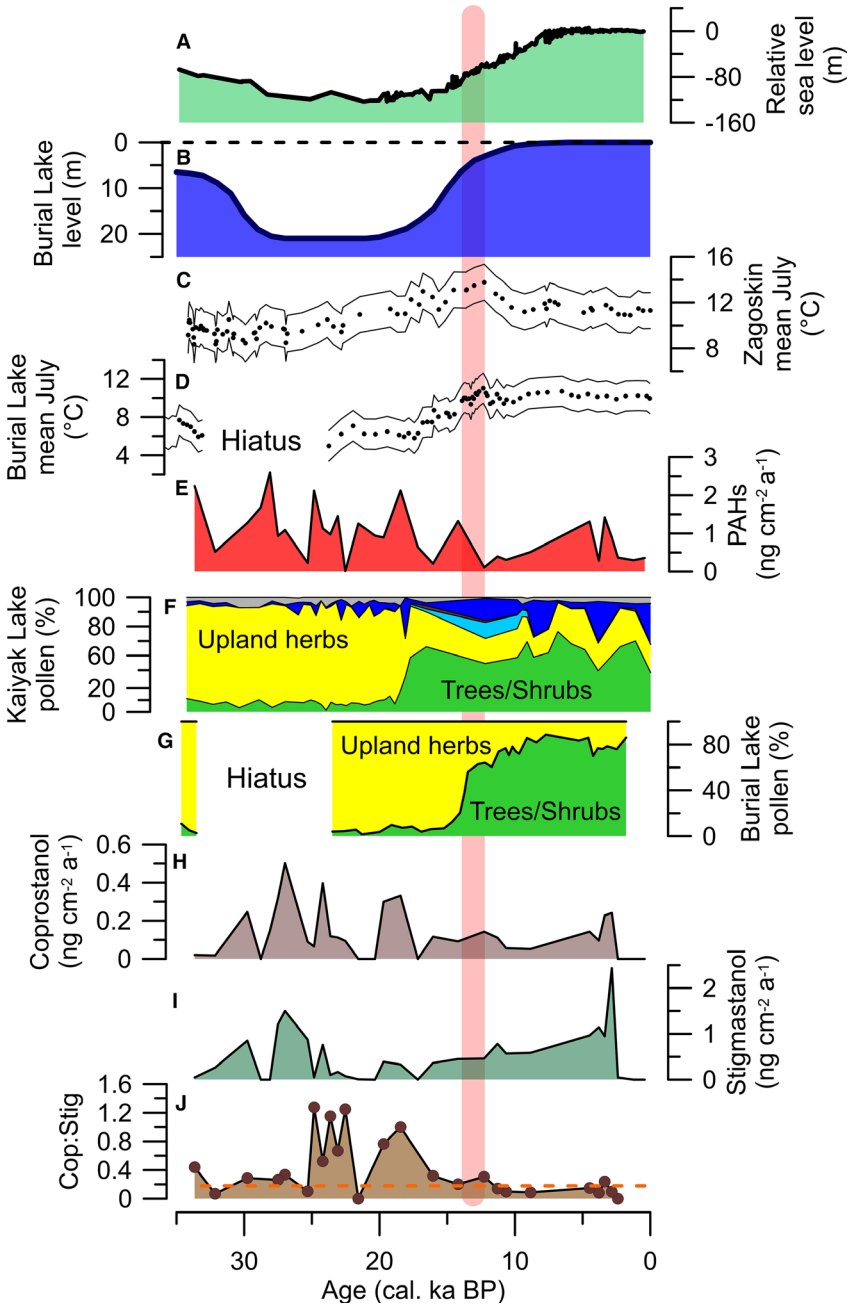


Fig. 5. Comparison of palaeolimnological data from Burial Lake and published palaeoecological and palaeoclimate records. Sea levels (A) rose dramatically during the deglaciation, flooding the Bering Land Bridge (Clark *et al.* 2009). Burial Lake levels (B) fluctuated in response to climate and basin fill (Finkenbinder *et al.* 2015, 2018). Chironomid-based palaeotemperature records from Zagoskin (C) and Burial Lakes (D) indicate lower July temperatures during the Last Glacial. Sample-specific prediction errors are marked as black lines. Elevated fluxes of PAHs in Burial Lake (E) coincide with palynological evidence for the mammoth steppe from Kaiyak Lake (F; green = trees/shrubs; yellow = upland herbs; cyan = aquatic vascular plants; blue = algal species; brown = terrestrial vascular cryptogams; gray = unidentified palynmorphs) and Burial Lake (G). Elevated fluxes of coprostanol (H) indicate human presence near Burial Lake during the Last Glacial period. Fluxes of stigmastanol (I) indicate consistent presence of herbivores near Burial Lake. Coprostanol:stigmastanol ratios (J) consistently exceed the 0.18 threshold value in both lakes during the Last Glacial period, indicating prolonged human fecal contamination. Red vertical bar depicts the timing of Ice Age megafauna in northeastern Beringia.

19 cal. ka BP at Lake E5 (Fig. 4). Our PAH results agree and indicate there was increased burning from 34 to 16 cal. ka BP (Fig. 4), though there is an absence of charcoal in Burial Lake sediments. Although the absence of charcoal might be due to the absence of wood fuels, experimental analyses indicate that non-wood tundra

plants (graminoids and forbs) produce nearly as much charcoal per fuel mass as do shrubs (Pereboom *et al.* 2020). Although the abundance of wood fuel in the mammoth steppe might be disputed (Willerslev 2014), it is unlikely to diminish the reliability of sedimentary charcoal as a palaeofire proxy. Like E5, Burial Lake would have experienced suppressed lightning ignition frequency during the Last Glacial (Vachula *et al.* 2019). The absence of charcoal in the Last Glacial Burial Lake sediments (Finkenbinder *et al.* 2015) coincident with increased fluxes of PAHs could indicate more regional vs. local (i.e. catchment) fire dynamics than in the case of Lake E5. Indeed, PAHs can be transported long distances in the atmosphere (Halsall *et al.* 2001). Moreover, recent work characterizing the source areas of sedimentary charcoal in the Alaskan tundra suggest that charcoal records in this region have a significant extra-local and regional fire history signal (Vachula *et al.* 2020). Previous work indicates that during the Last Glacial, significant inputs of dust to Burial Lake were likely sourced from exposed continental shelves composing the Bering Land Bridge (Dorfman *et al.* 2015), suggesting PAHs could have been sourced from this region as well. Notably, the Bering Land Bridge itself has been proposed as a mesic refugium for early humans in Beringia (Hoffecker *et al.* 2014), so it is possible the PAH signal reflects a population living on the Bering Land Bridge but visiting Burial Lake and its surroundings regularly. Dorfman *et al.* (2015) also identified a dust source change after 15 cal. ka BP indicative of a more local source of sediments, which could be true for PAHs as well. Notably, our PAH and faecal sterol data from Burial Lake suggest greater fire activity and influx of faecal matter (human and herbivore) during the deglaciation and Holocene than do those from Lake E5 (Fig. 4). However, the Noatak Basin may simply have experienced more frequent burning throughout the last 34 000 years than did E5. Historical records indicate the Noatak Basin experiences more fire activity than the central Brooks Range foothills (E5) due to more extreme fire weather conditions (humidity, temperature, precipitation, and wind speeds; French *et al.* 2015). Though it is difficult to determine how these variables might have varied between these two sites over the last 34 000 years, this agreement between modern observations and the palaeofire records suggests the vegetation around Burial may have been more susceptible to burning than that around E5. Similarly, herbivores and humans may have had a more pronounced presence near Burial Lake relative to Lake E5 during the deglaciation and Holocene. Elevated fluxes of stigmastanol and sitosterol in Burial Lake from 15 cal. ka BP to present suggest dense herbivore populations persisted during the Holocene (e.g. caribou) whereas they decreased near E5. Notably, fluxes of stigmastanol were low during the Last Glacial Maximum (Fig. 3) at Burial Lake, coincident with palaeozoological evidence for declines in megaherbivore populations during this interval (Matthews 1982; Sher *et al.* 2005; Mann *et al.* 2015). Thus, despite differences between Burial Lake and Lake E5 data, proxy results from both lakes support human presence in eastern Beringia during the Last Glacial.

Additionally, although the general trends of these faecal biomarkers and fire indicators in the two lakes agree, the total fluxes of PAHs and faecal sterols differ between the two lakes, with Burial Lake having lower fluxes by an order of magnitude (Fig. 4). These discrepancies are difficult to resolve. Burial Lake is approximately eight times larger in area than Lake E5, so differences in the efficiency of sediment transport and focusing could explain the lower fluxes. Similarly, preservation and diagenesis differences between the two lakes may add to the discrepancy (Biache & Philp 2013). Sedimentary organic matter content, and its effects on biomarker preservation, could explain some of this discrepancy. Indeed, percent weight of organic carbon in sediments from Lake E5 (6.2–12.7%; mean = 6.2%) were generally greater than in those from Burial Lake (1.2–7.8%; mean = 3.6%), though not sufficiently so to completely resolve this discrepancy. Though it is difficult to determine the cause of discrepancies of PAH and faecal sterols fluxes between Lake E5 and Burial Lake, it is promising that both records support human faecal input and increased burning during the Last Glacial. Vachula *et al.* (2019) posited that Lake E5 might have been one of the few sources of fresh water for megafauna in arid, glacial Beringia, and so might have attracted megafauna and humans alike. Indeed, such an Arctic glacial oasis might have similarly attracted and concentrated megafauna within the watershed of Burial Lake.

Our approach highlights the utility of palaeolimnological approaches as a means of inferring human presence in the absence of archaeological artifacts. The juxtaposition of the swift peopling and Beringian standstill hypotheses exemplifies disagreement between the fields of genetic anthropology and archaeology. At the core of this disagreement is the paucity of preserved material culture (e.g. stone or bone tools, fire pits) in Beringia during the Last Glacial, despite the finds at the Bluefish Caves (Morlan & Cinq-Mars 1982; Cinq-Mars & Morlan 1999; Morlan 2003; Bourgeon *et al.* 2017). However, the rarity of these artifacts ought to be expected as the deglaciation in Beringia was accompanied by landscape burial by melting (and occasionally temporary expansion) of alpine glaciers and the Laurentide Ice Sheet, as well as subsequent sea level inundation, which only compounds the difficulty of archaeological artifact recovery in remote permafrost regions (Hoffecker & Frederick 1996; Hoffecker *et al.* 2014). In light of these practical realities, we suggest that the geochemical-archaeological approaches undertaken with the E5 and Burial Lake sediments may represent a pragmatic means of reconciling these two hypotheses. Further, these

approaches highlight the utility of palaeolimnological records as complementary perspectives to traditional archaeological and genetic research seeking to understand human migrations of the past. However, more work is needed to properly benchmark and test the accuracy of the geochemical proxies presented in this study, preferably at sites where the archaeological record is better constrained.

Fire's role in the maintenance and productivity paradox of the mammoth steppe

The ecology of the mammoth steppe has puzzled palaeoecologists for decades, in particular the great abundance and diversity of megafauna and vegetation of the mammoth steppe relative to the low productivity expected of high latitude ecosystems in the Last Glacial, a problem termed the 'productivity paradox' (Vereshchagin & Baryshnikov 1982; Zimov *et al.* 1995, 2012; Yurtsev 2001; Bradshaw *et al.* 2003; Willerslev 2014). In the same areas today, tundra ecosystems support less diverse fauna and are less productive despite experiencing warmer and wetter interglacial climatic conditions. Palaeoecologists have offered several explanations for this paradox and the maintenance of the mammoth steppe. Aridity and decreased cloud cover associated with a more continental and cooler climate are thought to have promoted dry, well-drained and productive soils (Vereshchagin & Baryshnikov 1982; Guthrie 2001; Yurtsev 2001). Megafauna are also thought to have helped maintain the mammoth steppe by grazing and trampling shrubs, and to have promoted productivity by increasing nutrient cycling efficiency (Zhu *et al.* 2018). However, analyses of ancient DNA and nematode assemblages suggest that the woody component of mammoth steppe vegetation may be more significant than inferred from pollen records (Willerslev 2014). Clearly, further research is needed to better understand the ecology of the mammoth steppe.

Fire may also have promoted the productivity of the mammoth steppe by enhancing rates of nutrient cycling (most likely nitrogen) and helped to maintain the steppe by reducing plant litter accumulation and the growth of woody plants (Guthrie 2001), but little research has explored it as a possibility. The development of quantitative palaeofire reconstructions using sedimentary charcoal (e.g. Patterson *et al.* 1987; Clark 1988; Clark & Royall 1995, 1996) occurred at the same time as much of the work initially characterizing Beringian vegetation during the Last Glacial (e.g. Anderson 1985, 1988; Eisner & Colinvaux 1990, 1992; Anderson *et al.* 1994). Consequently, modern fire reconstruction methods and theory likely had not yet become part of the standard palaeoecological toolbox. For example, Eisner & Colinvaux (1990) noted elevated charcoal in the Last Glacial sediments of Ahaliorak Lake in Arctic Alaska but interpreted it as an indicator of aridity.

Our data suggest that fire and herbivory could have interacted to maintain the mammoth steppe and promote its productivity. Though it is difficult to decipher the dynamics of this no-analogue ecosystem, fire and herbivory have similar impacts on many modern ecosystems (Bond & Keeley 2005). For example, fire and herbivory partly determine the relative amounts of grassy and woody vegetation in savannah ecosystems (Van Langevelde *et al.* 2003; Smit *et al.* 2010; Holdo *et al.* 2012), and they may have done the same to limit shrub expansion in the herbaceous mammoth steppe (Zimov *et al.* 1995; Guthrie 2001; Blinnikov *et al.* 2011). However, ancient DNA analyses suggest that the mammoth steppe did have a significant shrub component (Willerslev 2014). Herbivore grazing promotes N enrichment in savannahs (Augustine *et al.* 2003) and reduces the losses of N to combustion in tallgrass prairie (Hobbs *et al.* 1991). Similarly, megafauna grazing is thought to have promoted the productivity of the mammoth steppe (Guthrie 1982; Schwartz-Narbonne *et al.* 2019). The role of fire in promoting ecosystem productivity is less clear (Pausas & Ribeiro 2013). Though fire volatilizes N in prairies, grasslands, rangelands and heathlands (Hobbs *et al.* 1991; Adams *et al.* 1994; Blair 1997; Snyman 2003; Henry *et al.* 2006), it promotes P availability and productivity in the same ecosystems (Butler *et al.* 2018). In shrub-grasslands and shrub steppes, grazing moderates fire activity by increasing fuel moisture, decreasing fuel abundance and decreasing fuel continuity (Davies *et al.* 2015, 2016, 2017). Though our data do not facilitate a complete analysis of the role of fire in the mammoth steppe, they demonstrate that fire did affect the ecosystem for millennia and highlight a topic needing further research.

The demise of the mammoth steppe and Ice Age megafauna in Beringia

The relative roles of humans and climate in the demise of the mammoth steppe and its megafauna are debated in the literature and are thought to have varied by region (Brook & Bowman 2002; Johnson 2002; Miller *et al.* 2005; Gill *et al.* 2009; Lorenzen *et al.* 2011; Sandom *et al.* 2014). In northeastern Beringia, climate change and subsequent landscape changes and habitat fragmentation are thought to have caused the extinction of megafauna (Mann *et al.* 2013, 2015), though this conclusion rests in part upon the assumption of swift peopling of the region at *c.* 13.5 cal. ka BP (though other sites suggest an earlier arrival to northeastern Beringia). This stands in contrast to global analyses indicating humans dominated climatic drivers of extinction (Sandom *et al.* 2014). To date, the timing of human arrival has not been reconciled between the date proposed by the BSH and the date of the megafauna extinctions in eastern Beringia.

Our data, in conjunction with published palaeontological and genetic data, suggest that humans could have influenced faunal population dynamics during the Last Glacial, but their impacts on the ultimate extinction agent of the mammoth steppe and its megafauna during the deglaciation were secondary to climate-driven vegetation changes. Our data place humans in eastern Beringia as early as 34 cal. ka BP, in agreement with the genetically inferred separation of the Ancient Beringian population *c.* 36 000 years ago (Raghavan *et al.* 2015; Moreno-Mayar *et al.* 2018). This suggests a long period of interaction between humans and megafauna, which would be expected to allow for coevolution and less severe extinctions (Sandom *et al.* 2014). Genetic evidence suggests that Beringian bison experienced precipitous population declines beginning 37 cal. ka BP (Shapiro *et al.* 2004) and that there was a local extinction of brown bears in Beringia from 35 to 21 ka (Barnes *et al.* 2002). The timings of these faunal population changes are conspicuous in light of our data and the BSH. Indeed, humans may have influenced bison populations via hunting and may have driven out omnivorous brown bear populations (Matheus 1995). However, herbivore megafauna extinctions in northeastern Beringia did not occur until the deglaciation, with mammoths disappearing 13.8 cal. ka BP and horses and bison remaining until 12.5 cal. ka BP (Mann *et al.* 2013). These extinctions are coincident with distinct increases in summer temperatures in eastern Beringia (Fig. 5), as inferred from chironomid assemblages (Kurek *et al.* 2009), as well as decreased aridity, as inferred from increased proportions of algal and aquatic vascular plant pollen and Burial Lake levels (Fig. 5). Geomorphological evidence for climate-driven peatland establishment and alluviation in flood-plains from 14 to 12.8 ka are thought to have fragmented habitats and caused the ultimate demise of these megafauna (Mann *et al.* 2010, 2015). Importantly, the timing of these climatic changes coincides with the ages of archaeological finds supporting the swift peopling hypothesis, which likely relate to human population expansion. It is therefore difficult to determine if humans or climate caused the ultimate demise of megafauna in Beringia; however, the extended period of cohabitation during the Last Glacial suggests humans, despite having potential impacts on megafauna populations during the Last Glacial, were secondary to climate.

Conclusions

Our analyses of biomarkers (faecal sterols and polycyclic aromatic hydrocarbons (PAHs)) preserved in the Burial Lake sediment core corroborate previous analyses of Lake E5 sediments. These analyses support the presence of humans in Beringia during the Last Glacial and suggest that they promoted fire activity. The timing of human presence evident in the Burial Lake and Lake E5 sediment records agrees with the Beringian Standstill Hypothesis. However, further research is required to determine if the human population identified by our analyses was indeed the Standstill population. Our data show that Ice Age megafauna and humans coexisted for millennia, suggesting that humans were not the primary cause of the extinctions that occurred at the end of the Last Glacial. Lastly, we show that the role of fire in the mammoth steppe has been overlooked in the palaeoecological literature, but that it may have been an important agent in the maintenance of this puzzling ecosystem's structure and productivity.

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Author contributions. – MBA and MSF collected samples. RSV analysed samples. RSV, MBA and YH designed the project. All authors contributed to the interpretation of data. RSV and JMR drafted the manuscript, which was reviewed and edited by all authors.

Data availability statement. – The data that support the findings of this study are available from the corresponding author upon reasonable request. They will also be made available for download from the NOAA's World Data Service for Paleoclimatology.

References

Abbott, M. B., Edwards, M. E. & Finney, B. P. 2010: A 40,000-yr record of environmental change from Burial Lake in Northwest Alaska. *Quaternary Research 74*, 156–165.

Adams, M. A., Iser, J., Keleher, A. D. & Cheal, D. C. 1994: Nitrogen and phosphorus availability and the role of fire in heathlands at wilsons promontory. *Australian Journal of Botany 42*, 269–281.

Anderson, P. M. 1985: Late Quaternary vegetational change in the Kotzebue Sound area, northwestern Alaska. *Quaternary Research 24*, 307–321.

Anderson, P. M. 1988: Late Quaternary Pollen Records from the Kobuk and Noatak River Drainages, Northwestern Alaska. *Quaternary Research 29*, 263–276.

Anderson, P. M., Bartlein, P. J. & Brubaker, L. B. 1994: Late Quaternary History of Tundra Vegetation in Northwestern Alaska. *Quaternary Research 41*, 306–315.

Argiriadis, E., Battistel, D., McWethy, D. B., Vecchiato, M., Kirchgeorg, T., Kehrwald, N. M., Whitlock, C., Wilmshurst, J. M. & Barbante, C. 2018: Lake sediment fecal and biomass burning biomarkers provide direct evidence for prehistoric human-lit fires in New Zealand. *Scientific Reports 8*, 12113, doi: https://doi.org/10.1038/s41598-018-30606-3.

Augustine, D. J., McNaughton, S. J. & Frank, D. A. 2003: Feedbacks between soil nutrients and large herbivores in a managed savanna ecosystem. *Ecological Applications 13*, 1325–1337.

Barnes, I., Matheus, P., Shapiro, B., Jensen, D. & Cooper, A. 2002: Dynamics of Pleistocene population extinctions in Beringian brown bears. *Science 295*, 2267–2270.

Biache, C. & Philp, R. P. 2013: The use of sterol distributions combined with compound specific isotope analyses as a tool to identify the origin of fecal contamination in rivers. *Water Research 47*, 1201–1208.

Blaauw, M. 2010: Methods and code for 'classical' age-modelling of radiocarbon sequences. *Quaternary Geochronology 5*, 512–518.

Blair, J. M. 1997: Fire, N availability, and plant response in grasslands: A test of the transient maxima hypothesis. *Ecology 78*, 2359–2368.

Blinnikov, M. S., Gaglioti, B. V., Walker, D. A., Wooller, M. J. & Zazula, G. D. 2011: Pleistocene graminoid-dominated ecosystems in the Arctic. *Quaternary Science Reviews 30*, 2906–2929.

Bliss, L. C. & Richards, J. H. 1982: Present-day arctic vegetation and ecosystems as a predictive tool for the arctic-steppe mammoth biome. *In* Hopkins, D. M., Matthews, J. V., Schweger, C. E. & Young, S. B. (eds.): *Paleoecology of Beringia*, 241–257. Academic Press, Cambridge.

Bonatto, S. L. & Salzano, F. M. 1997: A single and early migration for the peopling of the Americas supported by mitochondrial DNA sequence data. *Proceedings of the National Academy of Sciences 94*, 1866–1871.

Bond, W. J. & Keeley, J. E. 2005: Fire as a global 'herbivore': the ecology and evolution of flammable ecosystems. *Trends in Ecology and Evolution 20*, 387–394.

Bourgeon, L., Burke, A. & Higham, T. 2017: Earliest human presence in North America dated to the last glacial maximum: New radiocarbon dates from Bluefish Caves, Canada. *PLoS ONE 12*, e0169486, https://doi.org/10.1371/journal.pone.0169486.

Bradshaw, R. H. W., Hannon, G. E. & Lister, A. M. 2003: A long-term perspective on ungulate–vegetation interactions. *Forest Ecology and Management 181*, 267–280.

Brook, B. W. & Bowman, D. M. J. S. 2002: Explaining the Pleistocene megafaunal extinctions: models, chronologies, and assumptions. *Proceedings of the National Academy of Sciences 99*, 14624–14627.

Bull, I. D., Lockheart, M. J., Elhmmali, M. M., Roberts, D. J. & Evershed, R. P. 2002: The origin of faeces by means of biomarker detection. *Environment International 27*, 647–654.

Butler, O. M., Elser, J. J., Lewis, T., Mackey, B. & Chen, C. 2018: The phosphorus-rich signature of fire in the soil–plant system: a global meta-analysis. *Ecology Letters 21*, 335–344.

Cinq-Mars, J. 1990: La place des grottes du Poisson-Bleu dans la préhistoire Béringienne. *Revista de Arquelogia Americana 1*, 9–32.

Cinq-Mars, J. & Morlan, R. E. 1999: Bluefish caves and old crow basin: a new rapport. *In* Bonnichse, R. & Turnmie, K. L. (eds.): *Ice Age Peoples of North America: Environments, Origins, and Adaptations*, 200–212. Oregon State University Press for the Center for the Study of the First Americans, Corvallis, Oregon.

Clark, J. S. 1988: Particle motion and the theory of charcoal analysis: Source area, transport, deposition, and sampling. *Quaternary Research 30*, 67–80.

Clark, P. U., Dyke, A. S., Shakun, J. D., Carlson, A. E., Clark, J., Wohlfarth, B., Mitrovica, J. X., Hostetler, S. W. & McCabe, A. M. 2009: The last glacial maximum. *Science 325*, 710–714.

Clark, J. S. & Royall, P. D. 1995: Particle-Size Evidence for Source Areas of Charcoal Accumulation in Late Holocene Sediments of Eastern North American Lakes. *Quaternary Research 43*, 80–89.

Clark, J. S. & Royall, P. D. 1996: Local and regional sediment charcoal evidence for fire regimes in presettlement north-eastern North America. *Journal of Ecology 84*, 365–382.

D'Anjou, R. M., Bradley, R. S., Balascio, N. L. & Finkelstein, D. B. 2012: Climate impacts on human settlement and agricultural activities in northern Norway revealed through sediment biogeochemistry. *Proceedings of the National Academy of Sciences of the United States of America 109*, 20332–20337.

Davies, K. W., Boyd, C. S., Bates, J. D. & Hulet, A. 2015: Dormant season grazing may decrease wildfire probability by increasing fuel moisture and reducing fuel amount and continuity. *International Journal of Wildland Fire 24*, 849–856.

Davies, K. W., Boyd, C. S., Bates, J. D. & Hulet, A. 2016: Winter grazing can reduce wildfire size, intensity and behaviour in a shrub-grassland. *International Journal of Wildland Fire 25*, 191–199.

Davies, K. W., Gearhart, A., Boyd, C. S. & Bates, J. D. 2017: Fall and spring grazing influence fire ignitability and initial spread in shrub steppe communities. *International Journal of Wildland Fire 26*, 485–490.

Dorfman, J. M., Stoner, J. S., Finkenbinder, M. S., Abbott, M. B., Xuan, C. & St-Onge, G. 2015: A 37,000-year environmental magnetic record of aeolian dust deposition from Burial Lake, Arctic Alaska. *Quaternary Science Reviews 128*, 81–97.

Dyke, A. S., Moore, A. & Robertson, L. 2003: *Deglaciation of North America. Geological Survey of Canada, Open File 1574*, https://doi.org/10.4095/214399.

Eisner, W. R. & Colinvaux, P. A. 1990: A long pollen record from Ahaliorak Lake, Arctic Alaska. *Review of Palaeobotany and Palynology 63*, 35–52.

Eisner, W. R. & Colinvaux, P. A. 1992: Late Quaternary Pollen Records from Oil Lake and Feniak Lake, Alaska, U.S.A. *Arctic and Alpine Research 24*, 56–63.

Finkenbinder, M. S., Abbott, M. B., Finney, B. P., Stoner, J. S. & Dorfman, J. M. 2015: A multi-proxy reconstruction of environmental change spanning the last 37,000 years from Burial Lake, Arctic Alaska. *Quaternary Science Reviews 126*, 227–241.

Finkenbinder, M. S., Abbott, M. B., Stoner, J. S., Ortiz, J. D., Finney, B. P., Dorfman, J. M. & Stansell, N. D. 2018: Millennial-scale variability in Holocene aquatic productivity from Burial Lake, Arctic Alaska. *Quaternary Science Reviews 187*, 220–234.

French, N. H. F., Jenkins, L. K., Loboda, T. V., Flannigan, M., Jandt, R., Bourgeau-Chavez, L. L. & Whitley, M. 2015: Fire in arctic tundra of Alaska: past fire activity, future fire potential, and significance for land management and ecology. *International Journal of Wildland Fire 24*, 1045–1061.

van Geel, B., Aptroot, A., Baittinger, C., Birks, H. H., Bull, I. D., Cross, H. B., Evershed, R. P., Gravendeel, B., Kompanje, E. J. O., Kuperus, P., Mol, D., Nierop, K. G. J., Pals, J. P., Tikhonov, A. N., van Reenen, G. & van Tienderen, P. H. 2008: The ecological implications of a Yakutian mammoth's last meal. *Quaternary Research 69*, 361–376.

Gill, J. L., Williams, J. W., Jackson, S. T., Lininger, K. B. & Robinson, G. S. 2009: Pleistocene megafaunal collapse, novel plant communities, and enhanced fire regimes in North America. *Science 326*, 1100–1103.

Goebel, T., Waters, M. R. & O'Rourke, D. H. 2008: The Late Pleistocene dispersal of modern humans in the Americas. *Science 319*, 1497–1502.

Guthrie, R. D. 1982: Mammals of the mammoth steppe as paleoenvironmental indicators. *In* Hopkins, D. M., Matthews, J. V., Schweger, C. E. & Young, S. B. (eds.): *Paleoecology of Beringia*, 307–326. Academic Press, Cambridge.

Guthrie, R. D. 2001: Origin and causes of the mammoth steppe: A story of cloud cover, woolly mammal tooth pits, buckles, and inside-out Beringia. *Quaternary Science Reviews 20*, 549–574.

Halsall, C. J., Sweetman, A. J., Barrie, L. A. & Jones, K. C. 2001: Modelling the behaviour of PAHs during atmospheric transport from the UK to the Arctic. *Atmospheric Environment 35*, 255–267.

Henry, H. A. L., Chiariello, N. R., Vitousek, P. M., Mooney, H. A. & Field, C. B. 2006: Interactive effects of fire, elevated carbon dioxide, nitrogen deposition, and precipitation on a California annual grassland. *Ecosystems 9*, 1066–1075.

Hobbs, N. T., Schimel, D. S., Owensby, C. E. & Ojima, D. S. 1991: Fire and grazing in the tallgrass prairie: contingent effects on nitrogen budgets. *Ecology 72*, 1374–1382.

Hoffecker, J. F., Elias, S. A. & O'Rourke, D. H. 2014: Out of Beringia? *Science 343*, 979–980.

Hoffecker, J. F., Elias, S. A., O'Rourke, D. H., Scott, G. R. & Bigelow, N. H. 2016: Beringia and the global dispersal of modern humans. *Evolutionary Anthropology: Issues, News, and Reviews 25*, 64–78.

Hoffecker, J. F. & Frederick, H. W. 1996: Introduction to the Archaeology of Beringia. *In* West, C. F. & Robinson, B. S. (eds.): *American Beginnings: The Prehistory and Palaeoecology of Beringia*, 149–153. University of Chicago Press, Chicago.

Holdo, R. M., Mack, M. C. & Arnold, S. G. 2012: Tree canopies explain fire effects on soil nitrogen, phosphorus and carbon in a savanna ecosystem. *Journal of Vegetation Science 23*, 352–360.

Hu, F. S., Higuera, P. E., Walsh, J. E., Chapman, W. L., Duffy, P. A., Brubaker, L. B. & Chipman, M. L. 2010: Tundra burning in Alaska: linkages to climatic change and sea ice retreat. *Journal of Geophysical Research: Biogeosciences 115*, G04002, https://doi.org/10.1029/2009JG001270.

Johnson, C. N. 2002: Determinants of loss of mammal species during the Late Quaternary 'megafauna'extinctions: life history and ecology, but not body size. *Proceedings of the Royal Society of London, Series B: Biological Sciences 269*, 2221–2227.

Kurek, J., Cwynar, L. C., Ager, T. A., Abbott, M. B. & Edwards, M. E. 2009: Late Quaternary paleoclimate of western Alaska inferred from fossil chironomids and its relation to vegetation histories. *Quaternary Science Reviews 28*, 799–811.

Leeming, R., Ball, A., Ashbolt, N. & Nichols, P. 1996: Using faecal sterols from humans and animals to distinguish faecal pollution in receiving waters. *Water Research 30*, 2893–2900.

Lorenzen, E. D., Nogués-Bravo, D., Orlando, L., Weinstock, J., Binladen, J., Marske, K. A., Ugan, A., Borregaard, M. K., Gilbert, M. T. P. & Nielsen, R. 2011: Species-specific responses of Late Quaternary megafauna to climate and humans. *Nature 479*, 359–364.

Manley, W. F. 2002: *Postglacial Flooding of the Bering Land Bridge: A Geospatial Animation v1*. INSTAAR. http://instaar.colorado.edu/groups/QGISL/bering_land_bridge/.

Mann, D., Edwards, J., Chase, J., Beck, W., Reanier, R., Mass, M., Finney, B. & Loret, J. 2008: Drought, vegetation change, and human history on Rapa Nui (Isla de Pascua, Easter Island). *Quaternary Research 69*, 16–28.

Mann, D. H., Groves, P., Kunz, M. L., Reanier, R. E. & Gaglioti, B. V. 2013: Ice-age megafauna in Arctic Alaska: extinction, invasion, survival. *Quaternary Science Reviews 70*, 91–108.

Mann, D. H., Groves, P., Reanier, R. E., Gaglioti, B. V., Kunz, M. L. & Shapiro, B. 2015: Life and extinction of megafauna in the ice-age Arctic. *Proceedings of the National Academy of Sciences 112*, 14301–14306.

Mann, D. H., Groves, P., Reanier, R. E. & Kunz, M. L. 2010: Floodplains, permafrost, cottonwood trees, and peat: What happened the last time climate warmed suddenly in arctic Alaska? *Quaternary Science Reviews 29*, 3812–3830.

Matheus, P. E. 1995: Diet and co-ecology of Pleistocene short-faced bears and brown bears in eastern Beringia. *Quaternary Research 44*, 447–453.

Matthews, J. V. Jr. 1982: East Beringia during Late Wisconsin time: a review of the biotic evidence. *In* Hopkins, D. M., Matthews, J. V., Schweger, C. E. & Young, S. B. (eds.): *Paleoecology of Beringia*, 127–150. Academic Press, Cambridge.

Miller, G. H., Fogel, M. L., Magee, J. W., Gagan, M. K., Clarke, S. J. & Johnson, B. J. 2005: Ecosystem collapse in Pleistocene Australia and a human role in megafaunal extinction. *Science 309*, 287–290.

Moreno-Mayar, J. V., Potter, B. A., Vinner, L., Steinrücken, M., Rasmussen, S., Terhorst, J., Kamm, J. A., Albrechtsen, A., Malaspinas, A.-S., Sikora, M., Reuther, J. D., Irish, J. D., Malhi, R. S., Orlando, L., Song, Y. S., Nielsen, R., Meltzer, D. J. & Willerslev, E. 2018: Terminal Pleistocene Alaskan genome reveals first founding population of Native Americans. *Nature 553*, 203–207.

Morlan, R. E. 2003: Current perspectives on the Pleistocene archaeology of eastern Beringia. *Quaternary Research 60*, 123–132.

Morlan, R. E. & Cinq-Mars, J. 1982: Ancient Beringians: human occupation in the late Pleistocene of Alaska and the Yukon Territory. *In* Hopkins, D. M., Matthews, J. V., Schweger, C. E. & Young, S. B. (eds.): *Paleoecology of Beringia*, 353–381. Academic Press, Cambridge.

Mulligan, C. J. & Szathmáry, E. J. E. 2017: The peopling of the Americas and the origin of the Beringian occupation model. *American Journal of Physical Anthropology 162*, 403–408.

Nichols, J. 1990: Linguistic diversity and the first settlement of the New World. *Language 66*, 475–521.

Nichols, J. 2008: Language spread rates and prehistoric American migration rates. *Current Anthropology 49*, 1109–1117.

Oswald, W. W., Anderson, P. M., Brown, T. A., Brubaker, L. B., Hu, F. S., Lozhkin, A. V., Tinner, W. & Kaltenrieder, P. 2005: Effects of sample mass and macrofossil type on radiocarbon dating of arctic and boreal lake sediments. *The Holocene 15*, 758–767.

Patterson, W. A., Edwards, K. J. & Maguire, D. J. 1987: Microscopic charcoal as a fossil indicator of fire. *Quaternary Science Reviews 6*, 3–23.

Pausas, J. G. & Ribeiro, E. 2013: The global fire–productivity relationship. *Global Ecology and Biogeography 22*, 728–736.

Pereboom, E. M., Vachula, R. S., Huang, Y. & Russell, J. M. 2020: The morphology of experimentally produced charcoal distinguishes fuel types in the Arctic tundra. *The Holocene*, https://doi.org/10.1177/0959683620908629.

Pinter, N., Fiedel, S. & Keeley, J. E. 2011: Fire and vegetation shifts in the Americas at the vanguard of Paleoindian migration. *Quaternary Science Reviews 30*, 269–272.

Pitulko, V. V., Pavlova, E. Y. & Nikolskiy, P. A. 2017: Revising the archaeological record of the Upper Pleistocene Arctic Siberia: Human dispersal and adaptations in MIS 3 and 2. *Quaternary Science Reviews 165*, 127–148.

Pitulko, V. V., Tikhonov, A. N., Pavlova, E. Y., Nikolskiy, P. A., Kuper, K. E. & Polozov, R. N. 2016: Paleoanthropology: Early human presence in the Arctic: Evidence from 45,000-year-old mammoth remains. *Science 351*, 260–263.

Potter B. A., Holmes C. E. & Yesner D. R. 2013: Technology and economy among the earliest prehistoric foragers in interior eastern Beringia. *In* Graf K. E., Ketron C. V. & Waters M. R. (eds.): *Paleoamerican Odyssey*, 81–103, Texas A & M Press, College Station, Texas.

Prost K., Birk J. J., Lehndorff E., Gerlach R. & Amelung W. 2017: Steroid biomarkers revisited-improved source identification of faecal remains in archaeological soil material. *PLoS One 12*, e0164882, doi: https://doi.org/10.1371/journal.pone.0164882.

Raghavan M. & 99 others 2015: Genomic evidence for the Pleistocene and recent population history of Native Americans. *Science 349*, aab3884, doi: https://doi.org/10.1126/science.aab3884.

Rule S., Brook B. W., Haberle S. G., Turney C. S., Kershaw A. P. & Johnson C. N. 2012: The aftermath of megafaunal extinction: ecosystem transformation in Pleistocene Australia. *Science 335*, 1483–1486.

Sandom, C., Faurby, S., Sandel, B. & Svenning, J. C. 2014: Global late Quaternary megafauna extinctions linked to humans, not climate change. *Proceedings of the Royal Society B: Biological Sciences 281*, 20133254, https://doi.org/10.1098/rspb.2013.3254.

Schwartz-Narbonne R., Longstaffe F. J., Kardynal K. J., Druckenmiller P., Hobson K. A., Jass C. N., Metcalfe J. Z. & Zazula G. 2019: Reframing the mammoth steppe: Insights from analysis of isotopic niches. *Quaternary Science Reviews 215*, 1–21.

Scott G. R., Schmitz K., Heim K. N., Paul K. S., Schomberg R. & Pilloud M. A. 2018: Sinodonty, Sundadonty, and the Beringian Standstill model: Issues of timing and migrations into the New World. *Quaternary International 466*, 233–246.

Shapiro, B., Drummond, A. J., Rambaut, A., Wilson, M. C., Matheus, P. E., Sher, A. V., Pybus, O. G., Gilbert, M. T. P., Barnes, I. & Binladen, J. 2004: Rise and fall of the Beringian steppe bison. *Science 306*, 1561–1565.

Sher, A. V., Kuzmina, S. A., Kuznetsova, T. V. & Sulerzhitsky, L. D. 2005: New insights into the Weichselian environment and climate of the East Siberian Arctic, derived from fossil insects, plants, and mammals. *Quaternary Science Reviews 24*, 533–569.

Sikora M. & 54 others 2019: The population history of northeastern Siberia since the Pleistocene. *Nature 570*, 182–188.

Skoglund, P. & Reich, D. 2016: A genomic view of the peopling of the Americas. *Current Opinion in Genetics & Development 41*, 27–35.

Smit, I. P. J., Asner, G. P., Govender, N., Kennedy-Bowdoin, T., Knapp, D. E. & Jacobson, J. 2010: Effects of fire on woody vegetation structure in African savanna. *Ecological Applications 20*, 1865–1875.

Snyman, H. A. 2003: Short-term response of rangeland following an unplanned fire in terms of soil characteristics in a semi-arid climate of South Africa. *Journal of Arid Environments 55*, 160–180.

Szathmary, E. J. 1993: mtDNA and the peopling of the Americas. *American Journal of Human Genetics 53*, 793–799.

Tamm, E., Kivisild, T., Reidla, M., Metspalu, M., Smith, D. G., Mulligan, C. J., Bravi, C. M., Rickards, O., Martinez-Labarga, C., Khusnutdinova, E. K., Fedorova, S. A., Golubenko, M. V., Stepanov, V. A., Gubina, M. A., Zhadanov, S. I., Ossipova, L. P., Damba, L., Voevoda, M. I., Dipierri, J. E., Villems, R. & Malhi, R. S. 2007: Beringian Standstill and Spread of Native American Founders. *PLoS ONE 2*, e829, https://doi.org/10.1371/journal.pone.0000829.

Vachula, R. S., Huang, Y., Longo, W. M., Dee, S. G., Daniels, W. C. & Russell, J. M. 2019: Evidence of Ice Age humans in eastern Beringia suggests early migration to North America. *Quaternary Science Reviews 205*, 35–44.

Vachula, R. S., Sae-Lim, J. & Russell, J. M. 2020: Sedimentary charcoal proxy records of fire in Alaskan tundra ecosystems. *Palaeogeography, Palaeoclimatology, Palaeoecology 541*, 109564, https://doi.org/10.1016/j.palaeo.2019.109564.

Van Langevelde, F., Van De Vijver, C. A. D. M., Kumar, L., Van De Koppel, J., De Ridder, N., Van Andel, J., Skidmore, A. K., Hearne, J. W., Stroosnijder, L. & Bond, W. J. 2003: Effects of fire and herbivory on the stability of savanna ecosystems. *Ecology 84*, 337–350.

Vereshchagin, N. K. & Baryshnikov, G. F. 1982: Paleoecology of the mammoth fauna in the Eurasian Arctic. *In* Hopkins, D. M., Matthews, J. V., Schweger, C. E. & Young, S. B. (eds.): *Paleoecology of Beringia*, 267–279. Academic Press, Cambridge.

Waters, M. R. 2019: Late Pleistocene exploration and settlement of the Americas by modern humans. *Science 365*, eaat5447, https://doi.org/10.1126/science.aat5447.

West, F. H. 1996: *American Beginings: The Prehistory and Palaeoecology of Beringia*. 600 pp. University of Chicago Press, Chicago.

Willerslev, E., & 49 others. 2014: Fifty thousand years of Arctic vegetation and megafaunal diet. *Nature 506*, 47–51.

Young, A. M., Higuera, P. E., Duffy, P. A. & Hu, F. S. 2017: Climatic thresholds shape northern high-latitude fire regimes and imply vulnerability to future climate change. *Ecography 40*, 606–617.

Yurtsev, B. A. 2001: The Pleistocene "Tundra-Steppe" and the productivity paradox: the landscape approach. *Quaternary Science Reviews 20*, 165–174.

Zhu, D., Ciais, P., Chang, J., Krinner, G., Peng, S., Viovy, N., Peñuelas, J. & Zimov, S. 2018: The large mean body size of mammalian herbivores explains the productivity paradox during the Last Glacial Maximum. *Nature Ecology & Evolution 2*, 640–649.

Zimov, S. A., Chuprynin, V. I., Oreshko, A. P., Chapin, F. S., Reynolds, J. F. & Chapin, M. C. 1995: Steppe-tundra transition: A herbivore-driven biome shift at the end of the Pleistocene. *The American Naturalist 146*, 765–794.

Zimov, S. A., Zimov, N. S., Tikhonov, A. N. & Chapin, F. S. 2012: Mammoth steppe: a high-productivity phenomenon. *Quaternary Science Reviews 57*, 26–45.