**A new record of Bering Land Bridge paleoecology since the Last Glacial Maximum with biogeographic implications.**

# Matthew J. Wooller1,2\*, Émilie Saulnier-Talbot1,2, Ben A. Potter3, Soumaya Belmecheri4, Nancy Bigelow5, Kyungcheol Choy1,2, Les Cwynar6, Kimberly Davies7,8, Russ Graham9, Josh Kurek10, Peter Langdon7, Andrew Medeiros11, Ruth Rawcliffe1,2, Yue Wang12, John W. Williams12,13

**Author Affiliation:**

1.Water and Environmental Research Center, Institute of Northern Engineering, University of Alaska Fairbanks, Fairbanks, Alaska, USA. 2.Alaska Stable Isotope Facility, School of Fisheries and Ocean Sciences, University of Alaska Fairbanks, Fairbanks, Alaska, USA. 3.Department of Anthropology, University of Alaska Fairbanks, 308 Bunnell Building, Fairbanks, Alaska USA. 4.Laboratory of Tree Ring Research, University of Arizona, Tucson, Arizona, USA. 5.Alaska Quaternary Center, University of Alaska Fairbanks, Fairbanks, Alaska, USA. 6.Department of Biology, University of New Brunswick, Fredericton, New Brunswick, Canada. 7.Department of Geography and Environment, University of Southampton, Southampton, Hampshire, UK. 8.School of Geography, Earth and Environmental Sciences, Plymouth University, Plymouth, UK. 9.Department of Geosciences and Earth and Mineral Sciences Museum & Art Gallery, The Pennsylvania State University, University Park, Pennsylvania, USA. 10.Department of Geography and Environment, Mount Allison University, Sackville, New Brunswick, Canada. 11.York University, Toronto, Canada. 12.Department of Geography, University of Wisconsin-Madison, Madison, Wisconsin, USA. 13.Center for Climatic Research, University of Wisconsin-Madison, Madison, Wisconsin, USA. \*corresponding author e-mail: mjwooller@alaska.edu

**Corresponding author:** mjwooller@alaska.edu

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**Abstract:**

Paleoenvironmental records from the now submerged Bering Land Bridge (BLB) covering the Last Glacial Maximum (LGM) to the present are needed to document changing climates and connections with megafaunal and human biogeography in the region. We present the first terrestrial temperature and hydrologic reconstructions from the LGM to the present from the BLB’s south-central margin. We find that the timing of the earliest unequivocal and widespread human dispersals into eastern Beringia corresponds with a shift to warmer/wetter conditions on the BLB between ~14,700 and ~13,500 years ago associated with the early Bølling/Allerød interstadial (BA). These environmental changes could have provided the impetus for eastward human dispersal from western or central Beringia after a protracted human population standstill. Our data indicate substantial climate-induced environmental changes on the BLB since the LGM, which would have had significant influences on megafaunal and human biogeography in the region.

**Background:**

Major dispersal events throughout human prehistory have been linked to sea level and other major environmental changes (Montenegro et al. 2016, Timmermann and Friedrich 2016, Giampoudakis et al. 2017). Beringia, a region that includes easternmost Asia, westernmost northern North America, and the now-submerged Bering Land Bridge (BLB) (Fig. 1), provided the setting for the exchange of plants and animals between the two continents throughout the Pleistocene due to repeated exposure of the BLB, and was a key entry point for human dispersal into the Americas (Elias et al. 1996, Hoffecker et al. 2014).

New genetic and archaeological analyses of the initial peopling of the Americas indicate migration of Native American ancestors through Beringia sometime between 20,000-14,000 years ago, but the exact timing and specific routes remain unresolved (Llamas et al. 2016, Moreno-Mayar et al. 2018). Ancient Beringians, a newly discovered population of Native Americans, split off from other Native Americans about 20,000 years ago and are connected directly with the Denali complex, located throughout Alaska and adjacent regions between 12,500 and 6000 years ago (Moreno-Mayar et al. 2018).

The paleoenvironmental context of human adaptation and dispersal across Beringia includes the important roles of temperature, moisture, and vegetation (Giampoudakis et al. 2017), but remains speculative due to a distinct lack of paleoenvironmental data from the now-submerged BLB and since the LGM. However, most of the multiproxy data from eastern Beringia covers the Holocene (Kaufman et al. 2016) rather than the Late Glacial (Miller et al. 2010). Records of past terrestrial temperature and hydrologic changes from the central BLB since the LGM are non-existent and only a few reconstructions of past vegetation from this area have been published (Colinvaux 1967b, a, Graham et al. 2016, Wang et al. 2017). This is primarily because almost all records of terrestrial conditions on the south-central BLB are now submerged beneath the Bering Sea (Fig. 1). Instead, inferences about past environmental conditions have come from marine records (Caissie et al. 2010, Praetorius et al. 2015, Méheust et al. 2016), climate and vegetation models (Bartlein et al. 2015), lake sediments from the BLB’s perimeter(Kurek et al. 2009), and temporally limited terrestrial material preserved in marine sediments (Elias et al. 1996). Clearly, continued and enhanced paleoenvironmental information is needed from the BLB since the LGM to better define the physical setting for early human movements through Beringia and BLB biogeography. This study presents the first terrestrially-based reconstructions of temperature and hydrologic changes since the LGM at a site that is firmly within the boundary of the now-submerged south-central BLB and that has remained exposed above sea level since at least the LGM (Wang et al. 2017) (Fig. 1).

**Materials and methods:**

We analyzed a suite of abiotic and biotic proxies of past environmental conditions (SI 1) preserved in a dated (Graham et al. 2016, Wang et al. 2017) core of lake sediments taken from Lake Hill, on St. Paul Island (Fig.1). St. Paul Island is characterized by low relief, several freshwater lakes, no lotic systems and moderately productive moss-herbaceous tundra vegetation (Graham et al. 2016). The chronology for the core was established using radiocarbon dating and the vegetation history at the site was determined using pollen data, sedimentary ancient DNA and plant macrofossils (Graham et al. 2016, Wang et al. 2017). We used a chironomid-based inference model (Barley et al. 2006) (SI 1, SI 6 and 7) to reconstruct July air temperatures(Kurek et al. 2009). Diatom and cladoceran assemblage composition (SI 8-10) and oxygen isotopic analysis of chitinous chironomid headcapsules were used to infer hydrologic changes (Graham et al. 2016) (SI 1). Samples for all paleoecological and paleoenvironmental proxies were taken at identical depths, to minimize problems with proxy correlation. Extraction and processing of spores and pollen followed a modified version of the University of Minnesota LacCore protocol (Faegri et al. 1989). Cladocera, diatoms, and stable isotopic analyses were all conducted at Alaska Stable Isotope Facility (ASIF), University of Alaska Fairbanks. Preparation of diatom samples followed a modified protocol (Battarbee et al. 2001). Cladocera and chironomids were processed using previously published methods (Korhola and Rautio 2001, (Kurek et al. 2009) (Korhola and Rautio 2001). The oxygen isotope analyses of chironomid headcapsules were conducted using previously published methods (Wang et al. 2008). Bulk sediment samples were collected from the core at 16 cm intervals for isotopic and other geochemical analyses and processed according to previously published protocols (Wooller et al. 2012).

**Results:**

Here, we present a unique paleoenvironmental reconstruction from Lake Hill that extends from 18,500 years ago to the present (Fig. 2), which provides, for the first-time, multiproxy-based evidence from the BLB to compare with existing megafaunal and human biogeographic information. The Late Glacial portion of our record reveals a period of relatively warm and wet conditions during the Bølling/Allerød (BA - ~14,600 to ~14,000 years ago) (Rasmussen et al. 2006) that is bracketed by the cold and dry conditions associated with both Heinrich Stadial 1 (HS1; from 18,500 to ~14,600 years ago) and the Younger Dryas (YD; from 12,900 to ~11,650 years ago) (Hemming 2004, Rasmussen et al. 2006, Lohne et al. 2013) (Fig. 2). Between ~18,000 and 15,000 years ago, St. Paul Island was relatively cold and progressively drying (Fig. 2). Chironomid-inferred July air temperatures average about 5 oC for this period, a minimum for the record that is in agreement with previously published alkenone temperature estimates (Praetorius et al. 2015) (Fig. 2). Sea-surface temperatures (SSTs) also were at their coldest during HS1, with evidence of seasonal sea-ice expansion in the Bering Sea and the western North Pacific (Méheust et al. 2016) (Fig. 2). Increased aridity on the south-central BLB is supported by multiple indicators in the Lake Hill record of declining lake levels from ~17,700 until ~15,000 years ago (Fig. 2). This includes a trend towards higher δ18O values (Fig. 2), denoting increasing evaporative losses from Lake Hill (SI 1 and SI 2) severe enough to promote a decline in relative abundance of freshwater, planktonic diatoms and pelagic cladocerans, and an increase of a high conductivity-tolerant aquatic invertebrate species (i.e. *Alona circumfimbriata*) (Thienpont et al. 2013) by the end of HS1 (Fig. 2). At ~14,600 years ago, we document a relatively abrupt and short-lived (~1000 years) period of increased moisture and warmer conditions on the south-central BLB, corresponding to the BA (Fig. 2). Evidence includes nearly synchronous increases in pelagic cladocerans and planktonic diatoms, along with decreasing δ18O values during the BA, resulting from diminished evaporative losses from Lake Hill. Planktonic diatom species present during the BA include *Cyclotella tripartita* and *Asterionella formosa*, which in mainland Alaska lakes are observed to have water depth optima between 9.4 and 15.6 m (Gregory-Eaves I. et al. 1999), far deeper than the ~1.5 m water depth of Lake Hill today (SI 3). These changes co-occur with heightened vegetation productivity inferred from increased total pollen accumulation rates (Wang et al. 2017)and most notably by a marked increase in *Equisetum* spores (Fig. 2), indicating enhanced moisture in the area at this time. The BA period also saw a marked rise in July temperatures from ~5 oC to ~11 oC (Fig. 2e) on St. Paul Island and of SST in the northern North Pacific (Praetorius et al. 2015, Méheust et al. 2016), which accompanied a diminished extent of seasonal sea ice in the Bering Sea (Caissie et al. 2010, Méheust et al. 2016).

The relatively short-lived, warm and wet BA-period on the south-central BLB was followed by a marked shift to dry and cold conditions associated with the YD between 12,900 and 11,700 years ago (Fig. 2). This period of decreased temperatures over the Northern Hemisphere (Broecker et al. 2010) was accompanied by an expansion in seasonal sea-ice extent into the Bering Sea (Caissie et al. 2010) and western North Pacific (Méheust et al. 2016), and decreasing July temperatures and SST in the northern North Pacific (Praetorius et al. 2015) (Fig. 2). Lake levels at St. Paul Island declined so substantially during the transition from the BA into the YD that layers of loess and sand accumulated in the Lake Hill basin, containing insufficient remains of aquatic organisms to allow environmental inferences (Fig. 2). Trace amounts of well-preserved freshwater diatoms and no evidence of paleosols in the Lake Hill record during the YD indicate that an ephemeral aquatic habitat may have existed, but was regularly inundated with loess and sand. These YD-dated sediments also contained the degraded remains of marine diatoms (SI 4), most likely resulting from aeolian redeposition into the Lake Hill crater from deflating marine sediments from the dry, cold and exposed central BLB at this time. Degradation of these marine diatom frustules likely resulted from the same high wind velocities noted as scouring ventifacts found in archeological sites in Alaska dating to the YD period (Potter et al. 2017). These YD-dated sediments also have very low organic content and carbon to nitrogen ratios (C:N values) (SI 5), implying low terrestrial productivity (Gaglioti et al. In Press). The terrestrial pollen assemblages have very low pollen accumulation rates, and high abundances of non-local pollen types (*Picea*, *Pinus*), also indicating extremely low pollen and vegetation productivity on St. Paul Island during the YD (Wang et al. 2017). The July temperature reconstructions both into and out of the YD indicate that cold summer conditions prevailed (Fig. 2e). The onset of the Holocene at Lake Hill documents an increase in chironomid-inferred July temperatures, and high moisture availability reflected by a rapid and substantial increase in planktonic diatoms and pelagic cladocerans, as well as diminished evaporative losses inferred from decreasing δ18O values (Fig. 2). The planktonic taxa include those that are favored in deeper than present lakes (SI 1).

**Discussion:**

Our new multiproxy paleoenvironmental dataset allows us to evaluate the environmental context of Late Glacial human and the biogeography of some megafauna on the BLB. This includes human dispersals relating to a wide range of technologically related sites in northeast Asia and Beringia and to early Paleoindian populations south of the Ice Sheets. A wide range of genetic studies indicate a human population standstill between 25,000 and 16,000 years ago, in which Native American ancestors became genetically isolated from East Asians (Tamm et al. 2007, Llamas et al. 2016). The location of this standstill is debated; some researchers have argued for interior Northeastern Asia on the basis of archaeological evidence for human occupation during this period (Madsen 2015, Buvit and Terry 2016, Potter et al. 2017), while others have suggested Beringia based on human niche models (Giampoudakis et al. 2017), and the southern coast of central Beringia based on indirect estimates of biological productivity (Tamm et al. 2007, Hoffecker et al. 2014, Madsen 2015, Buvit and Terry 2016, Hoffecker et al. 2016, Llamas et al. 2016, Potter et al. 2017).

mtDNA analyses indicate population expansion related to colonization of the Americas sometime *after* 15,900 years ago, with 95% confidence intervals of 17,325-11,500 years ago (Llamas et al. 2016). The location of this ancestral population prior to this expansion remains unknown. However, it is likely to have been in Asia since we have evidence of human occupation there between 25,000-16,000 years ago, whereas we have limited evidence of humans in the Americas during this period (Madsen 2015, Buvit and Terry 2016, Potter et al. 2017). This migration period encompasses expansion north and east into Beringia, as well as further expansion south into North and South America. Although the location of Ancient Beringian populations prior to 11,500 years remains unresolved, they may have split from other Native Americans around 20,000 years ago in Asia (Scenario 1) or Alaska (Scenario 2). Current archaeological and paleoecological data clearly support the former (Moreno-Mayar et al. 2018 supplemental Sections 20-21 therein). There is a clear archaeological signal of expansion of people in Northeast Asia using Diuktai-related technologies after 17,000 years ago, connected with the earliest unequivocal site in Eastern Beringia, Swan Point dating to 14,200 years ago. While human occupations have been asserted for Last Glacial Maximum (LGM) times (Bourgeon et al. 2017), or pre-LGM, or even 130,000 years ago (Holen 2017), these remain equivocal (Braje, et al. 2017). More support has been given to sites dated to ~14,600-13,300 years ago, including Monte Verde and Paisley Caves (Adovasio 2013, Dillehay 2017), though some have also been criticized (Meltzer 2009, Fiedel 2013, Haynes 2016). While the technological connections between Diuktai culture and Paleoindian complexes is unclear, there is an unequivocal expansion of early Paleoindians using Clovis and related technologies between 13,400-12,680 years ago. These demographic patterns require explanation, and we evaluate here the relationships between the timing of these events (~14,500 years ago in eastern Beringia and 13,400 years ago in North America) and potential paleoenvironmental drivers or influences.

Increased aridity on the south-central BLB is supported by multiple indicators in the Lake Hill record from ~17,700 until ~15,000 years ago (Fig. 2). This much the same period, from 18,500 to 15,000 years ago, encompasses the latter part of the proposed standstill of ancestral Native American populations based on ancient DNA data (Llamas et al. 2016, Moreno-Mayar et al. 2018). Furthermore, the archaeological record indicates regional depopulation of Northern Siberia at this time (Goebel 2002). Our climatic inferences are also consistent with evidence for the relatively cold, dry and windier conditions on mainland Alaska at this time (Bigelow et al. 1990, Kunz and Reanier 1994, Edwards et al. 2001, Yesner 2001). Although southern archeological sites in Siberia persist south of the 58th parallel (Kuzmin and Keates 2016), evidence indicates that humans had not been migrating into the BLB region at the time of sustained cold and increasingly dry environmental conditions during the LGM and early deglaciation.

Our data supports the hypothesis that dispersal of humans into Alaska during the BA was associated with the widespread development of warmer and wetter conditions on the south-central BLB (Fig. 2), in much the same manner attributed to the environmental changes and their biogeographic implications following the YD, ~11,650 years ago (Guthrie 2006). For example, the earliest unequivocal occupations in Alaska (~14,200-13,100 years ago) were situated exclusively along large interior rivers, where humans exploited a wide range of resources, including wetland resources (waterfowl, fish), large ungulates (bison, wapiti), and possibly salmon (with direct evidence of exploitation after 11,800 years ago) (Yesner 2001, Potter et al. 2013, Choy et al. 2016). Warmer and wetter conditions associated with the onset of the Holocene may have affected the timing of eastward and westward dispersal of some animal species, such as moose, from the BLB (Guthrie 2001, Guthrie 2006).

Human dispersal across the BLB is posited to have been both a push and pull phenomenon (Yesner 2001). The ultimate “push” factor was the rising sea level that accompanied the release of water from melting ice sheets leading to the eventual and complete flooding of the BLB, which accelerated at the beginning of the Holocene Thermal Maximum (HTM), around 11,500 years ago (Yesner 2001). However, a chief environmental “pull” for early eastward human and mega-faunal dispersal across Beringia may have been ameliorating climate after the LGM, most notably the seasonal changes in moisture (Giampoudakis et al. 2017) associated with deglaciation that created suitable habitats for Northeast Asian hunter-gatherers (Yesner 2001), along with other environmental changes on the BLB and in eastern Beringia (Guthrie 2001, Kurek et al. 2009, Potter et al. 2017).

The warm and wet conditions on the BLB during the BA may also have promoted the development of some less favorable conditions for humans and the resources they relied upon on the BLB, which could have provided some impetus to move out of central Beringia. It has been postulated that even during the cold and dry LGM, the relatively low-lying BLB acted as a mesic barrier, inhibiting the dispersal of some open-habitat, obligate faunal species to disperse between eastern and western Beringia (Guthrie 2001, Meiri et al. 2013). Marked changes in moisture have been identified as an important attribute to mega-faunal turnover in Beringia (Graham et al. 2016, Rabanua-Wallace et al. 2017) and human niche dynamics in the Palaeoarctic (Giampoudakis et al. 2017). The progressively warmer and wetter conditions during the BA could have greatly transformed much of the southern BLB landscape into wetlands and peatlands, exacerbating the effects of the mesic barrier, reducing suitable local habitats for large grazers (bison, horse, mammoth) and promoting their dispersal into eastern Beringia. These moist environments would also have limited human ability to travel across the relatively low-lying landscape on the BLB and prompted humans to seek easier and better-drained terrains in interior Alaska. The *Equisetum*-spike in the Lake Hill record (Fig. 2i) is also consistent with an increased prevalence of wetland vegetation, at least locally at Lake Hill. *Equisetum* would have presented toxic forage for large grazers (Cortinovis and Caloni 2015) at this site and prompted faunal dispersal, also to seek more favorable habitats in upland and well-drained areas of interior eastern Beringia. Additional environmental factors “pushing” humans and some faunal taxa out of the relatively low-lying BLB region during the BA may have included an increased proliferation of mosquito populations, which are abetted by warmer and wetter conditions (Culler et al. 2015). Modern caribou herd movements are strongly influenced by the intensity of mosquito populations (Toupin et al. 1996, Morschel and Klein 1997) and caribou populations can be inhibited by the development of wetter and warmer conditions (Gunn and Skogland 1997, Mason et al. 2001). Movement of caribou and other faunal resources that were available to humans on the BLB could have subsequently prompted humans to move from the BLB as they tracked the geographic shift in the availability of these resources.

The greatest rate of land area loss from the BLB due to sea-level rise after the LGM occurred between ~10,000 and 8,500 years ago (Mann et al. 2001) (Fig. 2), which is at least 4,500 years later than the prevalent archeological evidence for the earliest human presence in Alaska (Llamas et al. 2016). This substantial temporal lag, combined with the well-constrained timing of environmental changes on the BLB preserved in the St. Paul Island record, strongly indicate that sea-level changes did not provide an initial environmental “push” corresponding to the earliest archeological evidence of human presence in Alaska. With the opening of the Bering Strait, between 13,000 and 11,000 years ago (Méheust et al. 2016) due to sea-level rise, came a notable amelioration in environmental conditions on St. Paul Island, the Bering Sea (Caissie et al. 2010) and the northern North Pacific (Fig. 2) due to oceanographic changes, and a maximum in Northern Hemisphere summer insolation (Laskar et al. 2004, Max et al. 2012, Bartlein et al. 2015). Conditions reverted to warm and humid in eastern Beringia during the HTM (Kaufman et al. 2016), which followed the cold and dry Younger Dryas interstadial. At Lake Hill, July air temperatures and relative moisture availability increased at this time (SI 1). These changes on St. Paul Island are accompanied by a similarly rapid increase in SST in the northern North Pacific (Praetorius et al. 2015) and a decrease in the extent of seasonal sea ice in the Bering Sea and western North Pacific (Méheust et al. 2016) (Fig. 2). Our evidence for warm early Holocene July air temperatures for the south-central BLB are also consistent with existing paleoecological evidence for relatively warm late-glacial summers on the BLB, compared with modern (onshore) values (Elias et al. 1997), and corresponding to the time of maximum summer insolation at 60 oN (Berger 1978, Bartlein et al. 1991). Archaeological data from interior Alaska indicate a decline in occupation sites during the YD, particularly between 12,900-12,500 years ago (only 1 known site), followed by a relative large increase in occupations after the YD, at the beginning of the HTM (14 known sites between 11,500-11,000 years ago) (Potter 2008), coupled with a diversification in resources used by humans in eastern Beringia (Guthrie 2006). This increase in archeological sites also correlates with the emergence of a new cultural group: the Denali complex or Paleoarctic tradition, that is genetically linked with Ancient Beringians, and may represent their initial migration into Alaska. Rapid climatic changes following the YD have previously been related to human dispersal into sites above the Arctic Circle in Alaska, termed Northern Paleoindians (Mann et al. 2001) and to faunal turnover in Beringia (Guthrie 2006).

**Conclusions:**

Paleo-geographic factors have been postulated to have had marked consequences for human dispersal into the Americas (Giampoudakis et al. 2017) and for faunal biogeography (Guthrie 2006, Graham et al. 2016, Rabanua-Wallace et al. 2017). Our new multiproxy-based temperature and hydrologic reconstructions from a terrestrial study location on the south-central BLB reveal relatively warm and wet conditions during the BA. We argue that these conditions could have provided environmental impetus for human movement, both across Beringia and, potentially, out of low-lying regions in the south-central BLB. The earliest archeological evidence for the presence of humans in Alaska (~14,200 years ago) thus corresponds with ecosystem, temperature and hydrologic changes in central and eastern Beringia and faunal range expansion into eastern Beringia (Guthrie 2006) during the BA, rather than with rising sea levels and the flooding of the BLB in later times. Some have argued for an inverse relationship between warmer climate and human populations between 12,500 and 7000 years ago in eastern Beringia (Mason et al. 2001). Our data supports this idea for some “push” impetus for human dispersal out of the south-central BLB and into interior Alaska during a warmer period. Human movement out of the BLB could in fact have been related to paludification and the development of extensive wetlands in the relatively low-lying terrain of this region, which might have impeded mobility and promoted intensified harassment of humans and game by mosquitoes during the warm and wet BA. Our results underscore the need for a deeper understanding of past environmental variability and its timing in Beringia since the LGM, to shed more light on the region’s complexity of early human archeology and megafaunal biogeography.

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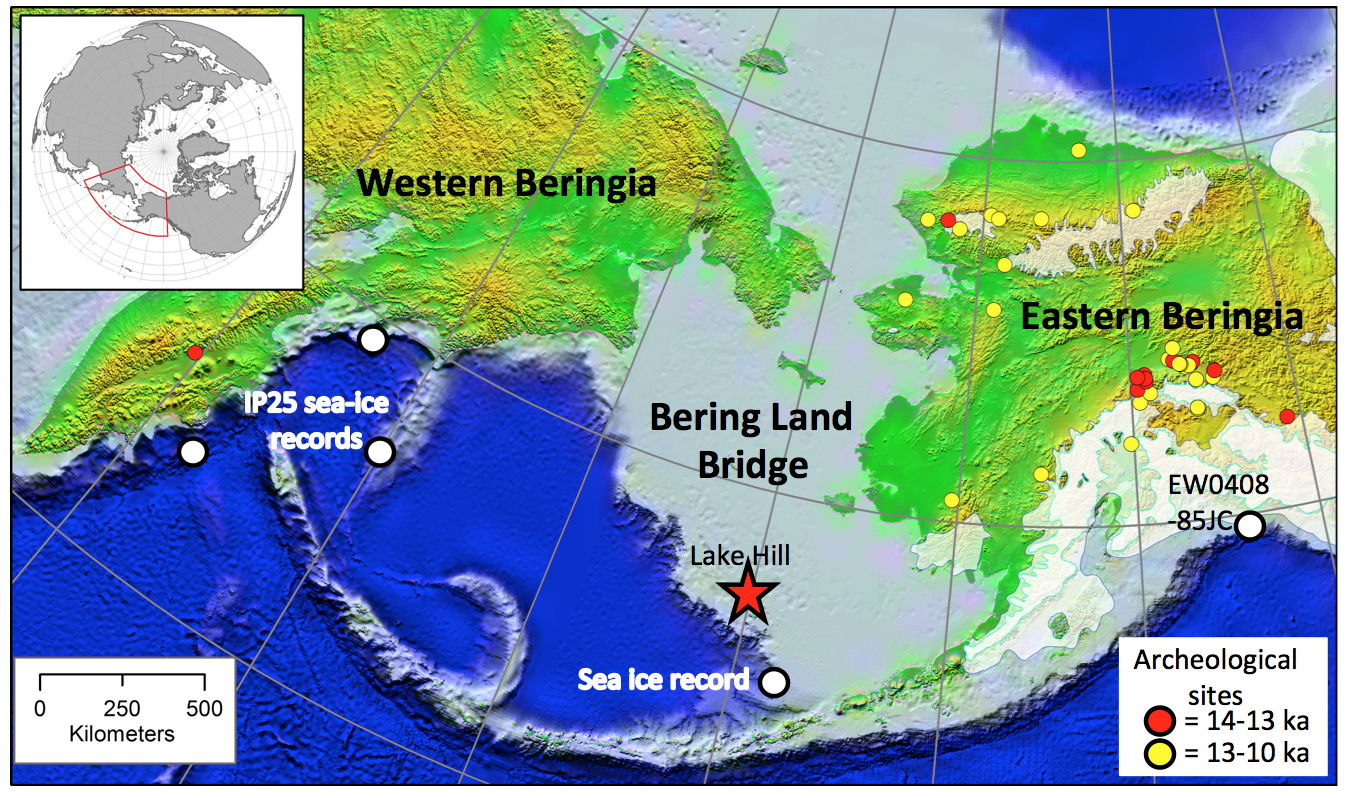
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**Figure Legends**

**Figure 1**. Location of St. Paul Island, Alaska and the locations of datasets referred to in the text (Caissie et al. 2010, Praetorius et al. 2015, Méheust et al. 2016, Potter et al. 2017).

**Figure 2.** Paleoenvironmental proxy data from St. Paul Island, Alaska and the vicinity referred to in the main text (sea ice presence = (Praetorius et al. 2015, Méheust et al. 2016), Bering Strait opens = (Elias et al. 1996), a = change in BLB surface area (Mann et al. 2001), b =archeological dates for Alaska between 16,000 and 9,000 years ago10, c = magnetic susceptibility Lake Hill sediments, d = Alkenone temperature in the N. Pacific 27, e-i from Lake Hill, respectively = chironomid inferred July temperature, planktonic diatoms % of assemblage, cladoceran data, oxygen isotope analyses of chironomid head capsules, *Equisetum* spore accumulation rates. No cladocerans or chironomids were evident during the YD in the St. Paul core and only trace amounts of freshwater diatoms (See main text for explanation) (Note the reversed scale for δ18O values).

**Figure 1.**



**Figure 2.**

