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Invited Review

Late quaternary environmental change in eastern Beringia

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ABSTRACT

Eastern Beringia (Alaska and western Yukon) is an extensive, high-latitude region of North America that remained largely unglaciated throughout the Quaternary. Consequently, its sedimentary deposits preserve long-term environmental records that have intrigued scientists for nearly a century. Recent advances in palaeoecological proxies and dating methods have proved critical in addressing long-standing questions about regional late Quaternary environmental change. At the same time, they have led to new and sometimes controversial hypotheses. This review covers recent discoveries and unresolved questions focused on the period 57,000–10,000 calendar years before C.E. 1950 (cal yr BP).

The middle Wisconsin interstadial (57,000–30,000 cal yr BP) was a period of relative warmth in eastern Beringia, compared with the late Wisconsin (30,000–14,000 cal yr BP). Early in the interstadial occasional *Picea* woodland was present amongst widespread shrub tundra. Palaeoecological, sedimentary and isotopic data indicate that climate was cooler and drier than the Holocene, with high rates of aeolian activity. Megafauna typically associated with the ‘mammoth steppe’ ecosystem (woolly mammoth [*Mammuthus primigenius*], horse [*Equus*] and steppe-bison [*Bison priscus*]) were present in some abundance.

The transition towards late Wisconsin cold-stage conditions (35,000–30,000 cal yr BP) coincided with the establishment of the Bering Land Bridge and featured expansion of spatially varied, herbaceous vegetation, sometimes associated with deep active layers. Sedimentary DNA (*seda*DNA) and macrofossil evidence show vegetation was not a prairie-like grassland, and the term “steppe-tundra” is a better descriptor. Permafrost pore-ice isotopic ($\delta^{18}O$) records suggest a step change in one or more climate drivers ca. 30,000 cal yr BP, by which time steppe-tundra was established across eastern Beringia. It remains uncertain whether *Picea* survived cold-stage conditions within isolated refugia, or whether it recolonized from south of the Laurentide-Cordilleran ice sheets. Genetic data suggest that *Picea* probably survived *in situ*; however, there is no definitive fossil evidence to support this.

The end-Pleistocene transition from steppe-tundra to shrub tundra began ca. 15,000 cal yr BP and took place within decades at local scales. The expansion of woody taxa coincided with rising sea levels, reduced sea-ice extent and an abrupt shift in atmospheric circulation that enhanced precipitation. During this time, Earth’s orbital configuration caused high early-summer temperatures and strong seasonality, creating growing conditions very different from today. The vegetation consisted of *Salix* and *Betula* shrub tundra with open areas of

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herbs and graminoids. During the deglacial warming trend, the Younger Dryas oscillation (12,800–11,700 cal yr BP) was variably expressed. It is generally evident in records affected by adjacent oceans but can be absent at sites in continental areas.

These past conditions and paleoenvironmental changes have implications for contemporary issues: hypotheses about Pleistocene mammalian extinction; sensitivity of eastern Beringia to major oceanic reorganizations and high-frequency climate variability; the nature of woody plant expansion with climate warming; grazing, hydroclimate and fire as controls over ecosystems; the efficacy of “Pleistocene rewilding” for carbon capture.

1. Introduction

The concept of Beringia was first defined by the Swedish biogeographer Eric Hultén (1937), who described a floristic refugium centred around the exposed Chukchi/Bering continental shelf (Fig. 1). During Pleistocene cold stages, such as the late Wisconsin (30,000–15,000 calendar years before C.E. 1950 [cal yr BP]), Beringia formed a northern subcontinental region now understood to have been the largest, continuous high-latitude terrestrial expanse to remain unglaciated during the Quaternary. It is usually defined as extending from the Kolyma River in Siberia to western Yukon (Hopkins, 1967, 1982; Guthrie, 2001), though some authors extend the boundaries to the Lena and Mackenzie rivers. The extent of the late Wisconsin land bridge was huge, measuring some 1000 km north to south, and the region has played a pivotal role in northern hemisphere biogeography and human history.

It has now been more than 40 years since David Hopkins and colleagues published the seminal book “Paleoecology of Beringia” (Hopkins et al., 1982). Since then, late Quaternary environmental change in Beringia has been discussed in numerous key papers, journal volumes and books (e.g., Ritchie, 1984; Elias and Brigham Grette, 2000; 2013; Guthrie, 2001; Anderson et al., 2004; Blinnikov et al., 2011). This foundational work has developed a framework for understanding biogeography and long-term environmental processes in the region.

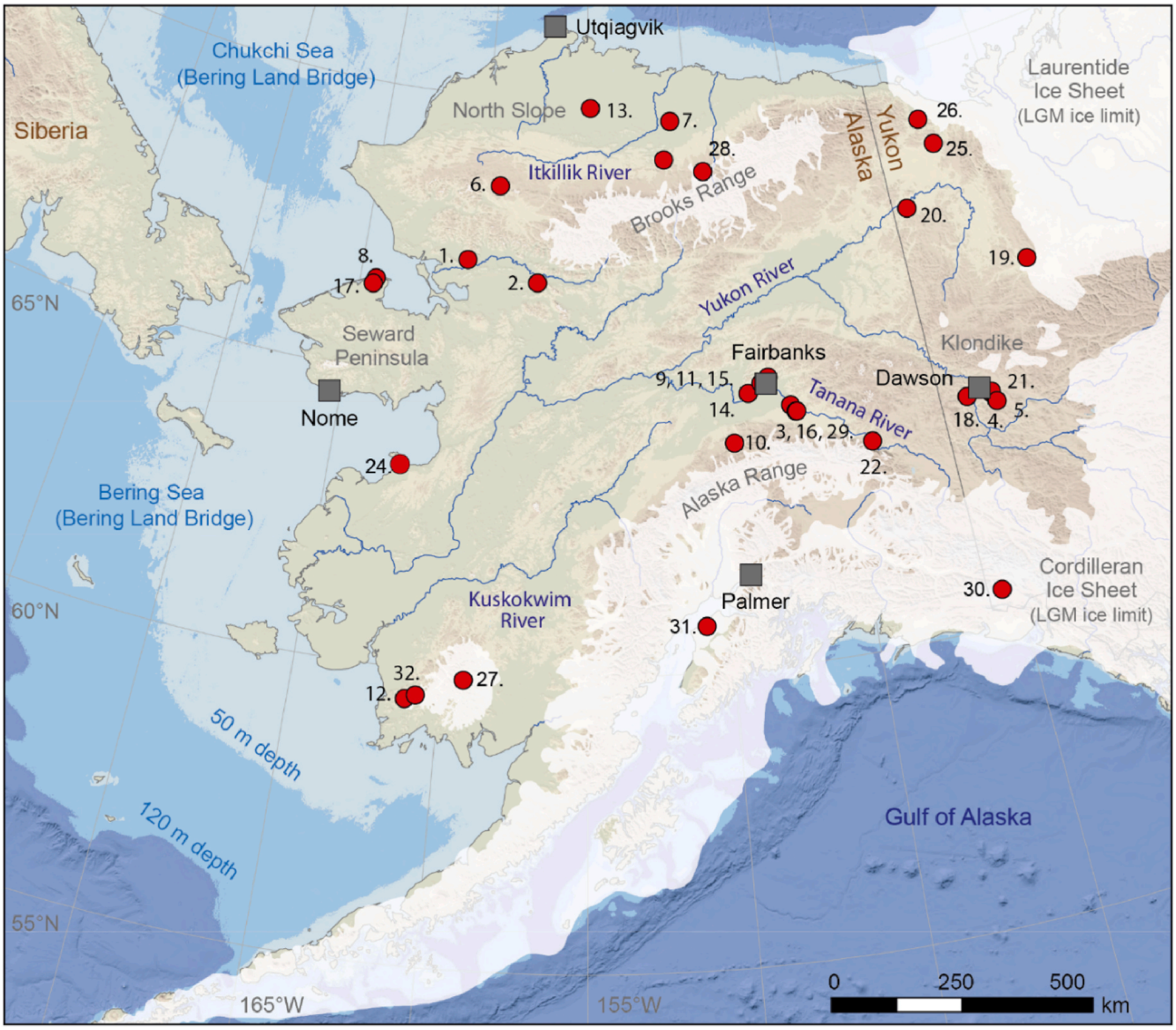

Fig. 1. Map of eastern Beringia, showing the key regions and study sites described in the text. Study sites are numbered with reference to Table 2: (1) Squirrel Lake, (2) Joe Lake, (3) Harding Lake, (4) Upper Goldbottom, (5) Hunker Creek, (6) Burial Lake, (7) Itkillik River, (8) Kitluk Pingo, (9) Isabella Basin, (10) Eightmile Lake, (11) CRREL Permafrost Tunnel, (12) Arolik Lake, (13) Carter Section, (14) Halfway House, (15) Gold Hill, (16) Chisholm Lake (Lost Lake), (17) Kitluk palaeosol, (18) Goldbottom Creek, (19) Doll Creek, (20) Bluefish River, (21) Lucky Lady, (22) Jan Lake, (24) Zagoskin Lake, (25) Hanging Lake, (26) Trout Lake, (27) Nimgun Lake, (28) Lake E5, (29) Birch Lake, (30) Logan Ice Core, (31) Discovery Pond, (32) Waskey Moraine Sequence. The approximate Last Glacial Maximum (late Wisconsin) ice limits are redrawn from Dalton et al. (2020). Base map data is from GEBCO (2023).

Scientific emphasis on the western and eastern regions of Beringia stems from both modern physical geography and political divisions, which have meant Beringian science has proceeded largely independently in each region for many decades. Hopkins, who strongly promoted a holistic approach to science in Beringia, accomplished a great deal by bringing scholars from the former Soviet Union and North America together (Elias and Dodds, 2016). Joint projects began with the advent of *glasnost* in the early 1990's (e.g., Lozhkin et al., 1993), and meetings included eastern and western Beringian researchers (Brigham-Grette and Elias, 2001). Later cooperative studies continued this approach (e.g., Kaplan et al., 2003; Lozhkin et al., 2007). Work has continued apace in both parts of Beringia, though in recent years cooperation has sadly been curtailed by geopolitics once again.

The region's current physiography takes the form of "divided twins", the regions of western (north-east Siberia, Chukotka) and eastern Beringia (northern Alaska and unglaciated Yukon and Northwest Territories) separated by the Bering and Chukchi seas (Fig. 1). At its centre is the Bering Strait, which is approximately 50 m deep at the oceanic sill and connects the Pacific and Arctic Oceans. During some previous glacial stages low eustatic sea level exposed the Bering Land Bridge, connecting eastern and western Beringia. This land connection allowed floristic exchange between the two continents (Swanson, 2003; Edwards et al., 2018), and humans, along with several old-world terrestrial mammals (e.g., bison [*Bison* spp.], wapiti [*Cervus* spp.] and moose [*Alces alces*]), colonised north-western North America via this route (Guthrie, 1990a; Meiri et al., 2014; Froese et al., 2017; Potter et al., 2017). During the late Wisconsin, eastern Beringia was also periodically isolated from the rest of North America by the coalesced Laurentide and Cordilleran ice sheets (Hopkins, 1982; Dyke et al., 2002), and Guthrie (2001) suggested that at this time the region is best viewed as an extension of Eurasia, rather than part of North America. Global eustatic sea-level records of the most recent glacial-interglacial cycle indicate that the late Pleistocene land bridge was exposed ca. 35,000 calendar cal yr BP and persisted until the onset of the Holocene (Lambeck et al., 2002; Jakobsson et al., 2017; Farmer et al., 2023; Mann and Gaglioti, 2024).

For older climatic cycles, the view of central Beringia as a seaway during interglaciations or a land bridge during glaciations may be overly simplistic. The height of the sill controlling land-bridge flooding has probably varied because of differing vertical displacement in response to isostatic depression and rebound (Pico et al., 2020), meaning older geographies are more ambiguous (Farmer et al., 2023; Mann and Gaglioti, 2024). Consequently, biogeographic and palaeogeographical models of the land bridge should not assume that the most recent patterns hold for earlier Quaternary intervals. In the same vein, eastern Beringia north of the Cordillera was not extensively glaciated during the most recent glacial cycles (Hamilton, 1986), but differing states of the ocean and atmospheric circulation created more extensive regional glaciations in the past. For example, the regional Anaktuvuk glaciation (ca. 500,000–600,000 years ago) covered a far greater area of northern Alaska than later Wisconsin glaciations and occurred at a time when sea level was relatively high (Huston et al., 1990; Brigham-Grette, 2001; Kaufman et al., 2001).

Since the publication of *Paleoecology of Beringia* (Hopkins et al., 1982), advances in our understanding of traditional palaeoecological proxies and dating methods, coupled with the emergence of novel proxies and techniques, have expanded our knowledge of eastern Beringia, though many questions, some controversial, continue to perplex researchers. Long-standing issues regarding the fundamental nature of past environments and, to some extent, past processes can now be addressed.

1. Interrelationships among climate and hydrology, vegetation, permafrost, the mammalian fauna and the carbon cycle.
2. Duration and extent of periods of boreal forest cover, whether refugia existed for *Picea* (spruce) and end-Pleistocene reforestation.
3. Pleistocene megafaunal extinctions and the potential role of large herbivores as modifiers of contemporary ecosystems and carbon dynamics.
4. The variable geographic expression of the Younger Dryas climate oscillation across Beringia and its relationship with North Atlantic and North Pacific events.

1.1. Modern vegetation and climate zones

Today, eastern Beringia spans low Arctic to northern boreal vegetation zones, with alpine tundra occurring above ~800 m elevation. Dominant vegetation types in northern and coastal lowlands are tussock-sedge, dwarf-shrub, moss tundra and sedge, moss, dwarf-shrub wetland. In southwest Alaska, sedge, moss, low-shrub wetland is common (Walker and Raynolds, 2018). Boreal forest, dominated by white and black spruce (*Picea glauca* and *P. mariana*), as well as several northern hardwoods (e.g., species of birch [*Betula*] and poplar [*Populus*]), occupies interior lower elevations south of the Brooks Range, extending along westward-flowing river drainages, but barely reaching the western shores of Alaska. Modern climate north of the Brooks Range is classified as Arctic. The interior of Alaska-Yukon experiences a cold continental climate with far warmer summers. Both northern and interior areas experience low levels of precipitation. Temperature in the west and south is moderated by maritime influences, and precipitation is higher. Station means are shown in Table 1. Note that air temperatures are warming rapidly across the region. For example, in Fairbanks, Alaska, mean Annual temperature increased by 2.2–2.4 °C between the 1930s–1940s and 2010–2019 (NOAA, 2022; Ballinger et al., 2023).

1.2. Past and present geography

Modern landscapes of eastern Beringia are characterised by varied climate, complex topography, and past environmental processes. In the past, changing climate and topography interacted to form a succession of landscapes and ecosystems different from those of today. While parts of the Alaska and Brooks Ranges were previously or are now glaciated, large areas of Alaska and Yukon remained ice-free throughout the Quaternary and comprise highly dissected, lower-elevation ranges and plateaus (Brigham-Grette, 2001, Fig. 1). The expanded landmass and orographic effects of the coastal ranges (Aleutian, Kenai, Chugach/-Wrangell, and St. Elias) and Alaska Range caused anticyclonic blocking of the westerlies and led to enhanced aridity and continentality (Péwé, 1975; Hopkins, 1982; Bartlein et al., 1998; Brigham-Grette, 2001; Kaufman et al., 2011). Lake-level reconstructions have revealed that lakes were typically low or desiccated throughout the late Wisconsin (e.g., Barber and Finney, 2000; Abbott et al., 2000, 2010; Finkenbinder et al., 2014). Major rivers, such as the Yukon and Tanana, flow through broad, low-lying tectonic basins, and form massive braided floodplains fed by glacial outwash from the Alaska, Wrangel and Brooks Ranges; this process was amplified in glacial periods. Past intervals of greater aridity led to widespread aeolian activity (Hopkins, 1982). Sand seas and dune fields, now mostly stabilized, formed in the interior basins, and in river valleys in western Alaska and on the North Slope of the Brooks Range (Carter, 1981; Hopkins, 1982; Lea and Waythomas, 1990; Gaglioti et al.,

Table 1
Climate means from 1991 to 2020 climate normals (NOAA, 2022).

	Mean Annual temperature	Mean July temperature	Mean January temperature	Mean annual precipitation
Utqiagvik (Barrow)	−10.2	5.4 °C	−24.1 °C	137 mm
Fairbanks	−2.0 °C	17.2 °C	−22.4 °C	296 mm
Dawson	−4.1 °C	15.7 °C	−26.0 °C	324 mm
Nome	−2.2 °C	11.1 °C	−14.7 °C	437 mm
Palmer	2.8 °C	13.5 °C	−9.2 °C	1152 mm

2018). Loess deposits are also common in interior areas and on the North Slope (Péwé, 1975; Muhs et al., 2003; Muhs and Budahn, 2006; Jensen et al., 2016). There are numerous lakes of different sizes and origins (Arp and Jones, 2008): thermokarst, topographic basins, volcanic maars, floodplain lakes, inter-dune ponds and lakes formed by glacial activity. The Arctic Coastal Plain and Yukon-Kuskokwim Delta feature flat, low-lying landscapes on which extensive wetlands developed during the Holocene (Jones and Yu, 2010). Here in particular, and in other lowland areas such as the North Slope, thermokarst lakes formed widely when climate became warmer and wetter during deglaciation and the onset of the Holocene (Walter et al., 2007; Edwards et al., 2016), having been rare until around 12,000 years ago. They continue to form, and drain, today (Jones et al., 2011).

1.3. *Future climates and landscapes*

Climate in eastern Beringia is projected to become far warmer than present during 21st Century, particularly in winter. More frequent extreme rain and snow events are also predicted, although with high quantitative uncertainty (Lader et al., 2017). Projections that include both precipitation and air temperature suggest that episodes of atmospheric drought may become more common, even though precipitation is expected to increase across the Arctic and subarctic later in the century (Bieniek et al., 2014; McCrystall et al., 2021). The status of the moisture balance is critical for surface processes and the trajectory of ecosystem change. For example, semi-arid portions of Beringia support mesic ecosystems because of low evapotranspiration and permafrost-impeded drainage, not because they are climatologically wet (Mann et al., 2002). This current uncertainty delivers several strikingly different future climate scenarios for eastern Beringia, and understanding past changes can help constrain projections.

Today, in dry parts of the interior such as the Yukon Flats, the precipitation minus evaporation (P-E) ratio is negative and trending towards stronger moisture deficits during recent millennia, although highly variable (Anderson et al., 2013, 2018). Further warming scenarios include moisture deficits that could have a widespread negative effect on northern forest health and productivity (Goetz et al., 2005), possibly affecting species composition. For example, summer drought in the more continental interior—and more widely in North America—has been shown to negatively affect white spruce growth (Barber et al., 2000; Sang et al., 2019). Fires are also likely to become more common with increasing warmth (Marlon et al., 2008; Lucash et al., 2023). Together with a more negative moisture balance and/or a change in fire weather characteristics (e.g., more lightning strikes) fire disturbance may shift forest composition towards early-successional deciduous taxa (Mann et al., 2012; Mack et al., 2021). Enhanced fire may even lead to open parkland (Rotbarth et al., 2025), a scenario first suggested by Chapin and Starfield (1997). For example, *Populus tremuloides* (aspen) sprouts after fire and dominates the transitional area of the moisture gradient from boreal forest to prairie (steppe) in the western Canadian interior, and indeed the steppe-forest transition in azonal boreal steppe sites today (Lloyd et al., 1994).

Alternatively, if moisture levels keep pace with future temperature increases, or indeed the moisture balance becomes more positive, a trend in expansion of shrub-tundra and white spruce (termed 'Arctic greening') may accelerate (Myers-Smith et al., 2011). Primary productivity in the boreal forest may be enhanced, particularly in more northern regions, because of permafrost thaw and better drained soils in some areas. A major increase in precipitation may also mitigate against a temperature-mediated increase in fire frequency and intensity, but this is uncertain (Abatzoglou and Kolden, 2011).

1.4. *Beringian depositional environments*

The absence of extensive glacial ice and presence of widespread permafrost (perennially frozen ground) means there is an excellent depositional record of Quaternary environments in eastern Beringia, including sequences that span several million years (Schweger et al., 2011), which in some cases remained frozen throughout several glacial-interglacial cycles (Froese et al., 2008; Reyes et al., 2010a). Deposits formed of primary airfall and re-transported loess, which are commonly associated with ice-rich syngenetic permafrost, are termed 'muck' in Alaska-Yukon mining parlance but are now more broadly known as 'yedoma' (Schirrmeister et al., 2013; Murton et al., 2015). Other deposits that preserve important fossils, palaeoenvironmental proxies and palaeogeographical evidence include aeolian sand, glacial and fluvial sediments, peat and palaeosols (Duk-Rodkin et al., 2010). Lake basins of different origins preserve continuous or semi-continuous sediment sequences, though few are as old as the oldest yedoma deposits (e.g., Heusser, 1965; Ager, 1975; Anderson et al., 2004).

Recorded fossil finds are rich in mammals, ranging from rodents to megafauna (animals weighing >44 kg). They typically take the form of bones, teeth, and other sub-fossils but also occasionally include frozen mummies (Guthrie, 1990b; Meachen et al., 2020). Other data sources include rodent middens (e.g., Zazula et al., 2007; Gaglioti et al., 2011) and buried land surfaces (e.g., Goetcheus and Birks, 2001; Zazula et al., 2006a; Wooller et al., 2011), which preserve plant macrofossils (e.g., Zazula et al., 2003) and insect remains (e.g., Matthews, 1974a; Elias, 2000). Novel approaches to palaeoenvironmental reconstruction include relict-water isotopes (δ^2H and δ^{18}O) in yedoma and lake sediments (e.g., Meyer et al., 2010; Mahony, 2015; Porter et al., 2016; King et al., 2021) and molecular proxies, including ancient DNA (e.g., Shapiro and Cooper, 2003; Murchie et al., 2021; Clarke et al., 2024). Yedoma records in particular are constrained by a mature tephrostratigraphic framework that anchors a regional chronology (Froese et al., 2009; Jensen et al., 2016; Davies et al., 2016; Monteath et al., 2017).

1.5. *Temporal scope of the review*

The temporal scope of this review is late Pleistocene to earliest Holocene: approximately 57,000 cal yr BP to 10,000 cal yr BP (Fig. 2). We begin our review around 57,000 cal yr BP as this marks the beginning of the middle Wisconsin interstadial and approximate limit of radiocarbon dating, before which establishing robust chronology becomes increasingly difficult. Eastern Beringian archaeology and later Holocene palaeoenvironmental data are not considered, as these extensive topics are reviewed elsewhere (e.g., Kaufman et al., 2016; Potter et al., 2017, 2022; Hoffecker et al., 2020).

We begin with the relatively long middle Wisconsin, which aligns approximately with Marine Isotope Stage Three (MIS3; 57,000–29,000 cal yr BP, Lisiecki and Raymo, 2005). Data are relatively sparse but indicate that conditions were warmer and moister than those of the late Wisconsin (broadly equivalent to MIS2; 29,000–14,000 cal yr BP, Lisiecki and Raymo, 2005). Nevertheless, both stages are associated with the northern megafauna (e.g., woolly mammoth [*Mammuthus primigenius*], horse [*Equus* spp.] and steppe-bison [*Bison priscus*]). We assess the latest findings and hypotheses about the composition and functioning of the steppe-tundra biome (mammoth steppe) and its collapse, a perennially fascinating topic. Whether the woody taxa that were present in the middle Wisconsin, particularly *Picea* (spruce), survived the late Wisconsin within eastern Beringian refugia remains an unresolved question.

Climatic and ecological events associated with global and regional deglaciation profoundly changed eastern Beringia between 15,000 and 10,000 cal yr BP. A warming climate driven by high summer insolation values, ice sheet decay, changing North Pacific and atmospheric conditions and major sea-level rise, promoted the development of widespread woody-dominated vegetation, extirpation of some megafauna taxa (e.g., horse and woolly mammoth), and major shifts in hydrology and carbon cycling. The opening of the ice-free corridor between Beringia and continental North America prior to 13,200 cal yr BP re-established biotic dispersal between continental North America and

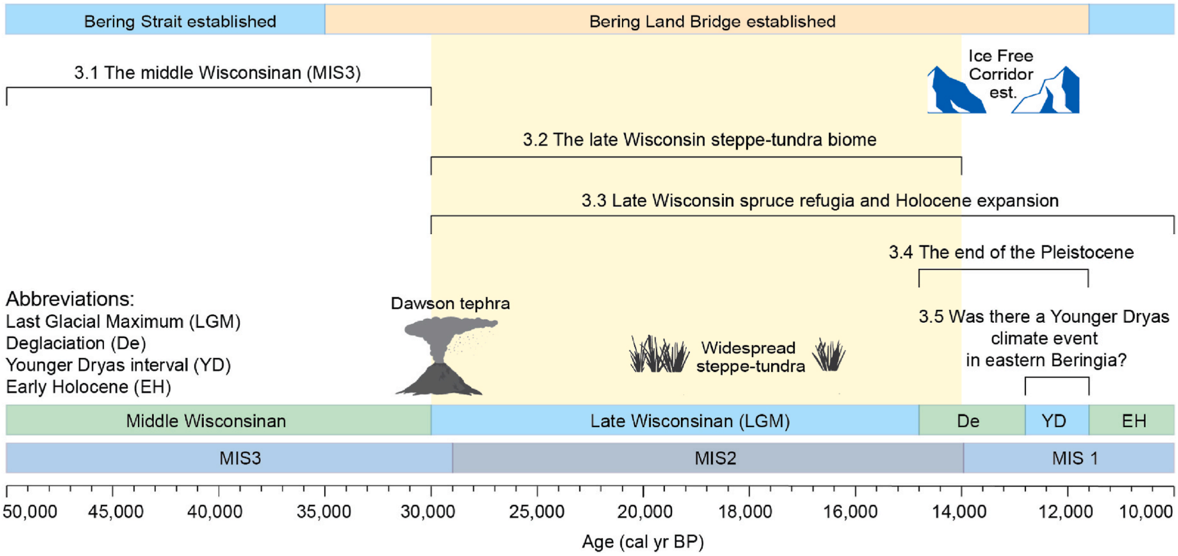

Fig. 2. The structure of this review including the major time-periods, key biogeographical events and chronological markers discussed in the text. Heading numbers refer to the corresponding sections in the review.

Beringia (Heintzman et al., 2016). Rising sea levels then breached the Bering Land Bridge by ca. 11,000 cal yr BP (Jakobsson et al., 2017; Pico et al., 2020; Mann and Gaglioti, 2024), separating Eurasia from North America. This was the last major biogeographic change of the late Quaternary in the region, and the end of a contiguous Beringia as conceived by Hultén (1937).

2. Materials and methods

The nomenclature used for different time periods in eastern Beringia varies substantially among studies and frequently includes terms that originate from North Atlantic and western European events. In some cases, these terms are now used to define chronological zones (e.g., the Younger Dryas chronozone; Mangerud, 2021) or climate oscillations that may or may not have direct equivalents in the western Arctic (e.g., Bølling-Allerød). Table 2 outlines the time periods discussed in this review. The rationale for the adopted nomenclature is described in Supplementary Information (Supplementary text, S1).

Our discussion is focussed on records that meet strict chronological criteria (see Supplementary text, S2 and S3; Table 3), which means that we do not describe much of the early literature in detail (see below for exceptions). While our general understanding of Beringia is founded on this earlier work, advances in dating methods have shown that many of the chronological approaches used in such studies were flawed, and this may explain findings that are inconsistent, or even contradictory (Abbott and Stafford Jr, 1996; Oswald et al., 2005; Gaglioti et al., 2014; Zazula et al., 2014). Particularly problematic are past radiocarbon dating approaches that provided chronologies for many palaeoenvironmental records. It is important to note that earlier authors recognized many of the chronological uncertainties that we describe here but faced methodological limitations that have now been improved upon. For example, the development of accelerator mass-spectrometer radiocarbon (AMS ^{14}C) dating has improved analytical precision for small mass samples, allowing discrete terrestrial macrofossils to be selected for dating. Similarly, the use of radiocarbon blanks allows contamination issues to be more closely scrutinised, improving the reliability of dates from samples of small mass (e.g., Kennedy et al., 2010) or near the radiocarbon limit (e.g., Reyes et al., 2010b; Martinez De La Torre et al., 2019).

Table 2
Nomenclature for different time-periods discussed in this review.

Age (cal yr BP)	Term used	Other terms/included intervals
71,000–57,000	Early Wisconsin	MIS4
57,000–30,000	Middle Wisconsin	MIS3
30,000–15,000	Late Wisconsin	MIS2, Last Glacial Maximum
15,000–11,700	Deglaciation	Late glacial, Bølling-Allerød, Younger Dryas, MIS1
11,700-8200	Early Holocene	MIS1

Many terrestrial palaeovegetation records are based on fossil pollen, which is by far the most common form of terrestrial palaeo data for the late Quaternary. While advances have been made in the interpretation of pollen data, it is important to note that in northern landscapes, particularly beyond treeline, it remains difficult to assess vegetation cover, because of the over-representation of high pollen producers such as *Betula* and *Alnus* and long-distance transport of pollen of forest taxa, such as *Picea* and *Pinus* (Birks and Birks, 2000; Binney et al., 2011). Under full- and late-glacial conditions, when pollen concentrations are typically lower than in the Holocene, differences in pollen productivity among herbaceous taxa may also skew taxon abundance patterns (Birks, 2003). We therefore include, wherever possible, macrofossil data, as recommended by Birks (2003) and sedimentary ancient DNA (*sed*aDNA; e.g., Murchie et al., 2021; Clarke et al., 2024), which has been shown to reflect local- or catchment-scale vegetation (Alsos et al., 2018; Edwards, 2020). Finally, we refer to modern pollen productivity estimates where relevant (e.g., Sugita, 2007).

3. Late quaternary environmental change in eastern Beringia

3.1. *The middle Wisconsin*

The middle Wisconsin represents a period of relative warmth in eastern Beringia that is broadly coeval with the Karginski interstadial in western Beringia (Anderson and Lozhkin, 2001) and MIS3 globally (Table 2). In eastern Beringia, this period is associated with the termination of early Wisconsin (MIS4) glaciation and the disappearance of herb-dominated vegetation (Zazula et al., 2011). Hopkins (1982) defines the middle Wisconsin duration from 65,000 to 30,000 cal yr BP. These dates broadly agree with ^{10}Be constraints on the maximum advance of early Wisconsin glaciers (59,700 ± 3600 yr BP, Tulenko et al., 2018), which exceeded late Wisconsin limits (Brigham-Grette, 2001), and the age and stratigraphic position of Dawson tephra (29,060–29,470 cal yr BP, Davies et al., 2016), which occurs near the onset of full-glacial

Table 3
Study sites described in the text. Site numbers (n.) correspond with numbering in Fig. 1. Note that the reference list for each site is not always exhaustive and primarily refers to the studies described in the main text. Abbreviations: *seda*DNA (sedimentary ancient DNA), MS (magnetic susceptibility), LOI (organic matter by loss on ignition), BSi (Biogenic silica), C/N (carbon to nitrogen ratio), XRF (elemental analysis by X-ray Fluorescence core scanning), TOC (total organic carbon), PS (particle size).

n.	Site	Lat (°N)	Long (°W)	Time-span (approx. cal yr BP)	Proxy(s)	Reference(s)
1	Squirrel Lake	67°06′00.0	160°22′48.0	180,000-present	Pollen	Berger and Anderson (2000)
2	Joe Lake	66°44′31.3	157°16′08.5	60,000-present	Pollen, LOI	Anderson et al. (1994); Berger and Anderson (2000)
3	Harding Lake	64°25′12.0	146°51′36.0	>30,000-present	Pollen, LOI, MS, BSi, C/N, XRF, PS	Nakao and Ager (1985); Finkenbinder et al. (2014)
4	Upper Goldbottom	63°54′00.0	138°59′24.0	45,000-5000	Ground ice isotopes, sedaDNA, TOC	Mahony (2015); Murchie et al. (2021)
5	Hunker Creek	63°57′00.0	139°56′24.0	31,000–29,000	Ground ice isotopes, TOC	Mahony (2015)
6	Burial Lake	68°25′48.0	159°10′12.0	38,000-present	Chironomid$_{temp}$, Chironomid δ^{18}O, pollen, XRF, MS, BSi, PS, Biomarkers	Kurek et al. (2009a); Abbott et al. (2010); Dorfman et al. (2015); King et al. (2021); Vachula et al. (2020)
7	Itkillik River	69°34′12.0	150°52′12.0	>35,000-5000	Pollen, TOC, Ground ice isotopes	Lapointe et al. (2017)
8	Kitluk Pingo	66°34′48.0	164°18′36.0	>45,000-9000	Pollen, TOC, C/N, MS, PS, Organic δ^{18}O	Wetterich et al. (2012)
9	Isabella Basin	64°54′00.0	147°39′00.0	>40,000-5000	Pollen, Macrofossils	Matthews (1974b)
10	Eightmile Lake	63°52′48.0	149°15′00.0	>40,000-present	TOC, TOC δ^{18}O, C/N, Biomarkers	Hutchings et al. (2019)
11	CRREL Permafrost Tunnel	64°57′00.0	147°37′12.0	45,000–14,000	Pollen, Macrofossils, Insects, CN, Organic^{13}C and^{15}N, Phytoliths, Ground ice isotopes	Sellman (1967, 1972); Hamilton et al. (1988); Shur et al. (2004); Bray et al. (2006); Wooller et al. (2007, 2011); Kanevskiy et al. (2022)
12	Arolik Lake	59°28′12.0	161°07′12.0	35,000-present	BSi, PS, MS, LOI, Pollen Tephra	Hu et al. (2006); Kaufman et al. (2003)
13	Carter Section	69°51′00.0	154°52′12.0	40,000–10,000	LOI, PS, Macrofossils, TOC, C/N	Gaglioti et al. (2018)
14	Halfway House	64°42′36.0	148°30′00.0	MIS5-MIS1	MS, Tephra	Jensen et al. (2016)
15	Gold Hill	64°51′36.0	147°55′48.0	MIS5-MIS1	MS, Tephra	Jensen et al. (2016)
16	Chisholm Lake (Lost Lake)	64°18′00.0	146°41′24.0	15,000-present	Pollen, sedaDNA, LOI, MS	Tinner et al. (2006); Clarke et al. (2024)
17	Kitluk palaeosol	66°28′48.0	164°24′00.0	ca. 21,000	Macrofossils, Insects	Höfle et al. (2000); Goetcheus and Birks (2001); Kuzmina et al. (2008)
18	Goldbottom Creek	63°55′48.0	138°58′12.0	ca. 30,000	Macrofossils, Insects, Tephra	Zazula et al. (2006a)
19	Doll Creek	65°57′00.0	135°56′24.0	16,000-present	Pollen	Ritchie (1982)
20	Bluefish River	67°22′48.0	140°21′36.0	23,000–19,000	Macrofossils, Megafauna, Pollen, Insects	Zazula et al. (2006b)
21	Lucky Lady	63°44′24.0	138°51′36.0	16,500-8000	Pollen, Ground ice isotopes, Insects, sedaDNA, Megafauna, TOC	Mahony (2015); Murchie et al. (2021); Monteath et al. (2023)
22	Jan Lake	63°33′52.7	143°55′03.3	14,500-present	Pollen, LOI, Macrofossils, Tephra	Carlson and Finney (2004); Monteath et al. (2017)
23	Squanga Lake	60°28′48.0	133°38′24.0	11,000-present	Ostracod δ^{18}O, Calcite δ^{18}O, LOI	Lasher et al. (2021)
24	Zagoskin Lake	68°54′00.0	151°18′00.0	>30,000-present	Pollen, Chironomid$_{temp}$, X-ray diffraction, PS	Ager et al. (2003); Kurek et al. (2009a)
25	Hanging Lake	68°21′00.0	138°21′36.0	17,000-present	Pollen, Chironomids	Cwynar (1982); Kurek et al. (2009b)
26	Trout Lake	68°49′48.0	138°45′00.0	16,000-present	Pollen, Chironomids	Irvine et al. (2012)
27	Nimgun Lake	59°33′36.6	160°46′00.2	15,000-present	Pollen	Hu et al. (2002)
28	Lake E5	68°38′24.0	149°27′36.0	30,000-present	Pollen, Charcoal, Biomarkers, δ^2H_{wax}	Vachula et al. (2019); Longo et al. (2020)
29	Birch Lake	64°18′50.2	146°39′57.0	16,000-present	Pollen, MS, LOI	Bigelow (1997); Abbott et al. (2000)
30	Logan Ice Core	60°36′00.0	140°30′00.0	16,000-present	Ice core isotopes	Fisher et al. (2008)
31	Discovery Pond	60°47′24.0	150°50′24.0	15,500-present	Pollen, BSi, MS, LOI	Kaufman et al. (2010)
32	Waskey Moraine Sequence	59°52′12.0	159°12′36.0	ca. 12,500	Geomorphology,^{10}Be	Young et al. (2019)

conditions in central Yukon (Froese et al., 2002; Zazula et al., 2006a).

Anderson and Lozhkin (2001) highlighted chronological issues related to the middle Wisconsin, the beginning of which lies beyond the reliable limit of radiocarbon dating. Trace contamination by modern carbon can cause deposits or faunal remains from earlier in the interval, or even the previous interglacial (MIS5e), to appear finite and be incorrectly ascribed to the later part of the middle Wisconsin (e.g., Zazula et al., 2014). Unsurprisingly, given these chronological limitations, firmly dated deposits from early in the middle Wisconsin are rare. Data from early in the interstadial come largely from lake-sediment records, where marked changes in pollen indicate climate amelioration (e.g., Anderson et al., 1994). These are imprecisely dated, and the continuity of the records is doubtful (Supplementary Text, S4), but they represent rare data from this interval. While pollen-based vegetation patterns remain a major source of information from which to infer past environmental conditions, the age, location and type of deposit affect reconstructions and contribute to inter-site variation. The middle Wisconsin record in eastern Beringia is particularly vulnerable to this source of noise as the total number of sites is low. In contrast, deposits from the latter half of the middle Wisconsin, between 45,000–30,000 cal yr BP, are more extensively studied and have better chronological constraints. The current discussion links key science questions to records with the most dependable chronologies.

3.1.1. *Middle Wisconsin environments ca. 57,000-45,000 cal yr BP*

Yedoma exposures at Upper Goldbottom, Lower Hunker and Upper Hunker in Klondike, Yukon, preserve sediments that older than 50,000 cal yr BP (the limit of radiocarbon) which very likely date to early in the interstadial (Mahony, 2015). The deposits include woody macrofossils and large ice wedges, indicating an open forest environment and continuous permafrost. They preserve abundant *in situ* fossils of horse and particularly steppe bison. The large ice wedges indicate higher moisture availability than overlying late Wisconsin (MIS2) deposits in which ice wedges are rare. Together, the available data are indicate warmer and wetter conditions compared with the early and late Wisconsin intervals, but cooler than today.

Several long lake-sediment records in eastern Beringia probably cover the whole middle Wisconsin, but their imprecise chronologies limit their interpretations. Comparison between these records and Lake El'gygytgyn in Chukotka (Brigham-Grette et al., 2007; Lozhkin et al., 2007), which preserves a continuous record from MIS5 to the present, suggests that hiatuses exist in the long Alaskan lake records, coinciding with MIS2 (and possibly MIS4) aridity (for more detail see Supplementary text, S4). Only two lakes in northwest Alaska, Squirrel Lake and

Joe Lake (Berger and Anderson, 2000; Anderson et al., 1994), appear to contain long middle Wisconsin records preceded by older MIS stages (MIS4 at Joe and back to MIS 5/6 at Squirrel). During the middle Wisconsin, *Betula* pollen values at both sites exceed 10 % and are as high as 40 % at Joe Lake (Fig. S1). These values, allowing for the relative over-abundance of *Betula* pollen compared with many other taxa (see sect. 2.0), indicate that birch shrubs formed part of the tundra vegetation in northwest Alaska in the earlier part of the middle Wisconsin. *Salix* was also present but, notably, *Alnus* was virtually absent, suggesting moisture levels were lower than during the Holocene.

3.1.2. Middle Wisconsin environments ca. 45,000-30,000 cal yr BP

Between 45,000–30,000 cal yr BP, sites at higher elevation and north of the Brooks Range record a form of shrub tundra, albeit one with a lower proportion of *Salix* and *Betula* pollen and more herb pollen than is typical for most modern and deglacial (ca. 15,000–10,000 cal yr BP) shrub tundra. The northernmost record, an exposure of yedoma and peat deposits on the Itkillik River (North Slope), was dated to ca. 34,000 cal yr BP and yielded herbaceous pollen assemblages. High *Picea* and *Pinus* inputs to this site were almost certainly from long-distance transport (Lapointe et al., 2017). At Burial Lake (~900 m elevation) between ca. 40,000 and 35,000 years ago, the vegetation was tundra, with a lower proportion of *Salix* and *Betula* pollen (*Betula* 5–10 % and *Salix* ca. 10 %) and more herb pollen than most modern shrub tundra (Abbott et al., 2010, Fig. 3). South of the Brooks Range, the lower-elevation sites Squirrel Lake and Joe Lake (see above) maintained *Betula-Salix* tundra into the later middle Wisconsin. In the far west, taberal yedoma sediments (i.e., thawed by an overlying lake, but not lacustrine) on Seward Peninsula dating between 33,000 and 31,000 cal yr BP show *Betula* and *Salix* of values < 10 % and dominance of Poaceae and Cyperaceae (Wetterich et al., 2012). Collectively, these data indicate that in northern and western Alaska shrub tundra, or herb tundra with or without sparse shrubs, characterized the latter part of the middle Wisconsin.

In Yukon, woody macrofossils are present in Klondike until around 36,000 cal yr BP suggesting the presence of shrub tundra (Mahony, 2015). Conversely, the radiocarbon-dated remains of black-footed ferrets (*Mustela nigripes*) and (likely) steppe ferret (*Mustela eversmanni*) indicate that grassland environments were also present in the region during the middle Wisconsin (Youngman, 1994). The absence of middens of arctic ground squirrel (*Urocitellus parryii*) prior to ca. 35,000 cal yr BP suggests that active layers were shallower than the following late Wisconsin cold stage (see 3.2.2.) as these animals require thaw depths of 0.9–1.0 m to burrow (Zazula et al., 2007).

In interior Alaska, near Fairbanks, valley-fill deposits from Isabella Basin contain woody plant remains dated to 36,700–35,970 cal yr BP (Matthews, 1974b; original radiocarbon dating replicated with AMS by Elias, 2000) provide evidence for valley-bottom evergreen boreal forest at this time. *Picea* contributes around 20 % of the pollen sum, and macrofossils show that arboreal birches (*Betula neoalaskana*) were growing locally. Matthews (1974b) interpreted the palaeoecological data as representing vegetation similar to present-day taiga but suggested local treeline elevations were lower than today. Within the watershed of Eightmile Lake, near modern treeline in the Nenana Valley, geochemical and sedimentological analyses of a permafrost core that has an earliest age of >35,000 cal yr BP show high carbon content, woody macrofossils and high ice content near the base. Carbon content declines markedly by 30,000 cal yr BP indicating lower productivity and colder/more arid conditions (Hutchings et al., 2019). The basal part of a sediment core from Harding Lake (Nakao and Ager, 1985) contains pollen of *Picea*, *Betula*, Ericales and Cyperaceae (but little *Alnus*), dated to >31,000 cal yr BP. However, Finkenbender et al. (2014) found no evidence of forest conditions at the base of their ca. 30,000-yr core as reported by Nakao and Ager (1985), and they note that the age of this material may be insecure, given there is a dating reversal in the original core. Furthermore, the sediment package likely varies across this large and complex lake basin. Given other data from interior Alaska (see above), a forested interstadial record at Harding Lake is possible but requires further investigation.

The Cold Regions Research and Engineering Laboratory (CRREL) Permafrost Tunnel complex near Fairbanks includes 500 m of excavated tunnels that dissect middle Wisconsin deposits; these are radiocarbon-dated to between 45,000 and 30,000 cal yr BP (Sellmann, 1967, 1972; Hamilton et al., 1988; Long and Péwé, 1996; Kanevskiy et al., 2022). Basal gravels are overlain by yedoma silt with large ice wedges and, in places, evidence of thermokarst. Pollen and insects from near the base of the silt indicate a dry, open meadow that contained herbs and some shrubs (graminoids 61 %, *Betula* 18 % and *Alnus* 9 %). Higher in the silt unit, truncated ice wedges are associated with more varied pollen and insect assemblages that include both mesic and xeric taxa. This unusual assemblage is interpreted as evidence for diverse, open meadow micro-habitats amongst active ice-wedge polygons (Hamilton et al., 1988). Wooller et al. (2007, 2011) describe a frozen land surface from another location within the tunnel, radiocarbon-dated to ca. 36,000 cal yr BP (consistent with other dating from the tunnel complex; e.g., Kanevskiy et al., 2022). Its vegetation and insect communities were similar to those described by Hamilton et al. (1988): graminoids (Cyperaceae and Poaceae) represent 70 % of the pollen assemblage and forbs are also important (Wooller et al., 2011). Fossil insects indicate both mesic and xeric conditions. Both vegetation records indicate trees are unlikely to have been present locally. Low abundances of pollen of *Betula*, *Picea*, and *Alnus* may represent sparse, more distant stands of woody vegetation, but may also be derived from reworking or older loess deposits (Hamilton et al., 1988; Wooller et al., 2011). Curiously, the landscape and vegetation reconstructed at this locality differ from that of the Isabella Basin, though the two localities are only 6 km apart and separated by 45 m in elevation. This may reflect chronological ambiguity in both profiles as it is unlikely either preserves a continuous record of the long (57,000–30,000 cal yr BP) middle Wisconsin, during which vegetation may have varied substantially. Alternatively, forest cover towards the end of the interstadial may have been spatially limited, perhaps confined to the larger river-valley systems, such as the Chena and Tanana drainage, which includes Isabella Basin.

Mesic taxa and evidence of thermokarst in the permafrost tunnel silt have been used to infer a climate optimum at the end of the middle Wisconsin (35,000–30,000 yr BP), termed the “Fox thermal event” (Hamilton and Fulton, 1990; Begét, 1990; Anderson and Lozhkin, 2001). The timing of this suggested climate optimum is inconsistent with other evidence (see below), which suggests cold-stage conditions by 30,000 cal yr BP, and it occurs during an interval of declining summer insolation and low atmospheric CO_2 (Berger and Loutre, 1991; Bereiter et al., 2015). New radiocarbon dates from macrofossils trapped within epigenetic, thermokarst-related cave ice place the period of thaw to no later than 35,000 cal yr BP (Kanevskiy et al., 2022). This older date is easier to reconcile with wider palaeoenvironmental and climate evidence. It may be, however, that the formation of thermokarst cave ice was related to local gully erosion caused by spring snow melt, which does not require a climate-based explanation (Shur et al., 2004; Bray et al., 2006).

3.1.2.1. Middle Wisconsin climate ca. 45,000–30,000 cal yr BP. Given that MIS3 is identified as a global period of interstadial conditions in ice-core and marine records and is a period of moderate summer insolation values in the Northern Hemisphere (Fig. 3), a key question concerns the extent of temperature amelioration and the level of aridity in eastern Beringia. MIS3 has an unusual insolation progression, with lower-amplitude summer optima compared with previous interglaciations such as MIS5 and MIS7 (Berger and Loutre, 1991, Fig. 3). It is therefore likely that the summer insolation optimum caused only modest warming. Well dated temperature estimates are rare for the middle Wisconsin in eastern Beringia. One source of quantitative temperature estimates that has been widely undertaken is based on fossil beetle assemblages (Elias, 2000, 2013). Values are established using the mutual climatic

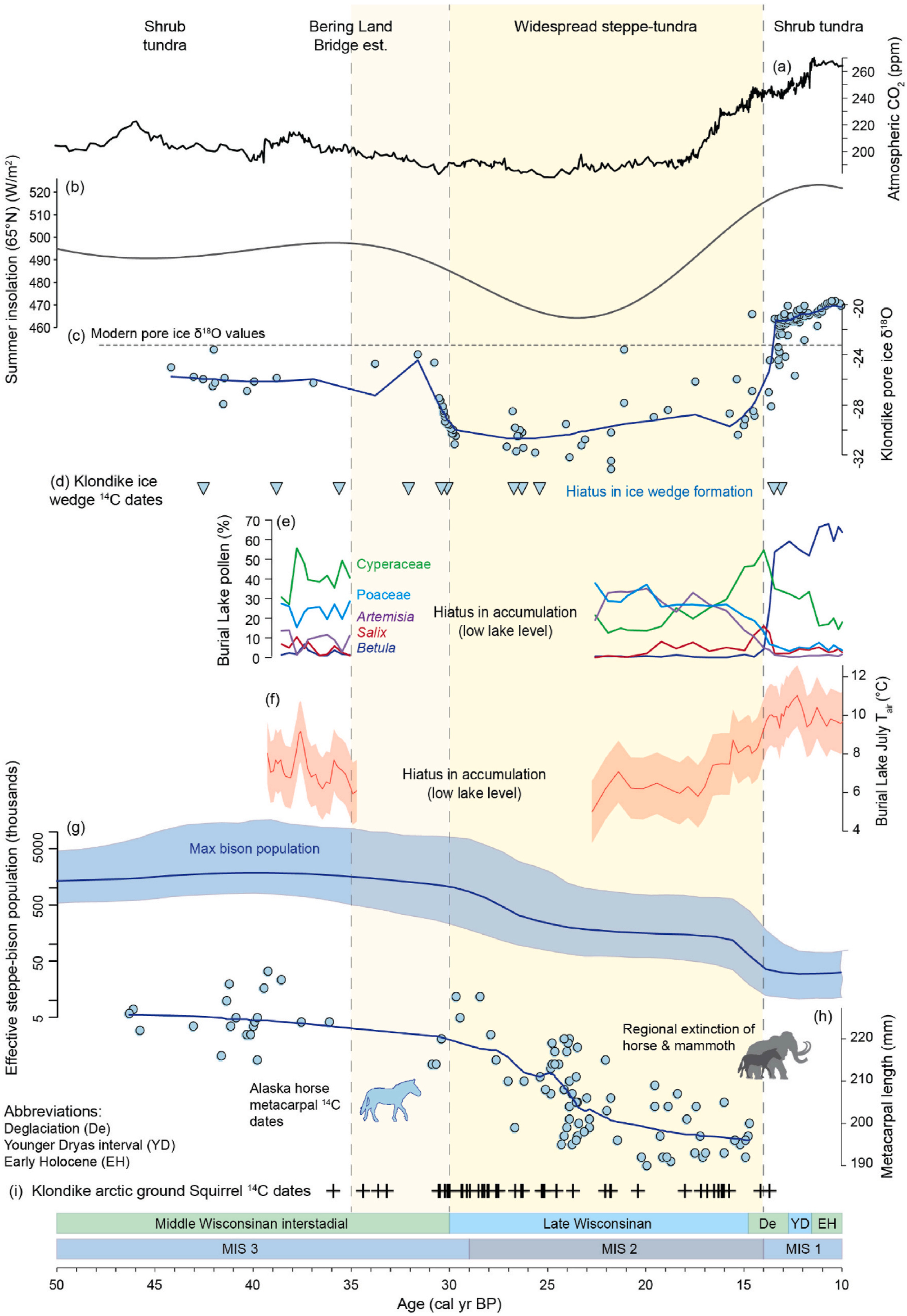

Fig. 3. (a) Atmospheric CO$_2$ concentrations (Bereiter et al., 2015). (b) Summer insolation at 65°N (Berger and Loutre, 1991). (c) Klondike pore ice $\delta^{18}O$ values (Mahony, 2015). (d) Klondike radiocarbon-dated ice wedges (Mahony, 2015). (e) Burial Lake pollen (Abbott et al., 2010). (f) Burial Lake chironomid July T$_{air}$ reconstruction (Kurek et al., 2009a). (g) Bison DNA skyline population estimate (Faulkner et al., 2020). (h) Radiocarbon-dated horse metacarpal measurements (Guthrie, 2003). Woolly mammoth and horse extinction dates are based on radiocarbon dating (Guthrie, 2003, 2006; Mann et al., 2013). (i) Klondike radiocarbon-dated arctic ground squirrel nests (Mahony, 2015).

range technique, which has been shown by later research to be subject to statistical biases (Bray et al., 2006). Furthermore, estimates are typically from samples with only a single associated radiocarbon date. These uncertainties notwithstanding, in assemblages that have been re-dated with AMS radiocarbon dating, a consistent pattern points to summer temperatures being lower than present during the middle Wisconsin, probably by several degrees (Elias, 2000, 2013). Further evidence for cool middle Wisconsin temperatures relative to the Holocene comes from Burial Lake, northwest Alaska. A chironomid-based temperature reconstruction from the site indicates that summer temperatures were ~4 °C lower than modern values between 40,000–35,000 cal yr BP (Kurek et al., 2009a).

The presence of shrub tundra and (probably) scattered forest during the middle Wisconsin indicates that effective moisture was higher than the preceding and following cold stages, when woody vegetation was largely absent and herbaceous vegetation dominated (Sanborn et al., 2006; Zazula et al., 2003, 2007, 2011). However, the scarcity of *Alnus* in most records suggests that conditions were drier than those of the moist Mid- and Late Holocene, when it was abundant and widespread. Furthermore, during the late Wisconsin, alpine glaciers in the Brooks Range retreated and ice-wedge formation ceased in areas of central Yukon, despite falling temperatures, indicating reductions in effective moisture (Briner and Kaufman, 2008; Mahony, 2015). Effective moisture changes are also evident in the lithostratigraphy of a sediment-core transect taken at Burial Lake, where relatively high lake levels at ca. 37,000 cal yr BP were followed by a major lowering of lake level between ca. 32,000 and 26,000 cal yr BP (Finkenbinder et al., 2015), shortly after the establishment of the Bering Land Bridge ca. 35,000 cal yr BP (Farmer et al., 2023). Fluctuating aeolian input to Burial Lake from ca. 36,000 cal yr BP implies variable aridity, at least seasonally (Dorfman et al., 2015). The combined data indicate moderately high P-E values and moderate temperatures throughout the middle Wisconsin, compared with lower P-E and cooler temperatures during the full glacial interval.

3.1.2.2. Climate variability. Ice, marine and terrestrial records in the North Atlantic region and North Pacific indicate that high-amplitude, short-term changes in climate occurred throughout MIS3 (e.g., Dansgaard et al., 1993; Rasmussen et al., 2014; Walczak et al., 2020). Well dated marine cores taken off southeast Alaska show episodes of ice-rafted debris deposition over the past ~40,000 years (Walczak et al., 2020). The record indicates multiple discharges of fresh water and ice into the North Pacific, at 18,000–17,000, 27,000–25,000, 30,500–29,500 and 42,000–39,500 cal yr BP, that appear to precede North Atlantic Heinrich events. Whether these rapid ocean oscillations affected eastern Beringian environments remains an open question.

Most regional palaeo records do not span sufficient intervals to identify MIS3 climate oscillations, and long lake-sediment cores do not show marked fluctuations (e.g., Joe Lake, Anderson et al., 1994; Fig. S1). The pore-ice isotopic record from yedoma deposits in Yukon (Mahony, 2015) does indicate minor summer temperature fluctuations between 45,000–30,000 cal yr BP. However, this record is of low resolution (centennial to several millennia; Fig. 3) and is derived from multiple sampling localities, each of which has site-specific influences on pore ice $\delta^{18}O$ values. As a result, it remains difficult to discern middle Wisconsin climate variation.

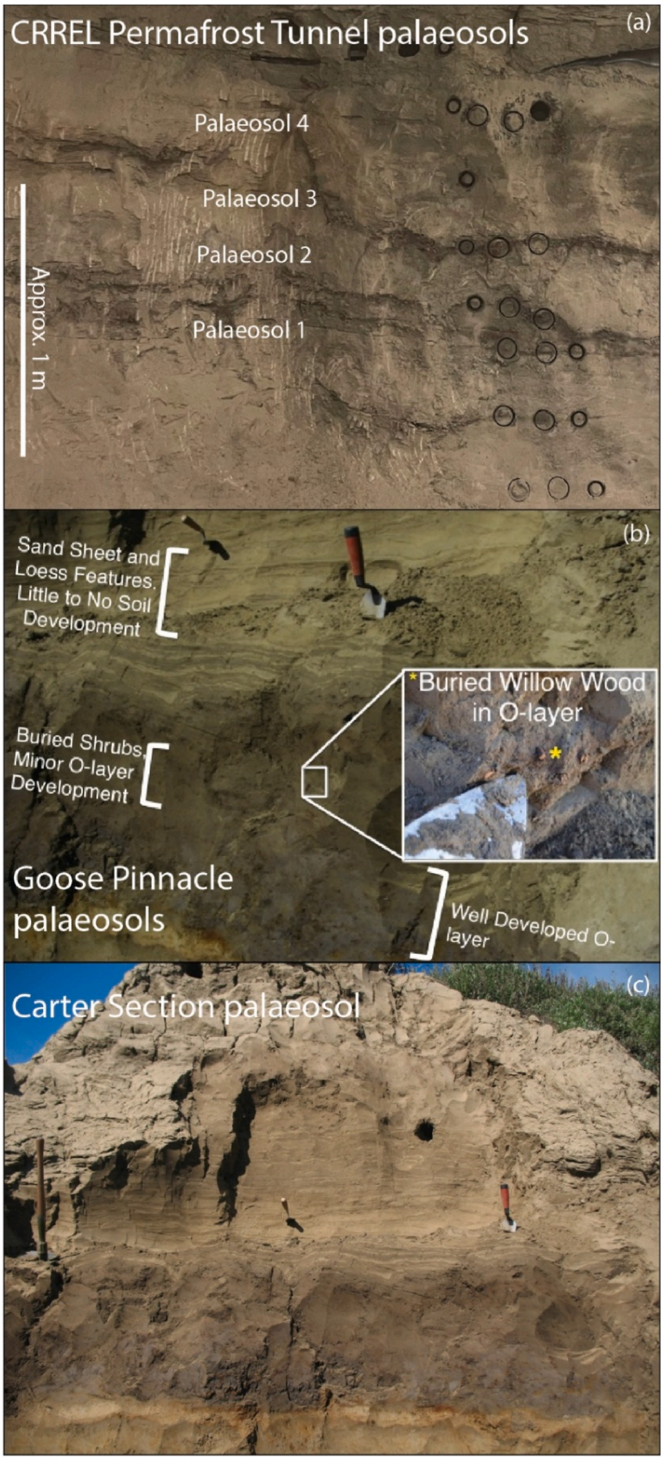

Fig. 4. (a) Alternating formation of palaeosols and loess in the CRREL permafrost tunnel. These date to ~45,000–30,000 cal yr BP and are typical of middle Wisconsin palaeosols preserved in the tunnel (photo credit: Duane Froese). (b) Palaeosol from the Goose Pinnacle Section (photo credit: Ben Gaglioti). (c) Middle Wisconsin palaeosol from the Carter Section (photo credit: Ben Gaglioti).

The strongest regional evidence of rapid environmental oscillations within the middle Wisconsin comes from well dated sequences of aeolian deposits on the Alaska North Slope (Gaglioti et al., 2018). The Carter Section along the Titaluk River includes three alternations of palaeosols and loess, particularly prominent between ca. 36,300 and 32,600 cal yr BP and showing ca. 1000-yr periodicity (Fig. 4). A more subtle alternation of plant-rich (including shrubs) and more minerogenic layers is evident higher in the section, with plant-rich layers dated to ca. 32,500 and 28,500 cal yr BP and occurring at a similar temporal rhythm into the late Wisconsin. While at any one locality, such patterns may reflect local changes in sediment supply, Gaglioti et al. (2018) suggest a match to palaeosol sequences in Tanana valley loess in interior Alaska dated to 39,000–36,000, 35,500–33,700 and 33,500–31,500 cal yr BP (Hamilton et al., 1988; Begét et al., 1990; Berger, 2003; Muhs et al., 2003, as cited by Gaglioti et al., 2018, Fig. 4). While these warm-wet episodes of pedogenesis, ice-wedge degradation and woody plant expansion may correspond with North Pacific ice-rafting events (Walczak et al., 2020) or Dansgaard-Oeschger events known from the North Atlantic (Svensson et al., 2008), demonstrating this requires higher-precision chronologies than are currently available from these sites.

The scarcity of evidence for MIS3 climate oscillations in eastern Beringia may indicate a regional insensitivity to ocean climate drivers. However, two sites in western Beringia suggest that the climate oscillations affected terrestrial environments. At Grand Lake (Elikchan-4), shifts in pollen, mirrored by marked changes in sediment properties (Minyuk and Subbotnikova, 2021), show vegetation varied between open and woody communities, which Lozhkin and Anderson (2011) hypothesised were a response to changes in North Pacific sea-surface temperatures and eustatic sea level. Further high-resolution pollen data at Lake Billyakh in the Lena River watershed (Müller et al., 2010) also show short periods of *Larix* and shrub dominance in an otherwise tundra-dominated sequence. At neither site, however, is the chronology good enough to make direct comparisons with North Atlantic or Pacific Ocean data, and it remains unclear whether these patterns reflect regional or hemispheric climate dynamics.

3.1.3. *The middle Wisconsin to late Wisconsin transition in relation to climatic and regional forcing*

The transition from middle to late Wisconsin and establishment of widespread steppe-tundra vegetation in eastern Beringia coincided with changes in several different hemispheric and regional climatic controls. Summer insolation (65°N), which is a key driver of growing-season conditions in the northern high latitudes, began to decline from ca. 35,000 cal yr BP (Fig. 3), and atmospheric CO_2 concentrations decreased from 40,000 cal yr BP (Bereiter et al., 2015). Changes in these controls coincided with falling sea levels, which exposed greater areas of the Bering Land Bridge (established ca. 35,000 cal yr BP; Farmer et al., 2023), and advances in the Laurentide ice sheet (Mann and Gaglioti, 2024). Both geographic changes are likely to have affected regional environments via shifts in atmospheric circulation and continentality (Bartlein et al., 2014, 2015; Löfverström et al., 2014). Responses could have been gradual or more abrupt, given the range of controls. The timing of observed environmental changes matches the trajectories of the drivers well and suggests eastern Beringia became progressively colder and drier during the millennia between 35,000 and 30,000 cal yr BP (Fig. 3).

In Yukon, the earliest robustly radiocarbon-dated arctic ground squirrel nest indicates that steppe-tundra vegetation and deep active layers were present (at least locally) from ca. 35,000 cal yr BP (Zazula et al., 2003, 2007). The nest lies beneath Dawson tephra, at Upper Goldbottom in Klondike, and is chronologically consistent with under- and overlying macrofossil radiocarbon dates in the sequence (Mahony, 2015). A composite Klondike pore-ice δ^{18}O record, which includes Upper Goldbottom, indicates that a substantial shift in atmospheric conditions had occurred by ca. 30,000 cal yr BP (Fig. 3), several thousand years after the local establishment of steppe-tundra (Mahony, 2015). This age divergence may represent variation in the progress of hemispheric and regional forcing factors through time. For example, Zazula et al. (2006b) and Monteath et al. (2023) hypothesise that the climate of central Yukon was strongly influenced by the Cordilleran-Laurentide ice sheet complex during the late Wisconsin. An extensive ice sheet can alter atmospheric circulation patterns, enhancing aridity in eastern Beringia via a diversion of jet-stream flow; it can also exert a cooling effect on areas adjacent to its margin (Bartlein et al., 1991; Löfverström et al., 2014). The exact status of the Cordilleran-Laurentide ice sheet complex at this time is poorly constrained (Pico et al., 2017; Gowan et al., 2021; Mann and Gaglioti, 2024), but the step change to lower pore-ice δ^{18}O values could reflect the onset of either a circulation effect or a proximity effect. Numerous arctic ground squirrel nests containing plant macrofossils, fossil insects and *seda*DNA typical of steppe-tundra date to ca. 30,000 cal yr BP and show that herbaceous vegetation was widely established by this time (Zazula et al., 2003, 2006a, 2007; Langeveld et al., 2018). It is likely that by 30,000 cal yr BP all the forcing mechanisms were driving cooling and drying, leading to growing conditions that favoured the expansion of steppe-tundra.

In Alaska, evidence for the middle Wisconsin – late Wisconsin transition is observed in loessal and lake-sediment records. At Arolik Lake (SW Alaska), proxies for aquatic productivity (OM, Bsi, C/N and δ^{13}C; closely linked with spring/summer temperatures) began to decline from ca. 33,000 cal yr BP (Kaufman et al., 2003). Steppe-tundra vegetation was present at Harding Lake before ca. 30,000 cal yr BP (Finkenbinder et al., 2014). Regional hydrology also shifted towards aridity, with a declining lake level at Burial Lake by ca. 35,000 cal yr BP (Finkenbinder et al., 2015) and a low stand at Harding Lake between 30,000 and 20,000 cal yr BP (Finkenbinder et al., 2014). Increased aridity is also indicated by magnetic susceptibility profiles from the Halfway House and Gold Hill loess exposures that show gradually declining trends from the later middle Wisconsin into the late Wisconsin, which Jensen et al. (2016) attribute to increasing wind intensity. This interpretation is consistent with evidence for increasing aeolian deposition at Burial Lake from ca. 36,000 cal yr BP (Dorfman et al., 2015).

3.1.4. *Middle Wisconsin summary*

The middle Wisconsin appears to have been a climatologically intermediate interval, having been cooler, drier and dustier than the Holocene, and yet both mesic and warm enough to have supported a diverse vegetation mosaic including shrub tundra and some woodland along major rivers. Tantalizing evidence of high-frequency climate variability in aeolian deposits, possibly matching those that characterize the higher northern latitudes in the Pacific or Atlantic/European sectors, invites further detailed investigation of continuous sediment archives, such as older lake basins and loess (yedoma) deposits. The shift towards full-glacial conditions occurred between 35,000–30,000 cal yr BP, although an abrupt shift in pore-ice δ^{18}O measurements from Yukon ca. 30,000 years ago may reflect a threshold linked with the growth of the Cordilleran-Laurentide ice sheet. Overall, the 30,000 cal yr BP date of Hopkins (1982) for the transition to the late Wisconsin and full-glacial conditions is largely supported by newer data and lies close to the MIS3-MIS2 transition defined by the marine isotope stack at 29,000 cal yr BP (Lisiecki and Raymo, 2005). Nevertheless, two decades since Anderson and Lozhkin (2001) summarised evidence on the middle Wisconsin, firm knowledge of the early part of the interstadial is still lacking, highlighting the continuing problem of attributing ages to deposits beyond the limit of radiocarbon dating.

3.2. *The late Wisconsin steppe-tundra biome*

For many, the cold-stage conditions of late Wisconsin Beringia and other unglaciated northern regions are the epitome of the “ice-age”. This interval includes the Last Glacial Maximum (LGM; ca. 25,000–17,000 cal yr BP) and has captured the attention of Beringian scientists, largely because of its close association with the grazing megafauna. But for this connection, the herb-dominated vegetation might not have received much attention; however, the nature of past interactions among herbivores and flora remains a palaeoecological puzzle relevant to contemporary ecology and conservation (Nagaoka et al., 2018). Information about ecosystem structure and function comes from pollen, plant macrofossils, plant *seda*DNA, vertebrate fossils and faunal aDNA. A largely missing piece of this puzzle is the effective quantification of both the mammalian population size and the vegetation biomass (productivity), which has led to quite different interpretations of this ancient ecosystem. Several terms are applied to this debate; commonly used examples are given in Table 4.

In early work, palynologists such as Colinvaux (1964) envisioned late Wisconsin vegetation as grassy, but unproductive, tundra. This interpretation became modified by the need to reconcile the presence of

Table 4
Vegetation terminology used in late Wisconsin steppe-tundra (mammoth steppe) discussion.

Term	Definition as used in this discussion
Tundra	Climate primarily too cold for trees. Forbs, grasses and shrubs present, or shrubs lacking.
Steppe	Climate primarily too dry for trees (temperate zone); grasses and forbs present.
Steppe-tundra	Cold and dry climate. Treeless vegetation with floristic elements of both steppe and tundra (Hibbert, 1982).
Tundra-steppe	As above; preferred by some authors.
Boreal steppe	Localised dry conditions preclude boreal trees; rare plant community with grasses and forbs present (Edwards et al., 2018).
Subarctic steppe	As above; preferred by some authors.
Mammoth steppe	Term linking megafauna and Pleistocene vegetation: grass-dominated vegetation and its fauna; an extinct biome (Guthrie, 1968, 1982).

megafauna with apparently limited vegetation biomass; termed the productivity paradox (as discussed in papers in Hopkins et al., 1982). Guthrie (1982, 1990b, 2001) described eastern Beringia as part of an extensive, largely treeless biome that stretched westward to Europe across unglaciated regions of Eurasia, which he termed “mammoth steppe”. Both Guthrie (1982, 1990b, 2001) and Schweger (1982) discussed the vegetation as a mosaic resulting from variations in topography, soil, and local climate, as did authors studying Asian plant communities (Yurtsev, 1982; Chytrý et al., 2019). While productive vegetation patches may have been scattered across the landscape, the very extent of this biome suggests resources would have been adequate for a highly mobile megafauna (e.g., Mann et al., 2013; Wooller et al., 2021). Unfortunately, the term mammoth steppe is often used to imply an extensive prairie-like grassland that overlooks important tundra elements of the palaeofloras (see below).

3.2.1. Palaeovegetation data

Pollen assemblages are the most abundant data type and underpin the reconstruction of late Wisconsin vegetation. They are dominated by three herbaceous groups: Poaceae (grasses) and Cyperaceae (sedges), which are collectively termed graminoids, and *Artemisia*. Graminoids are accepted as major components in many steppe and tundra communities while *Artemisia,* a large genus with many representatives in steppe communities, is sometimes interpreted as a steppe indicator (Birks, 2003), although it also occurs in tundra (Colinvaux, 1964; Chytrý et al., 2019). Based on modern ecological affinities of associated minor pollen taxa, the terms “tundra-steppe” or “steppe-tundra” became widely adopted, initially by Russian palynologists and botanists, to reflect the unusual, floristically mixed composition of the vegetation (Hibbert, 1982). Perhaps unsurprisingly, modern regional pollen assemblages across Alaska-Yukon have few close matches, underlining the “no-analogue” status, at least palynologically, of the vegetation (Anderson et al., 1989). Poor pollen analogues among most of today’s treeless plant communities likely reflect higher available moisture levels compared with the arid conditions of the late Wisconsin (Barber and Finney, 2000), and the ubiquitous, widely dispersed pollen of woody taxa such as *Picea* and *Betula* that masks the signal of local open vegetation (Binney et al., 2011).

Much of the uncertainty regarding the nature of steppe-tundra vegetation stemmed from the abundance of *Artemisia* in pollen records; was the late Wisconsin vegetation closer to steppe or tundra? In northern Asia today, *Artemisia* produces much more pollen than grasses (Cao et al., 2019), meaning that it is over-represented in pollen rain spectra compared with its actual contribution to biomass. Therefore, its presence at a site may mostly or entirely be derived from long-distance transport from steppe regions (Colinvaux, 1964). Macrofossil data, and more recently *sed*aDNA data, from easternmost eastern Beringia now confirm the late Wisconsin presence of *Artemisia frigida*, a widespread, disturbance-tolerant species that occurs today in boreal and temperate steppe (Zazula et al., 2003, 2006; Murchie et al., 2021). Given the genus was present, pollen spectra probably reflect vegetation with both tundra and steppe characteristics, as suggested by the diverse set of minor taxa, which are largely forbs (e.g., Ager, 2003).

Over the past two decades, plant macrofossil and *sed*aDNA studies have added further detail on the identity of late Wisconsin taxa. *Sed*aDNA data from yedoma exposures in Klondike, Yukon (Murchie et al., 2021), and a lake-sediment profile from interior Alaska (Clarke et al., 2024) show grass-forb dominance and include taxa typical of tundra communities (e.g., *Eritrichium*, *Bistorta vivipara*, *Hedysarum*, *Saxifraga*, *Papaver*) as well as those that are also found in boreal steppe today (e.g., *Potentilla*, *Anemone patens*, *Astragalus*), and the group Anthemideae, which includes *Artemisia*, and grasses such as *Bromus pumpellianus*, *Puccinellia*, and *Festuca*. *Salix* is present, uniquely among shrubs. Across Eurasia, *sed*aDNA assemblages of late-Wisconsin age are also consistently dominated by grasses and forbs (Willerslev et al., 2014; Wang et al., 2021). While forb abundance might partly (but not entirely) reflect *sed*aDNA representation or processing bias (e.g., Yoccoz et al., 2012), these records argue against grasses being ubiquitously dominant and indicate a far more important role for forbs; probably at least equal abundance. Notably, many decades previously, Ritchie (1982) studied pollen representation (see above) in northern Yukon and inferred forb-dominated vegetation from a detailed pollen record.

Arctic ground-squirrel middens are an exceptional source of ecological data. Midden materials, faecal pellets and food caches contain macrofossils, aDNA and insect remains (Zazula et al., 2003, 2007; Gaglioti et al., 2011; Langeveld et al., 2018; Cocker et al., 2025). The presence of ground squirrels also indicates warm summer soil conditions and a locally deep (0.9 m) active layer (Zazula et al., 2007). While these features seem inconsistent with palaeoecological and geomorphic evidence for colder climates during the late Wisconsin, Guthrie (1984, 2001) outlined several mechanisms to reconcile the data. Under arid, windy conditions, limited snowfall would have been unevenly distributed, leaving snow-free or thinly covered areas (as occur today in western Beringia on steep, windy, south-facing slopes; D. I. Berman, pers. comm. 1992). Coupled with low cloud cover, and in the absence of waterlogged organic soils, soil temperatures could warm rapidly in Spring, creating a deep active layer (Baughman et al., 2015). Fossil remains of the endemic thermophilous weevil (*Connatichela artemisiae*; see below) which today is only found on dry, south-facing slopes in Yukon and easternmost interior Alaska and is closely associated with *Artemisia frigida* (see above; Anderson, 1984, 1997), and of saiga antelope (*Saiga tatarica*), which cannot tolerate even moderate snow depth (Harington and Cinq-Mars, 1995), support this hypothesis (e.g., Berman et al., 2011; Monteath et al., 2023).

A few localities provide exceptional snapshots of preserved late Wisconsin landscapes. They record small-scale topographic variation and, possibly, larger-scale differences across eastern Beringia (i.e., closer to tundra in the west and steppe in the east). The Kitluk palaeosol is a vegetated land surface on the Seward Peninsula, Alaska, currently under shrub-tussock tundra, that was buried beneath the Devil Mountain Lake tephra and preserved in permafrost ca. 22,000 cal yr BP (Fig. 5). It is classified as an inceptisol, formed in aggrading loess, with little Ca leaching and an active layer of about 50 cm (Höfle et al., 2000); this indicates cold, dry and seasonally dusty conditions. A diverse macrofossil flora represents heterogeneous local communities (Goetcheus and Birks, 2001). At some localities the surface is hummocky, suggesting strong frost action, and inter-hummock crevices contained prostrate willow (*Salix arctica*; estimated at 30–50 % ground cover). Otherwise, the vegetation comprised forbs (estimated at 25–40 % ground cover), graminoids (estimated at 30–50 % ground cover; *Kobresia myosuroides* often dominant), and diverse bryophytes (estimated at 60–70 % ground cover; Fig. 5). Numerous rodent droppings attest to small-mammal activity. Fossil insects from beneath the tephra are consistent with the vegetation assemblage and include *Lepidophorus lineaticollis*, a weevil

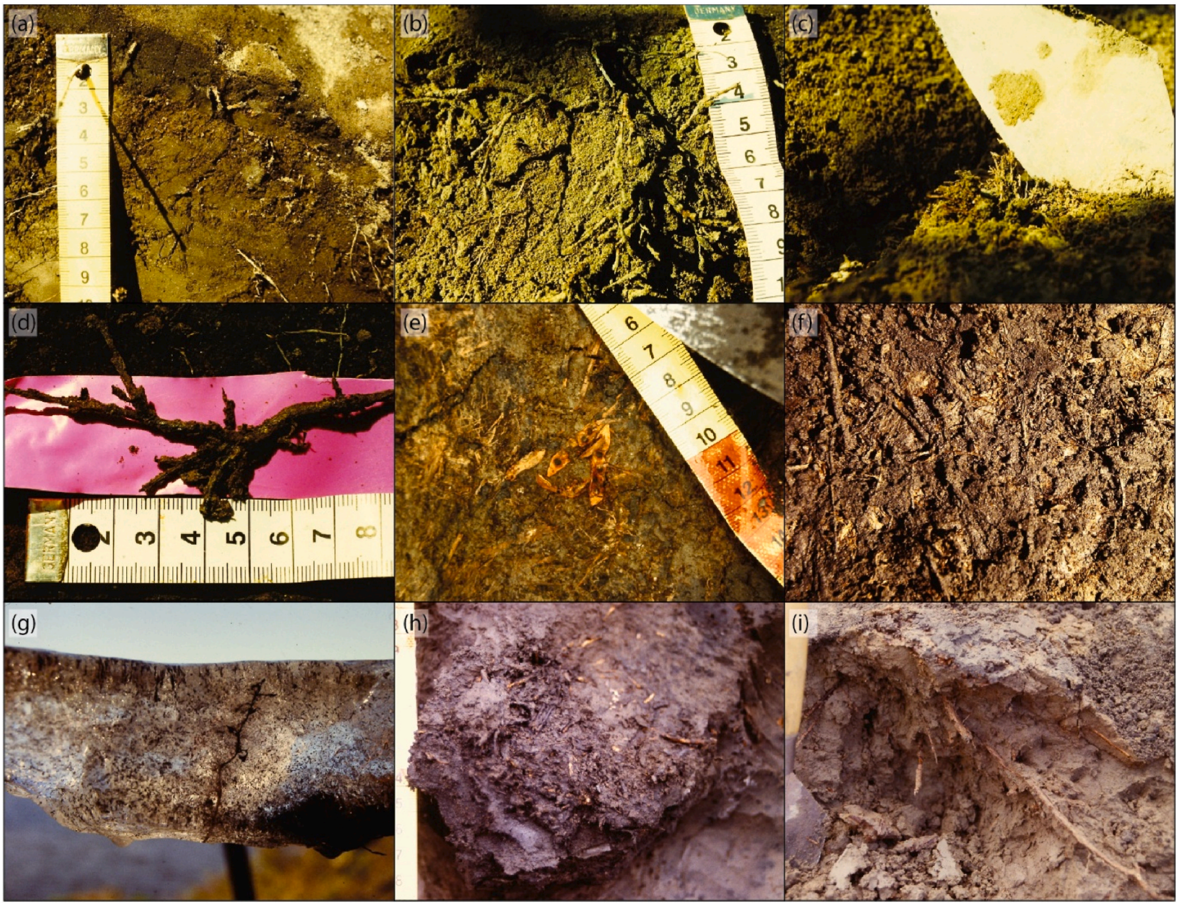

Fig. 5. Hummocky buried land surface of the Kitluk palaeosol preserving prostrate willow and a sedge tussock. Photo credit: Claudi Thompson.

closely associated with steppe-tundra vegetation and contemporary south-facing tundra slopes with dry, warm soils, and *Morychus* spp., a pill-beetle linked with *K. myosuroides* (Kuzmina et al., 2008). The ecological assemblage is consistent with the sedimentological interpretation for a dry, calcareous tundra, based on the abundance and ecology of the tundra forbs, but the biomass remains uncertain. The prostrate *Salix* here and the presence of *Salix* in *sed*aDNA records from yedoma indicates willow was part of the upland flora (not just limited to watercourses), which is a strong tundra signal.

An older *in-situ* vegetation assemblage lies immediately beneath Dawson tephra at Goldbottom Creek, Yukon (29,060–29,470 cal yr BP; Zazula et al., 2006a; Davies et al., 2016). It documents local-scale vegetation heterogeneity related to slope and drainage. Macrofossils reveal a graminoid-dominated, riparian community (e.g., *Alopecurus*, *Carex* spp.) with *Equisetum* and bryophytes. In contrast, macrofossils from nearby arctic ground squirrel middens located in loess on interfluves include taxa found in contemporary boreal steppe and/or open, dry or disturbed habitats (e.g., *Anemone patens* var. *multifida*, *Phlox hoodii*, *Plantago* cf. *canescens*, *Artemisia frigida*) and grass genera such as *Elymus* and *Festuca*. Other taxa are more typical of tundra (e.g., *Bistorta vivipara* and *Draba*) are also present. These macrofossils are similar to those identified in two middens collected near Fairbanks, interior Alaska, dating to ca. 21,500 cal yr BP (Gaglioti et al., 2011). Macrofossils included steppe-adapted forbs (*Phlox hoodii* and *Bupleurum triradiatum*), graminoids (*Bromus pumpellianus* and *Hordeum* spp), and tundra graminoids and forbs. Notably, *Salix* and *Betula* spp. are absent from this flora.

At the Lucky Lady placer gold mine, Yukon, a series of permafrost exposures (Murchie et al., 2021; Monteath et al., 2023; Cocker et al., 2025) with low pore-ice δ^{18}O values (Fig. 3) preserve *sed*aDNA, pollen and insect assemblages that indicate hyper-aridity in easternmost Beringia ca. 16,500 cal yr BP. Notably, Poaceae pollen values are low (<5 %) whereas *Artemisia* values are high (42–54 %). This contrasts with data from the Kitluk palaeosol where *Artemisia* macrofossils are absent, although *Artemisia* pollen was present at low levels (range 0.3–11.7 %) in all samples analyzed (n = 30) and Poaceae pollen was typically 15–30 % (Goetcheus and Birks, 2001; Goetcheus Wolf, 2001).

3.2.2. *Biogeography of tundra and steppe—the role of climate*

A broader, geographical view of steppe-tundra is as a biome: an extensive, recognizable assemblage of plants, animals, and soils, ultimately determined by climate, but highly variable within the larger whole. Using moisture and temperature gradients as a bioclimatic framework, Kaplan et al. (2003) mapped northern plant communities, as defined by structure and function (Fig. 6), providing a mechanism to explore the climate space of late Quaternary steppe-tundra. Today, tundra has limited net primary productivity (NPP), mainly due to available growing degree-days (GDD). If snow depth is low, most woody taxa except low-growing shrubs such as some *Salix* spp., cannot survive winter cold, consistent with the observation that trees and most shrubs were virtually absent from eastern Beringia during the late Wisconsin. For this reason, the xeric end of a tundra moisture gradient will favour forbs and grasses; with higher moisture, tundra shrubs may be present. Above the NPP threshold for tree growth, boreal forest occurs, with evergreen conifers tending to dominate moister regions and deciduous conifers (e.g., *Larix* spp.) or broadleaves (e.g., *Populus tremuloides*) occurring where climatic or physiological drought is more likely. Under warmer growing seasons but even higher moisture deficits, trees eventually give way to steppe vegetation. Therefore, under dry climates, vegetation varies from grass-forb tundra (lower GDD) to steppe (higher

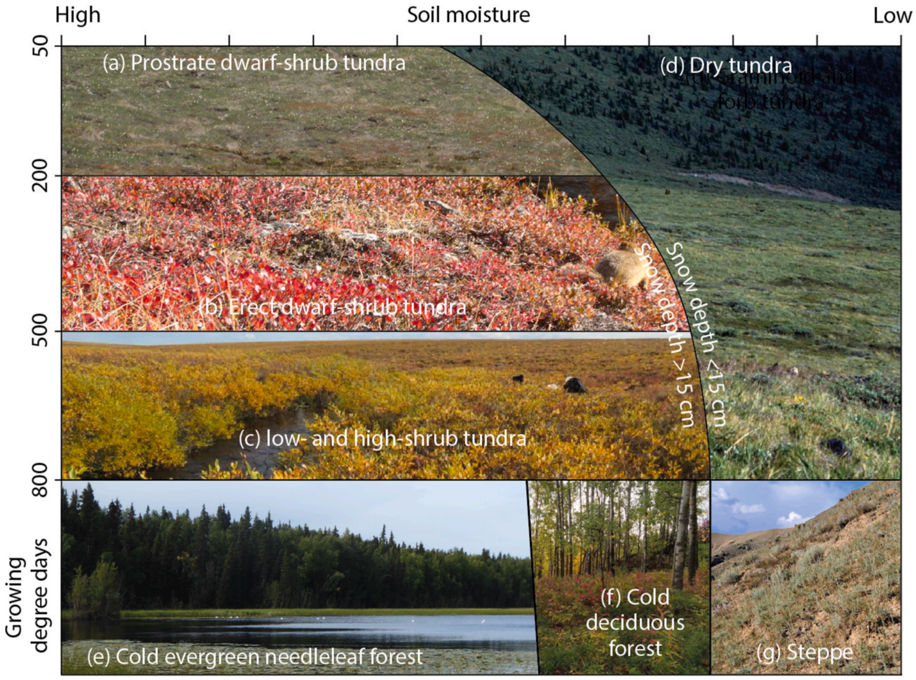

Fig. 6. Bioclimatic scheme of eastern Beringian vegetation after Kaplan et al. (2003), based on soil moisture and growing degree days above 5 °C. Illustrated by modern eastern Beringian vegetation communities located on temperature and soil-moisture gradients related to lat/long, substrate, slope and aspect. Vertical and sloping line indicates the ca. 15 cm snow depth, a critical moisture requirement for shrubs. Horizontal lines indicate approximate temperature-controlled boundaries between vegetation types. Photo credits: Claudi Thompson, Mary Edwards, Scott Armbruster and Ben Gaglioti.

GDD), depending on latitude or elevation. Today, at a local scale, the dry end of the temperature climate gradient reflects a vegetation gradation from dry forms of tundra to steppe (Edwards and Armbruster, 1989; Lloyd et al., 1994; see below). With the absence of a boreal forest barrier at a continental scale, as in the late Wisconsin, admixtures of steppe and tundra species along such a gradient would be expected. Pan-arctic palaeovegetation patterns for 21,000 cal yr BP simulated using a dynamic vegetation model and global palaeoclimate model output (Kaplan et al., 2003) are dominated by treeless vegetation types: forms of tundra, including a dry variant, “grass-forb tundra” related to the cooler and drier part of the moisture gradient, but also “shrub tundra” on the moister end, and steppe (particularly in Asia).

A different perspective on how climate may have affected vegetation relates to the rapid, high-amplitude climate fluctuations evident in the Greenland ice-core records (e.g., Dansgaard-Oescher events; Dansgaard et al., 1993; Maslin et al., 2001), which indicate long-term periods of climate instability in the North Atlantic and European regions. If such instability also affected eastern Beringia, as suggested by Mann et al. (2019), the composition of the steppe-tundra might reflect temporal climate fluctuations at centennial to millennial scales. Large climate swings may have led to the dominance of disturbance-tolerant species with broad niches—taxa with high reproductive rates and good dispersal characteristics. In other words, the steppe-tundra may have been part of a disequilibrial system, rather than one existing under relatively stable, cold, dry climate conditions. Against this hypothesis is the nature of many Arctic taxa: long-lived, often clonal, with long generation times, and limited sexual reproduction (Brochmann et al., 2013). Nevertheless, the hypothesis challenges Beringian Quaternary scientists to demonstrate climate instability occurred in the region during the late Wisconsin and to further define the ecological niches of taxa of the steppe-tundra flora.

3.2.3. Modern vegetation analogues

While there is no widespread modern vegetation type related to cold, dry climate space, as most modern northern tundra regions are moist, at smaller spatial scales elements of contemporary landscapes may provide analogues for the Beringian steppe-tundra. The composition of the steppe-tundra would have varied spatially depending on floristic region and landscape-scale or local controls, as does the modern vegetation of Alaska and Yukon (as well as Eurasia). Potential small-scale analogues from northern regions are azonal patches within the contemporary dominant vegetation formations of boreal forest and moist tundra. At the warmer end of an open-landscape temperature (and productivity) continuum is modern subarctic steppe, typically found on steep, south-facing slopes where local aridity strongly affects soil moisture (Murray et al., 1983; Lloyd et al., 1994; Edwards et al., 2018, Fig. 7). Open grass-forb communities in colder, but dry environments, which contain a mixture of boreal steppe and tundra taxa, are occasionally found at higher elevation (but below treeline) on dry mountain slopes (Edwards and Armbruster, 1989). Dry alpine tundra occurs above treeline (Viereck et al., 1992). In highly continental Siberia, Yurtsev’s (1982) “cryoxeric” communities contain drought-tolerant and cold-tolerant taxa. Exposed, high-elevation fellfields mark the cold, low-productivity end of the continuum (Cwynar, 1982; Ritchie and Cwynar, 1982). While these communities occupy small areas compared with forest and moist tundra today, late Wisconsin variants of these open communities would have likely dominated a treeless vegetation mosaic, as anticipated by both Schweger (1982) and Young (1982). Mountainous central Asia, which lies latitudinally at the southern margin of the treeless steppe-tundra biome, provides a range of high-elevation vegetation analogues at the warm end of the temperature gradient that show floristic gradations between steppe and tundra (Chytrý et al., 2019). Disturbed slopes, dry mountain desert steppe, and steppe (all with bare ground) and dry alpine grassland share overlapping taxa, many genera of which occur in late Wisconsin records.

3.2.4. Non-climatic and “top-down” controls over the steppe-tundra

While it has long been recognized that vegetation-soil communities are influenced by the animals that inhabit them (e.g., Collinson, 1977; Walter, 1979), it has recently been argued that vegetation patterns are inadequately defined by climatic variables alone, and that broader ecosystem dynamics can impose “top-down” controls over vegetation

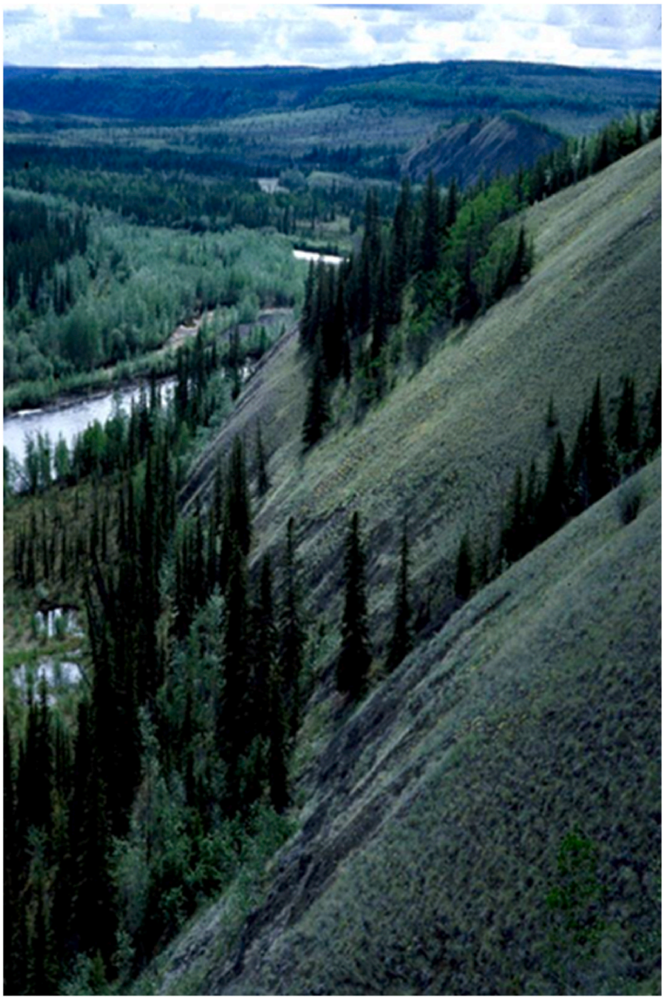

Fig. 7. Patches of boreal steppe amongst boreal forest on steep, south-facing slopes in interior Alaska (photo credit: Scott Armbruster).

composition at a large scale. This is particularly evident in temperate steppe and tropical savanna ecosystems where large herbivore populations still exist (e.g., Moncrieff et al., 2016). In eastern Beringia, megafauna such as woolly mammoth, horse and steppe-bison may have acted as keystone species in the steppe-tundra ecosystem—supporting a floristically diverse and nutritious forage through snow clearance, browsing, trampling and nutrient loading (Owen-Smith, 1987, 1988; Zimov et al., 1995, 2012; Johnson, 2009). Arctic ground squirrels may also have acted as small-scale ecosystem engineers, helping to maintain a floristically rich sward around burrow networks, as they do today on warm, south-facing slopes in northern Alaska and Yukon (Walker et al., 1991; Zazula et al., 2006a; Blinnikov et al., 2011; Wheeler et al., 2013). This view of the steppe-tundra implies that interactions can be disruptive, but also constructive, even mutualistic, with plants and animals to some extent interdependent.

Other indirect controls over vegetation include large-scale nutrient input via loess deposition, fire, and atmospheric composition. In the unglaciated north, loess deposition was a source of nutrient input over large areas during periods of more arid climate (Muhs and Budahn, 2006). Today, localized dust influx is associated with enhanced vegetation productivity and changes in plant community composition (Laxton et al., 1996; Auerbach et al., 1997). Fire is probably underestimated worldwide as a key top-down factor (Bond and Keeley, 2005). In eastern Beringia, the few available late Wisconsin palaeofire records show inconclusive patterns (Higuera et al., 2009; Pautler et al., 2013; Vachula et al., 2019, 2020); the nature and frequency of burning during the cold stage prior to climate amelioration remains a key unanswered question. Finally, low atmospheric CO_2 concentrations (180–220 ppm) that characterised the glacial interval may have interacted with other stressors to influence plant growth (Cowling and Sykes, 1999; Sage and Coleman, 2001; Gerhart and Ward, 2010). The combined effects of aridity and low CO_2 can reduce water-use efficiency and thus growth rates; some studies show substantial growth reduction in C-3 plants at LGM CO_2 levels (Street-Perrott et al., 1997; Prentice and Harrison, 2009). Shifts in C-allocation (i.e., to greater above-ground biomass) and developmental phenology have also been observed (Gerhart and Ward, 2010).

3.2.5. How productive was the steppe-tundra?

Pollen data typically imply low productivity in the steppe-tundra, but megafauna remains require productivity to have been high enough to support large mammals (Colinvaux and West, 1984; Colinvaux, 1986; Guthrie, 1985, 1990b): the "productivity paradox" (see papers in Hopkins et al., 1982). Past net primary productivity (NPP) is hard to quantify. Pollen accumulation rates during the late Wisconsin indicate relatively low pollen productivity compared with the Holocene but are subject to several biases: i) forbs with insect pollination or vegetative propagation, both common in tundra, are underrepresented in pollen records compared with wind-pollinated woody species (e.g., *Betula*, *Picea*), ii) pollen accumulation rates are site-dependent and rely on accurate estimates of sedimentation rates (which are rare in eastern Beringia because of chronological ambiguity), and, possibly, iii) herbivores consumed fertile shoots (Guthrie, 2006).

In "Paleoecology of Beringia" (Hopkins et al., 1982) and the Quaternary Science Reviews (volume 20) special issue edited by Elias and Brigham-Grette (2001) there is much informed speculation on the consumable biomass of the vegetation, but it remains a largely unanswered question. Guthrie (1984, 2001) suggested that a longer growing season, plus varied topography, enhanced spatial and temporal variability in plant growth and thus overall available forage. It should also be noted that low concentrations of CO_2 likely reduced plant productivity, while biomass reallocation through megafaunal excretion may have partially countered this (see sect. 3.2.4), but what is less clear is how forage quality may have differed from present (Gerhart and Ward, 2010). While biomass estimates from potential modern analogues are rare, Chytrý et al. (2019) obtained values for central Asian mountain plant communities that may provide partial analogues. Mean above-ground biomass ($g\ m^{-2}\ a^{-1}$) for disturbed slopes and desert-steppe was 50, for steppe 100, and for dry alpine grassland 200. They suggest the latter two are high enough to support grazing populations. Further, levels of N and P and other essential nutrients were high enough for good nutrition (all values are, necessarily, for modern CO_2 levels).

Estimating animal population sizes from fossil frequency data can be problematic and extrapolating from bones to plant biomass even more so (e.g., Zimov et al., 2012; Mann et al., 2013). Recent radiocarbon-dating studies have shown that the frequency of megafauna fossils varies with time, and this has been used to infer relative past population sizes (e.g., Sher et al., 2005). Guthrie (2006) observed from fossil evidence that steppe bison were absent, or rare, in eastern Beringia during the late Wisconsin, a finding that was replicated by Monteath et al. (2021) and Kelly et al. (2021). Combined DNA and Bayesian reconstructions of steppe-bison genetic history indicate that in Beringia population diversity (and size) peaked ca. 37,000 cal yr BP, before declining over the course of the late Wisconsin (Shapiro et al., 2004; Drummond et al., 2005; Faulkner et al., 2020, Fig. 3). Using measurements of radiocarbon-dated horse metacarpal bones Guthrie (2003) suggested rapid reductions occurred in body size in Alaska populations during deglacial shrub expansion. Re-plotting these data with the IntCal20 Northern Hemisphere radiocarbon calibration curve (Reimer et al., 2020) shows that the reduction in metacarpal lengths takes place from ca. 30,000 cal yr BP, around the onset of the late Wisconsin, indicating that these animals faced nutritional pressures at this time (Fig. 3). Although inferring population and animal sizes from radiocarbon-dated fossils is subject to numerous assumptions and taphonomic biases, the replication of this pattern in different areas of eastern Beringia, and in different datasets (e.g., DNA, radiocarbon frequencies and metacarpal lengths) does suggest that some megafauna populations declined during the late Wisconsin (Fig. 3), implying a reduction in NPP.

It is also possibile that population size estimates are insecure because of range dynamics of some key taxa. Mann et al. (2013) hypothesised that if climate fluctuations reflecting Dansgaard-Oescher events affected eastern Beringian megafaunal populations, average numbers based on bone counts may be misleading if they reflect only intermittent presence, as animals became extirpated from northernmost land areas during intervals with the harshest conditions. Strontium and oxygen isotope profiles from woolly mammoth tusks suggest that mammoths may have travelled large distances during their lifetime in response to seasonal changes and resource availability (Wooller et al., 2021). Together, these lines of evidence indicate that although late Wisconsin steppe-tundra was productive enough to support megafauna, at times much of it may have been a marginal environment for these animals, with populations periodically reduced or absent in some areas of eastern Beringia during periods of extreme cold and/or aridity.

3.2.6. *Can the steppe-tundra be restored?*

“Pleistocene” rewilding advocates using top-down ecosystem controls to change ecosystem structure and function to resemble a state that existed prior to substantial human impact. It has recently been suggested that the reintroduction of large herbivores (e.g., horse and bison) to Beringian landscapes might return soil, permafrost and vegetation to something similar to the late Wisconsin steppe-tundra ecosystem (Zimov, 2005; Beer et al., 2020; and see review in Macias-Fauria et al., 2020). The proposed consequences include a reduction in permafrost thaw and associated greenhouse gas emissions, thus providing a “nature-based” contribution to the slowing of global warming. These ideas are based partly on the proposal of Zimov et al. (1995, 2012) that herbivore presence can control vegetation composition to the extent that the steppe-tundra vegetation might have been maintained into the Holocene if the megafauna had not been diminished or extirpated by human actions. In this scenario, herbivore population decreases due to hunting at the end of the Pleistocene led to ecosystem cascades, including the change in vegetation to woody, less palatable communities. Observations at experimental sites with large numbers of herbivores and simulations with a land-surface model indicate that animal-trampling of snow can modify the surface enough to slow permafrost thaw, whereas enhanced thaw would be the natural trajectory on these landscapes with continued warming (Beer et al., 2020).

Beringian rewilding proposals are variously criticized. The suggestion that the Beringian ecosystem of 15,000 years ago could be restored under modern conditions assumes that critical interactions and processes have not changed (Nogués-Bravo et al., 2016). Restoration of the steppe-tundra depends on a range of conditions and drivers, and ecological interactions are complex; if key features are omitted from an ecological scenario/simulation, expected outcomes may not occur (Liu et al., 2022). Oliveira-Santos and Fernandez (2010) remind us of Pimm’s (1991) concern that a community at any given time reflects evolutionary interactions against a unique background of arrivals and extinctions; after thousands of years, and when different species are involved, it would be difficult to predict ecological outcomes in the target system. What we do know about past and present conditions shows that re-establishment of extensive steppe-tundra is unlikely.

Attempts to rewild modern Beringian landscapes would take place under a climate with far greater precipitation and atmospheric CO_2 levels than those of the late Wisconsin (Barber and Finney, 2000) and with different range of soil types (see sect. 3.4); all of which favour woody vegetation. Furthermore, evidence from the palaeo record indicates that the steppe-tundra was not maintained by megafauna and that the introduction of large herbivores is unlikely to cause substantial vegetation changes. Reanalyses of radiocarbon evidence by Monteath et al. (2021) showed that shrubs expanded prior to the eventual extinction of major megafauna taxa, indicating that megafaunal decline is more likely a response to shrub expansion, rather than a cause. Notably, during the middle Wisconsin, mammal populations were possibly higher than those of the late Wisconsin, but eastern Beringian vegetation was a mixture of herb tundra, shrub tundra, and woodland, rather than extensive steppe-tundra (see section 3.1; Sher et al., 2005; Mann et al., 2013; Faulkner et al., 2020; Kelly et al., 2021).

It is also uncertain if the reintroduction of large mammals would prevent carbon emissions. During the dry and windy late Wisconsin, incipient soils developed on accreting aeolian deposits across broad areas at lower elevations (e.g., Höfle et al., 2000); they were mineral-rich but carbon-poor (frozen deposits usually contain <5 % total C content; Murton et al., 2015). Today, in contrast, peatlands and organic-rich soils are widespread, and beneath the active layer drainage is impeded (i.e., paludification). Under such conditions in rewilding scenarios during the warm, wet summer season, the ground surface would be heavily trampled and warmed, accelerating the breakdown of Holocene histosols from the land surface. There is a risk, then, that far more carbon would be released than would be preserved by maintaining a higher permafrost table. Even assuming that it would be feasible to populate extensive areas with the requisite densities of large grazing mammals (Macias-Fauria et al., 2020; Ylänne and Stark, 2025), an intermediate result of disturbance could be exacerbated thermokarst, which would create an impossible substrate for large, small-hoofed mammals (Guthrie, 1984, 2001). Rather than restoring an ancient ecosystem, a new one of unknown properties seems more likely (Oliveira-Santos and Fernandez, 2010; Nogués-Bravo et al., 2016).

3.3. *Late Wisconsin spruce refugia and Holocene expansion in eastern Beringia*

Two species of spruce dominate the contemporary evergreen boreal forest in Alaska and Yukon: *Picea glauca* (white spruce) and *P. mariana* (black spruce). Of these, white spruce tends to favour better-drained landscapes, and distributions extend further north and west, whereas black spruce can tolerate shallower active layers and wetter soils. Both are found on river floodplains (Viereck et al., 1992). Remarkably, after decades of research, the jury is still out on the presence of either species during the late Wisconsin. The evidence is ambiguous and comes from three main sources: radiocarbon-dated macrofossils, fossil pollen and contemporary population genetics.

The cold, dry late Wisconsin would have been unfavourable for woody taxa (see sect. 3.2), particularly trees, and earlier researchers hypothesised that spruce became regionally extinct in eastern Beringia during this time, re-establishing from populations south of the Laurentide-Cordilleran ice sheets following deglaciation (Hopkins et al., 1981). Alternatively, spruce may have survived in eastern Beringia throughout the late Wisconsin in refugia where conditions were warm and/or moist enough to support local populations. In this hypothesis, modern analogues for their refugia might be mesic river valleys in the northern prairies (Hogg, 1994; Hogg and Schwarz, 1997), or on floodplains at the northern edge of spruce distribution in Alaska today, where taliks provide permafrost-free and well-watered ground conditions (Viereck, 1979). Notably, some of the earliest post-glacial spruce macrofossil and pollen sites lie in, or near, major river systems (e.g., Mackenzie, Yukon, Tanana; Hopkins et al., 1981), all of which are possible refugial areas. Refugia—if they occur—can alter the impact of post-glacial spruce migration, with extant isolated populations playing a greater or lesser role in large-scale forest expansion (Giesecke and Bennett, 2004; Edwards et al., 2014). Constraining past migration rates is important for understanding how fast spruce may migrate to equilibrate with anthropogenic warming in the future; also important is understanding how critical small populations (i.e. outposts) may be in establishment and spread (Väliranta et al., 2011).

Only macrofossils provide direct evidence of spruce presence, and these are in short supply (Hopkins et al., 1981; Edwards et al., 2014). In Alaska, spruce macrofossils (undiff.) are dated to ca. 36,000 cal yr BP at Isabella Basin (Matthews, 1974b; Elias, 2000). In Yukon, at several sites both black and white spruce fossils (from two arctic ground squirrel middens, plus a stump) have ages younger than 30,000 cal yr BP (see Zazula et al., 2006c and references therein). The youngest date is on two spruce needle fragments from Bluefish River, Yukon, dating to ca. 26,850 cal yr BP (24,530 ± 180 ^{14}C yr BP; Beta-193791). Macrofossil evidence for the presence of spruce during the LGM is unlikely to be reliable. Hopkins et al. (1981) report spruce dated to ca. 16,300 cal yr BP and ca. 19,200 cal yr BP (13,500 ± 310; GSC-2341 and 15,900 ± 160 ^{14}C yr BP; I-3083), but these are bulk-sediment samples that include spruce needles, and they are therefore likely to reflect reworked/old carbon (see Supplementary Text S2; Zazula et al., 2006c). Otherwise, macrofossil finds, ranging from northern Northwest Territories to interior Alaska, are typically ca. 11,000 cal yr BP or younger (Zazula et al., 2006c; Edwards et al., 2014). An exception is a ca. 13,380 cal yr BP date on cones from Twin Lakes (11,500 ± 160 ^{14}C yr BP; GSC-1514) in Northwest Territories, but this is strikingly early and has not been replicated (Hopkins et al., 1981).

Most pollen data are also ambiguous about the timing of spruce migration into eastern Beringia and the likelihood of refugia, due to the propensity for long-distance transport of spruce pollen grains by wind. Today, *Pinus* and *Picea* pollen can occur many hundreds of kilometres beyond mapped treelines in North America (Binney et al., 2011). Therefore, pollen can be unreliable as direct evidence of spruce presence, particularly at low values (<5 %). Furthermore, early *Picea* pollen found at some lake sites may have been reworked from middle Wisconsin sediments as lake levels rose during deglaciation and eroded old surfaces (Ager, 1975). In mapped summaries of older pollen data (Brubaker et al., 2005), *Picea* pollen occurs in scattered locations at low levels from 19,000 cal yr BP (usually 5% or less, which does not reliably suggest local presence). Better dated pollen evidence from sites in the Brooks Range, interior Alaska, and Yukon studied over the past two decades with AMS dating record a *Picea* pollen rise nearer 10,000 cal yr BP or slightly later (e.g., Tinner et al., 2006; Higuera et al., 2009; Irvine et al., 2012; Edwards et al., 2014), as does the *seda*DNA record at Chisholm Lake, interior Alaska (Clarke et al., 2024). One of the earliest well dated records is the Lucky Lady yedoma sequence, in central Yukon, which shows *Picea* pollen values of 14 % from ca. 11,900 cal yr BP (Monteath et al., 2023). Other temporal mapping of pollen data has shown i) rapid migration of spruce through the ice-free corridor (Ritchie and MacDonald, 1986; see below) and ii) a general east-west expansion of high spruce pollen values in the Holocene, with dates typically younger in the west (Ritchie, 1984; Edwards et al., 2014). It is notable that between 11,000 and 9000 cal yr BP, values at many sites increase markedly across Alaska, except in the far west (Edwards et al., 2014).

Modern genetic studies of eastern Beringian spruce populations provide an indirect line of evidence on past *Picea* distribution. Anderson et al. (2006) sequenced white spruce chloroplast DNA (cpDNA) from 24 forest stands distributed across northwest North America. Results are ambiguous: Alaska haplotypes, several unique to that region, are differentiated from haplotypes from outside Alaska. The observed variation may predate the late Wisconsin, reflecting mutation, sorting, and genetic drift through repeated glacial cycles (long-term presence) or, conceivably, they could reflect similar, but post-glacial processes. Anderson et al. (2011) updated the 2006 study by using nuclear microsatellites to refine insights into postglacial histories. New data supported the broad phylogeographic patterns uncovered in the original study, two-way genetic exchange between Alaska and the rest of North America, and patterns indicating genetic drift and gene flow that suggest periods of isolation and of mixing. Microsatellites indicated several cryptic refugia and a mix of (historically) large and small populations in eastern Beringia. A population in interior Alaska, north of Fairbanks (65.56 °N, 148.98 °W), may have been a source for the spread and expansion of white spruce after the late Wisconsin; however, the same study also identified a Canadian site (Riding Mountain) that had a similarly unusual (refugial-type) genetic pattern, but was under ice in the LGM and thus post-glacial in origin, probably a founder population. By analogy, unusual Alaskan populations might also reflect early post-glacial populations. Studies on *Picea abies* in Fennoscandia using modern genetic patterns, but also linking these to specific markers recovered from ancient, clonal trees, buried wood and well dated lake-sediments, strongly indicate that founder populations spread into central Fennoscandia from refugial areas further east early in the late-glacial period, and that in some places their descendants remained dominant in the modern landscape (Parducci et al., 2012). This record indicates that spruce has the capacity to extend its range and establish new populations extremely rapidly.

The *Picea* story still lacks clarity in eastern Beringia. If refugial populations existed, the extent of their role in regional forest expansion is unclear. Possibly, Pleistocene populations were highly restricted to optimal sites (e.g., talik, perennially flowing springs, topographic shelter), and they may have become adapted to cool, arid climatic conditions greatly different from the Holocene, and thus not resilient in the face of major climate change (Edwards et al., 2014). Subsequently, refugial populations would have encountered large, genetically diverse in-migrating populations, leading to gene flow and genetic mixing and a nuanced pattern of modern genetic variation, consistent with the findings of Anderson et al. (2006, 2011). Furthermore, there is a low probability of finding firm evidence of such populations in the vast landscape of eastern Beringia. Three scenarios remain possible: spruce survived in refugia and later spread, it survived but populations did not expand, or it was absent during the late Wisconsin.

If spruce was eliminated entirely during the late Wisconsin, the opening of the deglacial ice-free corridor between the Cordilleran and Laurentide ice sheets is the point at which it could have re-entered eastern Beringia. At its opening (prior to 13,200 cal yr BP; Heintzman et al., 2016), the ice-free corridor was almost certainly not conducive for *Picea* growth (Pedersen et al., 2016). Extremely rapid migration via the ice-free corridor seen in pollen records appears to reflect fast northward dispersal in a few centuries after 10,700 cal yr BP (Ritchie and MacDonald, 1986) but could also reflect inaccuracies associated with non-AMS, bulk-sediment dating. The radiocarbon-dated Twin Lakes spruce macrofossil (ca. 13,600–13,100 cal yr BP; Hopkins et al., 1981) broadly coincides with the opening of the ice-free corridor (before ca. 13,200 cal yr BP; Heintzman et al., 2016), but all other reliably dated macrofossils and pollen records suggest a later appearance, making Holocene migration a more likely scenario. There remains a weak geographical trend of the oldest dates occurring in the far northeast, the northern end of the ice-free corridor (e.g., at Lucky Lady; Monteath et al., 2023), so it may be the case that early establishment of one or more founder populations occurred, though major expansion of spruce forest in the region was delayed by several millennia. As described above, the major increases in *Picea* pollen values occurred between 11,000 and 9000 cal yr BP, suggesting that the main expansion of spruce occurred well after migration routes from the southeast were available and the earliest identified trees were present. Given the coincidence of increasing moisture levels at this time (see below) and the demonstrated modern growth response of *Picea* to restricted moisture (e.g., Barber et al., 2000; McGuire et al., 2010; Cahoon et al., 2018), expansion may have been limited by climatic conditions in the earliest Holocene.

Another possible refugium is the now flooded Bering Land Bridge. Mapped pollen data indicate that spruce arrived later in the far west (7000-2000 cal yr BP; Edwards et al., 2014), and it is therefore intriguing that a spruce macrofossil from northern Seward Peninsula dates to 9560-9010 cal yr BP (Kitluk Pingo; Wetterich et al., 2012). A pollen record from a river valley near Nome has well preserved *Picea* pollen dated to 13,500–12,000 cal yr BP (Hunt et al., 2013). In contrast, an 18,000-year record of pollen, plant macrofossils and *seda*DNA from St

Paul Island (south-central land bridge) shows no evidence of the local presence of *Picea* or large shrubs (Wang et al., 2017). If there were spruce populations on the land bridge, what happened to them as sea-level rose? Future investigations may be guided by palaeodrainage identifications from bathymetric surveys of Bering and Chukchi Seas (e. g., Bond, 2019). Some of these hypotheses could certainly be tested by a current effort aimed at coring sediments from ancient lake basins that existed on the Bering Land Bridge during the late Wisconsin. Questions regarding the existence, or otherwise, and fate of land-bridge refugia could usefully be addressed by further palaeo-records from the region and genetic studies of modern spruce populations in far-western Alaska.

3.4. *The end of the Pleistocene*

The end of the Pleistocene saw almost every aspect of the eastern Beringian environment destabilized as global ocean-atmospheric circulation patterns adjusted to ice sheet melting, atmospheric CO_2 and sea-level rise, and sea-ice retreat. Major ecological changes in eastern Beringia include a transformation of vegetation, large-scale turnover in faunal communities and permafrost thaw.

3.4.1. *Reorganisation of climate and geography*

Although summer insolation had been increasing since ca. 21,000 cal yr BP, North Pacific Ocean-atmospheric circulation patterns that characterized the glacial period reorganized later, at ca. 14,000 cal yr BP, bringing a substantial increase in moisture to eastern Beringia. An early series of equilibrium palaeoclimate simulations (COHMAP members, 1988) indicated major adjustments in atmospheric circulation over North America between 15,000 and 12,000 cal yr BP. In a conceptual model for Beringian regional climate, Bartlein et al. (1991) proposed that eastern Beringian moisture increased ca. 14,000–13,000 yr BP as the Laurentide ice sheet diminished to the point where it no longer sustained a glacial anticyclone, leading to the return of a westerly flow across eastern Beringia. A more recent transient simulation (Transient Climate Evolution [TraCE]: National Center for Atmospheric Research, Community Climate System Model version 3) supported this hypothesis (Bartlein et al., 2014; Lora et al., 2016). In the simulation, a large North American ice sheet is crucial to maintaining aridity in eastern Beringia via a south-east anticyclonic flow and deflection and/or splitting of the northern jet-stream track. A reduction in glacial ice thickness of 500–1000 m, coincident with the separation of the Cordilleran and Laurentide ice sheets, is linked with rapid atmospheric reorganisation at about 14,000 cal yr BP. The result is northward movement of the westerly jet and increasing moisture delivery to eastern Beringia. The most recent glacial chronology (^{10}Be, radiocarbon and OSL) is consistent with these simulated changes in atmospheric circulation: the main phase of Cordilleran–Laurentide ice sheet saddle collapse occurred between 15,400 and 13,800 cal yr BP (Stoker et al., 2022; Reyes et al., 2024), and by ca. 13,000 the southwestern Laurentide ice sheet had retreated >1250 km to the Cree Lake Moraine (Norris et al., 2022).

Increased rates of moisture delivery were further enhanced after ca. 14,000 cal yr BP by sea level-rise and by a shift from perennial to seasonal sea ice in the eastern Bering Sea starting ca. 15,000 cal yr BP as regional sea-surface temperatures increased by ∼3 °C (Caissie et al., 2010). The extent of the land bridge rapidly diminished due to marine inundation, shifting the position of the coast inland and bringing marine moisture sources closer to the interior; the land bridge was probably breached by ca. 11,000 cal. yr. BP (Jakobbsen et al., 2017; Mann and Gaglioti, 2024). By 10,000–9000 cal yr BP, the coastline approached its modern configuration in most areas (Manley, 2002), with substantial climate and vegetation shifts indicated at sites influenced by encroaching seas (Ager, 2003; Ager and Phillips, 2008; Wooller et al., 2018). An equilibrium experiment using a regional climate model showed that under 11,000 cal yr BP boundary conditions the flooding of the Bering Land Bridge markedly reduced seasonality in eastern Beringia, bringing cooler summers and warmer winters (Bartlein et al., 2015). Thus, replacement of land by sea in the latest Pleistocene and Early Holocene is implicated as a major climate control in eastern Beringia, though the eastward extent of this effect and the time at which the seaway became a detectable climatic influence are both uncertain (Bartlein et al., 2015; Mann and Gaglioti, 2024).

3.4.2. *Palaeohydrology*

Although temperature rise is often considered the dominant feature of deglaciation, moisture dynamics are a critical element of the Pleistocene-Holocene transition in eastern Beringia (Mann et al., 2002). Lake-level studies have established that lakes in smaller and/or shallower catchments were dry during the late Wisconsin and did not begin to fill until deglaciation, while less hydrologically sensitive lakes show substantial lowering (e.g., Abbott et al., 2000; Barber and Finney, 2000; Mann et al., 2002; Finkenbinder et al., 2014, 2015; Dorfman et al., 2015). For example, at Jan Lake, an endorheic lake in interior Alaska, Barber and Finney (2000) used lake-level changes to estimate a 35–70% reduction in late Wisconsin precipitation compared with the Holocene (ca. 90–195 mm a^{-1}, compared with ca. 300 mm a^{-1} today). While the overall trend during deglaciation is one of increasing moisture and increasing lake levels, detailed data suggest that water levels underwent oscillations or step changes (Abbott et al., 2000; Mann et al., 2002). Many lakes, including those of thermokarst origin in discontinuous permafrost, did not reach maximum levels until much later in the Holocene (e.g., Abbott et al., 2000; Mann et al., 2002; Barber and Finney, 2000; Anderson et al., 2018, 2019). In Yukon, a steady decline in oxygen isotope values of lacustrine calcite in Squanga Lake between ∼11,000 and 8000 cal yr BP is interpreted to reflect rising moisture (Lasher et al., 2021). Small, shallow lakes in Yukon began to fill during deglaciation and showed their largest rise between 11,000 and 10,000 cal yr BP, but they did not consistently overflow until between 8000 and 5000 cal yr BP (Anderson et al., 2005; Pompeani et al., 2012).

Additional insights into moisture dynamics across the Pleistocene-Holocene transition are indicated by isotopic changes measured on chironomid chitin δ^{18}O at Burial Lake (northwest Alaska). Several large δ^{18}O shifts (∼5 ‰) can be aligned with lake-level changes and overall moisture balance, although in complex ways (King et al., 2021). The lake's δ^{18}O values reflect a combination of meteoric source water, lake hydrology (i.e., P-E balance, basin characteristics, overflowing status) and growing-season temperature. Negative δ^{18}O values between ca. 20,000–16,000 cal yr BP reflect cold, arid conditions when the lake was shallow and closed with an extended duration of ice cover. Rising δ^{18}O values at the onset of deglaciation reflect increasing moisture and higher lake levels, but the lake was still a closed basin; higher oxygen isotope values result from substantial evaporation. Within the period ca. 14,000–11,000 cal yr BP, rising summer temperatures (indicated by changing chironomid assemblages) and continued evaporative enrichment led to the highest δ^{18}O values as the closed lake's level stabilized temporarily. Coincident with final opening of the Bering Strait at ca. 11,000 cal yr BP, higher precipitation and reduced evaporation is reflected as a rapid decline in lake δ^{18}O values, as the lake rose to the modern overflowing level. These results show the complexity of hydrologic change during deglaciation, which would have had impacts on terrestrial and lacustrine ecosystems.

3.4.3. *Permafrost and carbon dynamics*

Changes in hydrology, palaeogeography and the cryosphere during deglaciation combined to affect the carbon cycle. From the onset of deglaciation, Pleistocene carbon was released into the atmosphere as greenhouse gasses (Zimov et al., 1997) and entered ecosystems as particulate organic carbon and dissolved organic carbon. Lipid biomarker records from sediment cores from the Bering Sea indicate pronounced reworking and carbon mobilisation early in the deglaciation (ca. 15,000 cal yr BP), probably associated with meltwater runoff via the Yukon River that increased riverbank erosion of permafrost soils (Meyer et al., 2019). Subsequently, intense coastal erosion, particularly during meltwater pulses 1A (ca. 14,000 cal yr BP) and 1B (ca. 11,000 cal yr BP), further mobilized carbon from thawing permafrost. On land, permafrost thaw increased due to warming and greater moisture levels (Mann et al., 2002), which promoted ponding of surface water and development of thermokarst lakes in frozen, unconsolidated deposits across the region (Hopkins, 1949). The consequent thaw and decomposition of material underlying lakes led to a release of stored carbon, much of it as methane (CH_4; Zimov et al., 1997; Walter et al., 2007, 2008). A large component of this carbon was ancient, deriving from the sediments into which thermokarst lakes eroded (Walter Anthony et al., 2016). Further thaw of widespread late Wisconsin yedoma and other deposits across eastern Beringia is likely to become a positive feedback to contemporary climate warming (Douglas et al., 2021; Walter Anthony et al., 2024).

In permafrost-affected regions, the age and amount of carbon mobilized from permafrost substrates into aquatic systems is highly variable and depends upon climate. Using the age-offset approach, which entails dating of paired macrofossil and bulk-sediment samples, on exposed lake sediments in the northern Brooks Range, Gaglioti et al. (2014) recorded modern offsets of ~2000 yr but higher offsets (3000–5000 yr) during the deglacial warm period (14,500–12,900 cal yr BP) and the warm Early Holocene (11,700–9000 cal yr BP). This they attribute to enhanced permafrost thaw and release of older stored carbon. At Burial Lake, northwest Alaska a recent study has revealed the temporal complexity of carbon storage and release as climatic conditions changed and affected permafrost dynamics over the past 40,000 years. Using age-offsets and ramped pyrolysis-oxidation radiocarbon analysis, Sinon et al. (2025) recorded variations in both the quantity and relative age of organic carbon mobilized from permafrost. They concluded that erosion is a key driver of both carbon age and amount. The highest age offsets (~9000 yr) are linked with erosion (rather than thaw) of ancient carbon held in the soil profile during the LGM. On the modern landscape, near-contemporary terrestrial carbon reaches the lake via subsurface flow, and age offsets are low (2000 yr), as observed by Gaglioti et al. (2014). From deglaciation to present, the contribution of near-contemporary organic carbon to the lake increased from 53 % to 88 %. Both permafrost thaw and the degree and type of erosion appear to influence carbon mobilization, and these, in turn, depend on features such as vegetation cover, thickness of soil organic layers, disturbance and precipitation. Today, both thaw and erosion may be dampened by dense vegetation cover and organic soils; this may delay changes related to Arctic warming (Gaglioti et al., 2014).

A further concern in a warming Arctic is the release of mercury (Hg) compounds from previously frozen soils, some of which are strong biotoxins; arctic soils are globally significant mercury reservoir (Lim et al., 2020). Also at Burial Lake, Griffore et al. (2025) showed major changes in mercury release coincident with the temperature and moisture increases that characterized the deglacial climate transition. Notably, Hg concentrations rose with increased moisture and warming ca. 14,000 cal yr BP and reached their highest levels when precipitation increased further near the onset of the Holocene, ca. 11,000 cal yr BP. In the past, summer rainfall appears to have been the strongest driver of Hg mobilization; given precipitation is expected to increase with rising anthropogenic emissions (see sect. 1.3), this result raises concern for the future.

3.4.4. End-Pleistocene changes in landscape and biota

Terminal Pleistocene changes after ca. 15,000 cal yr BP affected many aspects of the eastern Beringian landscape and biota. The xeric, well-drained soils and graminoid-forb vegetation that characterised areas in the east and interior, and the herbaceous tundra areas in the west were widely replaced by woody shrubs (*Betula* and *Salix* spp.) at ca. 14,000 cal yr BP (Anderson et al., 2004; Monteath et al., 2021). Woody shrub expansion may have been completed within a few decades (certainly a few centuries) at local scales (Bigelow, 1997; Monteath et al., 2023). Prior to expansion, *Salix* was probably widespread in prostrate form, whereas *Betula* was likely confined to widespread, but local refugia (Brubaker et al., 2005), where snow depth was sufficient to provide adequate moisture and protection from winter temperatures (Kaplan et al., 2003, Fig. 6). Peatlands and thermokarst lakes also developed rapidly during this period (Guthrie, 2001; Anderson et al., 2004; Walter et al., 2007; Jones and Yu, 2010; Edwards et al., 2016; Farquharson et al., 2016). Within the same period, grazing megafauna populations declined, with woolly mammoth and horse becoming absent in the regional fossil record before the onset of the Holocene (Guthrie, 2006; Mann et al., 2013). These widespread environmental changes coincided with the arrival of hunter-gatherer groups in the interior of eastern Beringia, ca. 14,000 years ago (Potter et al., 2017, 2022). The southern portion of the land bridge may have supported human populations prior to this (e.g., Hoffecker et al., 2014), but, as described above, environmental conditions had also begun to change rapidly along coastal areas as well.

Initially, the vegetation probably maintained a mosaic pattern at the landscape scale. Pollen accumulation rates from dated lake sediments provide temporal sequences of pollen flux to a site; although still affected by differential pollen productivity among taxa and subject to accurate chronology, they can be less biased than percentage data. They show that graminoid and herbaceous taxa continued to form an important part of the vegetation community, even as the vegetation became increasingly dominated by shrub species, which often exceed 50 % of the pollen sum (e.g., Ritchie, 1982; Bigelow and Edwards, 2001). The development of the REVEALS algorithm for land-cover estimation uses extensive documentation of relative pollen productivity estimates (PPEs; Sugita, 2007); it further aids pollen interpretation of land cover, allowing semi-quantitative estimates to be made from fossil pollen records. A reassessment of late Pleistocene pollen records from interior Alaska using a REVEALS calibration shows lower *Betula* and *Salix* cover, and higher graminoid and forb cover (Hopla et al., 2019; Hopla, 2020). This raises the possibility that while the landscape was inexorably changing, open, non-woody vegetation was still an important part of the mosaic; if so, openness may have supported the continuance of megafauna populations in isolated refugia (Haile et al., 2009; Murchie et al., 2021) or have partly been the consequence of their presence—or both.

Increases in *Betula* and *Salix*, the two dominant shrub-tundra taxa, show different temporal patterns across the region, though in each case *Salix* tends to increase before *Betula* (Anderson et al., 2004; Monteath et al., 2021, Fig. 8). These taxa could have responded to increases in either (or both) temperature and moisture. Of the two, *Salix* is more likely to show enhanced productivity with temperature increase, but little moisture enhancement, given that several prostrate species in the genus can survive in low-snow conditions, while *Betula*, which occurs as a dwarf (or larger) shrub, would require sufficient snow cover (i.e., moisture increase) to expand and persist (Kaplan et al., 2003). Comparison between pollen data and chironomid-inferred temperatures from the same cores reveals these temporal patterns along with (likely) regional drivers. In eastern (Yukon) sites a rapid rise in temperature is evident between 15,000–14,000 cal yr BP (Hanging and Trout Lakes; Kurek et al., 2009b; Irvine et al., 2012, Fig. 8), whereas in western (Alaska) sites (Burial and Zagoskin Lakes; Kurek et al., 2009a, Fig. 8), the temperature rise was more gradual. *Salix* expands almost synchronously with initial temperature rise at the eastern sites and at Burial Lake (Abbott et al., 2010, Fig. 8), but at all sites the rise in *Betula* took place between 600 and 1000 years later (Fig. 8). At Burial Lake, *Betula* also lags *Salix*, but expands during a gradual increase in chironomid-inferred air temperature (Abbott et al., 2010; Kurek et al., 2009a). At Zagoskin Lake (Ager, 2003; Kurek et al., 2009a, Fig. 8), *Salix* is present throughout the record and only shows gradual fluctuations, while *Betula* shows a sharp increase (the chronology of Zagoskin may be offset towards too-old dates due to bulk-sediment dating, but the trends at this site are clear). These spatial patterns suggest that in Yukon the abrupt rise in temperature at ca. 15,000–14,000 cal yr BP may reflect the cessation of the ice-sheet cooling effect as the Laurentide ice sheet retreated, whereas western temperature trends were not affected by

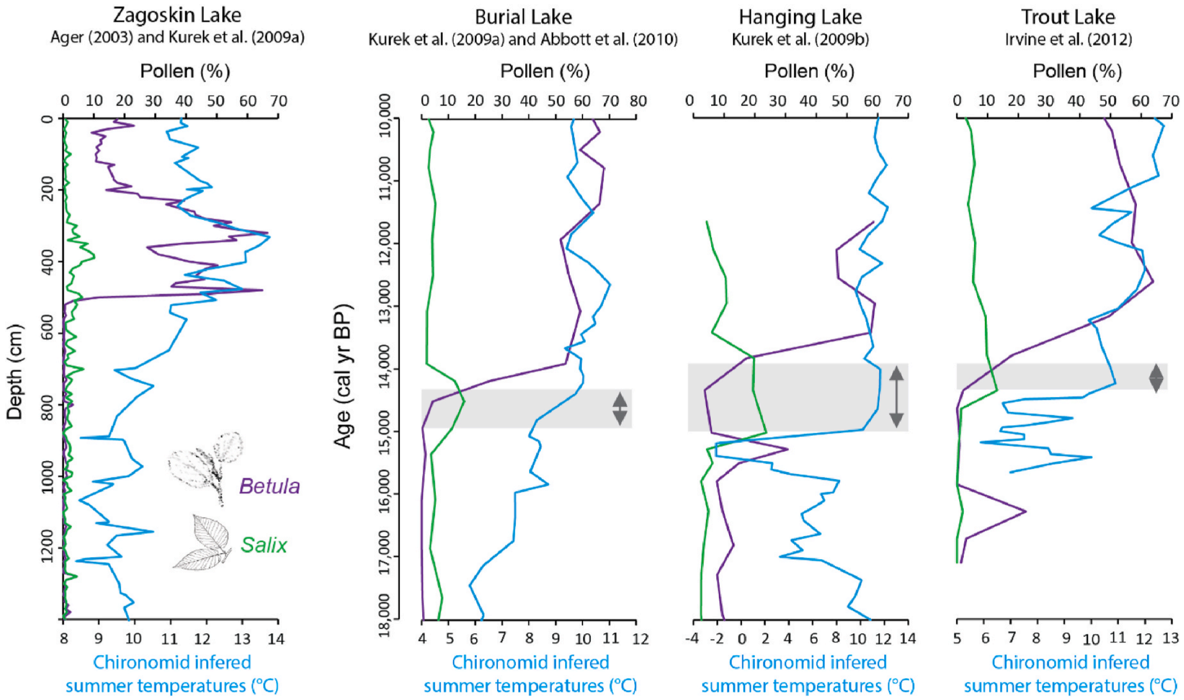

Fig. 8. Lake records where pollen and chironomid assemblages have been quantified from the same sediment core. Gray bars indicate a lag between *Salix* and *Betula* expansion. Note that chironomid-inferred extreme cold temperatures at Hanging Lake are likely to be caused by seasonal ice/snowpack meltwater from near the site (Kurek et al., 2009b).

proximity to the ice sheet, but may instead have been moderated by a gradual shift to greater maritime dominance. The differing east-west patterns suggest that *Salix* directly responded to a combination of increasing temperatures and the onset of slightly moister conditions, whereas *Betula* did not respond to the initial temperature rise, but rather, it responded to a moisture threshold being passed with changes in atmospheric circulation (Bartlein et al., 1991). We note that although modern pollen production of *Betula* in the subarctic varies positively with temperature (Anderson et al., 1991), soil moisture is now high, which was not the case in the late Pleistocene, when moisture appears to have been a strong control over vegetation structure and composition.

The past dynamics of shrub expansion invite comparison with vegetation responses to current warming. Today, across many (but not all) areas of the northern high latitudes, enhanced NPP (Arctic greening) is recorded by satellite data and field observations (e.g., Myers-Smith et al., 2011; Walker et al., 2012; Berner et al., 2020). This is attributed to greater growth and productivity of shrub taxa, which in turn is a response to increases in summer temperatures, but also to other drivers, such as disturbance, permafrost dynamics, changes in herbivory and snow cover (Myers-Smith et al., 2011). Additionally, woody taxa have been extending their distributions northward with warming temperatures (Sturm et al., 2001; Tape et al., 2006). It is expected that expansion will continue, changing the structure and function of northern ecosystems—including those that occupy the northernmost parts of eastern Beringia. Current changes invite comparison with the transformation of deglacial landscapes from steppe-tundra to shrub tundra and deciduous woodland. While there are some notable similarities between late Pleistocene and modern shrub expansion (e.g., speed of landscape transition and associated faunal turnover; Tape et al., 2006, 2022; Monteath et al., 2023) past changes do not provide a perfect analogue. Most palaeo records cover many centuries, but at relatively low resolution, while modern observations (including photo pairs) cover perhaps 50–100 years at most, and in both cases—ancient and modern—our understanding of these transitions is incomplete.

In the past, rapid shifts in summer temperature (probably at least 4 °C), moisture and shrub expansion occurred, perhaps within a few decades, similar to modern observations, but other changes took longer and were more gradual (Figs. 3 and 8). While northern high-latitude growing-season temperature trajectories may somewhat align between the past and today, moisture patterns are different: at the end of the Pleistocene moisture increased from low levels and was critical for shrub expansion (see above), whereas modern moisture levels are already high, and their future trajectory is a challenge to predict (see section 1.3). Atmospheric CO_2 conditions were also different, with values rising ($<$280 ppm in the late Pleistocene), whereas today they exceed 420 ppm and will increase further, affecting productivity and winter warming. Late Pleistocene shrub tundra initially expanded across minerogenic soils that had developed under the steppe-tundra. Subsequently, with shrub encroachment under a moistening climate there was a trend towards paludification (Mann et al., 2002, 2015; Jones and Yu, 2010), which encouraged rising permafrost tables over time.

Modern conditions therefore pose different ecological and physiological challenges to plants, particularly expansion into highly paludified soils, making the deglacial shrub expansion an imperfect analogue for the rates of shrub proliferation expected in the future. It is interesting to note that within the range of modern conditions, greater productivity increases have been observed on non-acidic, relatively nutritious soils under a more continental climate with lower winter moisture (Walker et al., 2012). Furthermore, simple projections of suitable bioclimate considerably over-estimate the actual spread of woody taxa, highlighting that climate is not the only driver influencing a shift toward woody tundra. Liu et al. (2022) concluded that both fire and propagule (e.g., fruits and seeds) dispersal affected shrub expansion. Fire can have both positive and negative effects on shrub establishment under current conditions. In northwest Alaska, a positive feedback loop between shrub dominance and fire occurs, likely related to productivity and thus fuel availability, whereas tussock tundra shows little shift towards shrub expansion (Gaglioti et al., 2021). During deglaciation (ca. 14,000 cal yr BP), when moisture levels were far lower, Higuera et al. (2009) report increasing fire occurrence (based on macro-charcoal) after the transition from steppe-tundra conditions to shrub tundra; in part driven by the abundance of flammable *Betula* shrubs. This is consistent with increasing fuel availability driving an increase in fire, but finer details about the evolution of fire with the vegetation mosaic (see section 3.2) are not discernible.

3.4.5. *What happened to the megafauna?*

The Pleistocene-Holocene transition is associated with turnover in the eastern Beringian megafauna community that included regional extirpations (e.g., woolly mammoth and horse) and new arrivals (e.g., moose and wapiti) from Eurasia (Guthrie, 1990a, 2006; Mann et al., 2013, 2015; Monteath et al., 2021). Around the same time, rapid changes in hydroclimate coincided with shrub tundra expansion (see sect. 3.4.2 and 3.4.4) and the first appearance of well documented and dated archaeology (e.g., tools and hearths; Potter et al., 2017, 2022). Given the nearly synchronous changes in climate, vegetation, megafauna communities and human arrival, it is tempting to connect these into a web of interaction, particularly through the idea that human action exacerbated the decline of some large mammals through hunting or habitat modification (e.g., Fordham et al., 2022). However, as the drivers of each planetary warming (i.e., interglaciations and major interstadials) are continually changing, every climate shift will be associated with unique circumstances (Mann et al., 2019; Meltzer, 2020), and in eastern Beringia the causes of megafauna extirpations remain uncertain. The following arguments concerning this community turnover invoke either “top-down” ecological processes, such as human-caused extinction, or “bottom-up” processes, typically landscape and vegetation responses to climate change that negatively affected the herbivores’ environment (see section 3.2.4).

It is possible that human hunting caused regional megafauna extirpations (Martin, 1967), which led to vegetation change through a loss of top-down controls (see section 3.2.4). While direct lines of evidence, such as Pleistocene kill sites, have not been identified in eastern Beringia, early archaeological records in the Tanana valley, interior Alaska, suggest that palaeolithic hunters were actively using megafauna as resources and may have established their seasonal hunting camps to coincide with congregations of woolly mammoths (e.g., Wygal et al., 2022; Rowe et al., 2024). Megafauna remains found in these archaeological settings could have been scavenged; however, tools found in the same context are nearly identical to those from Upper Palaeolithic sites in Siberia (Gómez Coutouly and Holmes, 2018), where woolly mammoth hunting is well documented (Zenin et al., 2006). Therefore, it is conceivable that human hunting contributed to regional megafaunal extirpations.

Alternatively, climate-driven processes may have diminished grazing megafauna populations that were adapted to open, well drained landscapes as their preferred habitat disappeared with widespread paludification (i.e., became covered by moist, organic soils and wetlands; Guthrie, 1990b, 2006; termed “death by peat” hypothesis by Mann et al., 2015). This shift to wetter soil conditions was compounded by the spread of unpalatable woody plant taxa (e.g., *Betula*) that produce anti-herbivory toxins (Guthrie, 1984, 2001). Species that survived into the Holocene (e.g., caribou [*Rangifer tarandus*] and muskoxen [*Ovibos moschatus*]) were better adapted to moister facies of the landscape (e.g., lower foot loading; Guthrie, 1990b; Mann et al., 2013). In this climate-driven scenario, rapid biogeographical change, including the submergence of the Bering Land Bridge, wiped out escape routes to other, more favourable regions in Eurasia. In the case of woolly mammoth, this may have been particularly important given the extensive lifetime ranges of these animals (Wooller et al., 2021; Rowe et al., 2024).

More subtle transformations, hard to detect using the palaeoecological record, underlie other environmental hypotheses for megafaunal decline; for a detailed exposition, see Mann et al. (2019). In the hypothesis of Guthrie (1984), long growing seasons led to phenological niche separation and a diverse flora with low levels of competition. Intra-seasonal changes continually refreshed a landscape mosaic of palatable forage plants. By the start of the Holocene, shorter growing seasons, climatic stability and a reduced disturbance regime led to more phenological overlap, competition, increased anti-herbivory compounds, and forage that was unpalatable for non-ruminants such as mammoth, horse and steppe-bison. The phytochemical characterization of Holocene forage is undoubtedly correct, but the postulated change in growing-season length as a driver is less secure. A simpler explanation is that the large deglacial climate shift was probably enough to drive compositional dominance from a non-woody, perennial-dominated flora that was grazing- and disturbance-adapted (e.g., grasses and Asteraceae, including *Artemisia*) to woody vegetation characterized by a defended, browsing-adapted flora (Monteath et al., 2021).

Mann et al. (2019) expand the idea of temporal disturbance to centennial/millennial scales involving the climate variability recorded in the Greenland ice cores (Rasmussen et al., 2014). They take the idea beyond plant phenology and ecological strategy to different aspects of the megafaunal environment (e.g., disturbed substrates, incipient soils, fluctuating climate) arguing that the highly mobile megafaunal taxa coped with such disruptions effectively. Possibly, this led to evolutionary trends whereby the biology of megafauna taxa became progressively fitted to these “non-equilibrium” conditions, leaving them vulnerable to longer periods of stability. When considering the individualistic character of each deglaciation, the Holocene is characterized by marked overall stability; this may have facilitated the transformation of the extensive steppe-tundra into today’s latitudinal and altitudinal vegetation zones, which formed poorer habitats to which the megafauna was poorly adapted.

These scenarios, in which environmental change drove megafauna extirpations, also leave space for a human driver where hunting might have contributed to the demise of populations already in decline (e.g., Fordham et al., 2022). The role of humans is likely to remain disputed, but given the huge geographical area of Alaska-Yukon and limited population sizes of high-latitude peoples (Burch, 1980; Mann et al., 2013), it seems unlikely that palaeolithic hunters could have caused regional extirpations of megafauna unless they contributed to an underlying trend driven by other changes.

3.5. *Was there a Younger Dryas climate event in eastern Beringia?*

The Younger Dryas climate event (approximately coeval with Greenland Stadial 1) saw strong cooling in the North Atlantic region between 12,800–11,700 cal yr BP (Mangerud, 2021; Reinig et al., 2021) and is arguably the best studied example of abrupt Pleistocene climate change. It was probably driven by substantial freshwater discharges from glacial Lake Agassiz that disrupted the Atlantic Meridional Overturning Circulation (Broecker et al., 1989; Clark et al., 2001; Murton et al., 2010), although other mechanisms, including freshwater discharge into the Pacific (Praetorius et al., 2020), volcanism (Baldini et al., 2018) or (more controversially) asteroid impact (Firestone et al., 2007; strongly refuted by Holliday et al., 2023) have been proposed. Similar climatic events are observed in older deglaciation sequences, however, suggesting that the Younger Dryas did not require a unique catastrophic onset and instead was more like a Heinrich Event (Broecker et al., 2010). It is also important to note that environmental changes in Beringia may have been driven (all or in part) by Columbia River megafloods that caused strong sea-surface cooling in the North Pacific, rather than a North Atlantic driver (Praetorius et al., 2020).

The Younger Dryas was first described in Scandinavia as a period of regional cooling, but the term is now used to infer both a chronozone and—informally—a climate oscillation of almost global extent (Mangerud, 2021). While marine records from the northeast margins of the North Pacific clearly show a Younger Dryas oscillation in sea-surface temperatures (Praetorius et al., 2020) terrestrial evidence from eastern Beringia is sometimes weak, or even absent, in some records, raising the question if there was a regional Younger Dryas event at all. This may reflect the fact that many climate and biogeographical drivers (e.g., summer insolation, sea-level change and continentality) affected environments in eastern Beringia at this time, and in some cases may have overridden the expression any Younger Dryas signal.

Kokorowski et al. (2008) summarised palaeoecological data throughout this interval and found that in southern and coastal Alaska, the Younger Dryas climate event was expressed as pronounced cooling, in contrast with records from interior or northern Alaska, which indicated more limited responses, if any. Mann and Gaglioti (2024) undertook a similar review of the northwest coast of North America and also found stronger evidence for a Younger Dryas climate event in areas adjacent to the ocean. Re-analysis of well dated proxy records in eastern Beringia confirms geographic variation (Fig. 9). Younger Dryas cooling is evident in sites in southern Alaska and southern Yukon, as well as sites north of the Brooks Range, with clear changes in isotopic measurements (e.g., Epstein, 1995; Meyer et al., 2010; Jones et al., 2014; Gaglioti et al., 2017), glacial extent (Young et al., 2019), vegetation composition (Hu et al., 2002; Mann et al., 2002, 2010), hillslope processes (Mann et al., 2010) and aquatic productivity (e.g., Hu and Shemesh, 2003; Hu et al., 2006; Kaufman et al., 2010, 2011). Proxy responses in the interior, however, are typically weakly expressed or are not evident at all (Fig. 9). For example, a pronounced climate event is not evident in pollen percentage records (Bigelow, 1997; Bigelow and Edwards, 2001), although principal component analysis (PCA) of high-resolution data shows a partial shift towards vegetation communities associated with steppe-tundra in two interior records (Bigelow and Edwards, 2001). Furthermore, pollen accumulation rates suggest that vegetation productivity was reduced, even if climate forcing was not sufficient to cause turnover in vegetation communities (e.g., Birch Lake and Lost Lake; Fig. 9). Oxygen-isotope values at Burial Lake indicate increased aridity during the Younger Dryas although chronomid-inferred summer temperatures remain high; (King et al. (2021) suggest this reflects enhanced seasonality (colder winters and still-warm summers). Terrestrial deposits have yielded ambivalent data. In the Alaskan interior, brGDGT

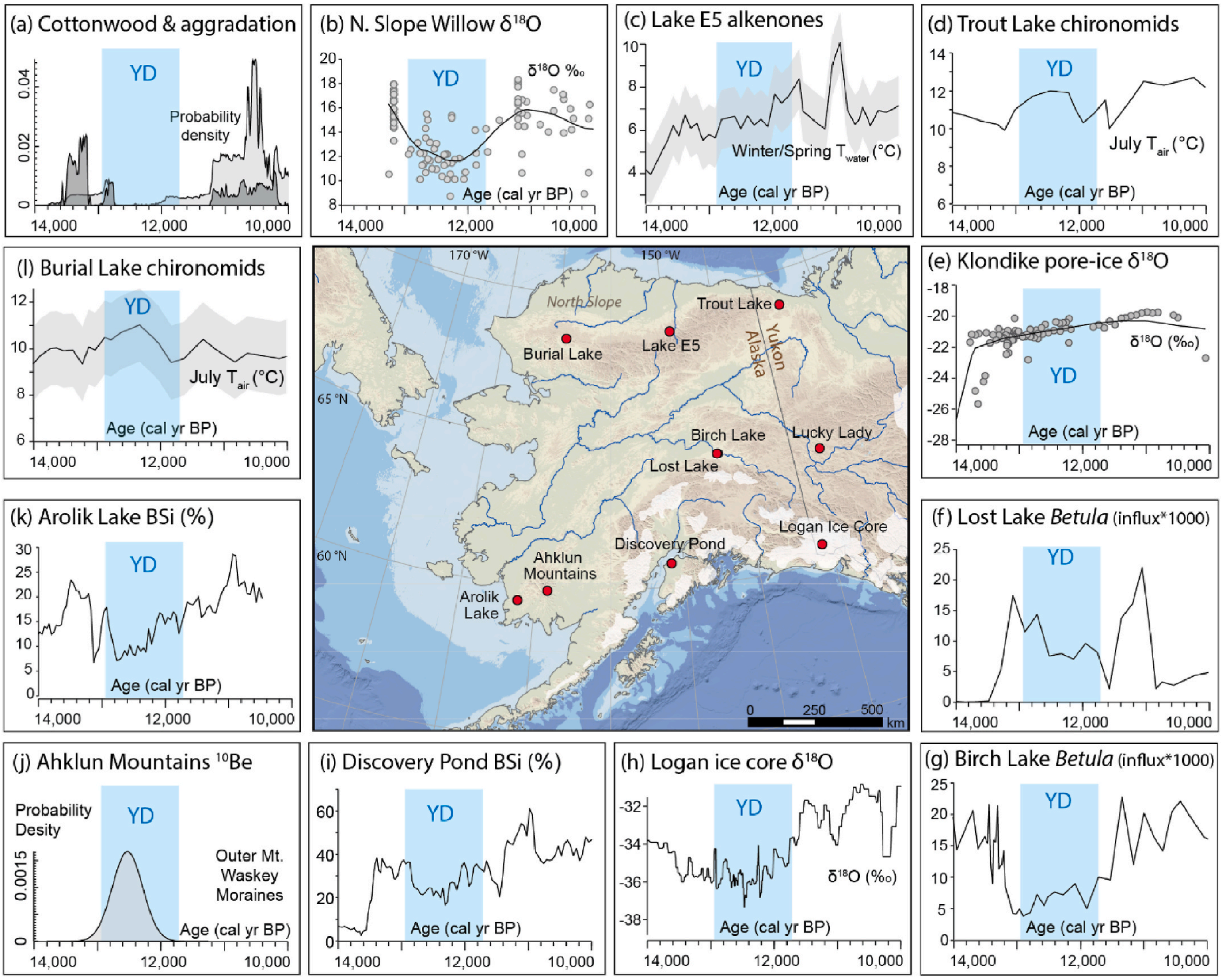

Fig. 9. Selected palaeo records spanning the Younger Dryas (YD) time-period (12,800–11,700 cal yr BP). (a) Probability-density curves from North Slope (Mann et al., 2002) for the radiocarbon ages of cottonwoods (*Populus balsamifera*) at locations beyond their present range limits (pale gray) and for radiocarbon ages of floodplain aggradation in the Arctic Foothills (dark gray) (Mann et al., 2010). (b) $\delta^{18}O$ measurements from willow cellulose on the North Slope (Gaglioti et al., 2017). (c) Reconstructed winter-spring lake water temperatures from Lake E5 (Longo et al., 2020). (d) Chironomid-reconstructed air temperatures from Trout Lake (Irvine et al., 2012). (e) Klondike pore-ice record ($\delta^{18}O$) (Mahony, 2015). (f) *Betula* influx (grains cm^{-2} yr^{-1}) from Lost Lake pollen analysis (Tinner et al., 2006). (g) *Betula* influx (grains cm^{-2} yr^{-1}) from Birch Lake pollen analysis (Bigelow, 1997). (h) $\delta^{18}O$ measurements from the Logan ice core (Fisher et al., 2008). (i) BSi (%) values from Discovery Pond (Kaufman et al., 2010). (j) ^{10}Be dating from Mt. Waskey moraine sequence (Young et al., 2019). (k) BSi (%) values from Arolik Lake (Hu et al., 2006). (l) Chironomid-reconstructed air temperatures from Burial Lake (Kurek et al., 2009a). Approximate ice limits are redrawn from Dalton et al. (2020). Base map data from GEBCO (2023).

measurements through the late glacial reveal generally high temperatures and no clear variation related to the Younger Dryas (Kielhofer et al., 2023), neither does a permafrost oxygen-isotope time series from Yukon (Monteath et al., 2023).

It is possible that this pattern is derived from differing spatial expressions of the Younger Dryas climate event and/or the seasonal sensitivities of palaeoenvironmental proxies. Firstly, the climate forcing of the Younger Dryas is hypothesised to have been more pronounced during winter (Denton et al., 2005, 2010). In contrast, the majority of palaeoenvironmental proxies capture summer (i.e., growing season) signals (e.g., pollen and chironomids). Therefore, it might be expected that most palaeoenvironmental proxy records outside the most strongly affected areas are insensitive to winter cooling. Further, during the Younger Dryas summer insolation was higher than present (Fig. 3), and in continental areas of eastern Beringia this may have negated any summer cooling. Existing data that do indicate cooling are at the margins of eastern Beringia, where climate may have been more strongly affected by ocean conditions than the interior. For example, Gaglioti et al. (2017) hypothesised that $\delta^{18}O$ values from willow cellulose on the North Slope were sensitive to changes in sea-ice extent over the Arctic Ocean and the expanding Bering Sea (as sea levels rose). Similar water-isotope variations from North Slope of Alaska suggest Younger Dryas climate changes included temperature, moisture source and atmospheric circulation patterns (Epstein, 1995; Meyer et al., 2010). Coupled with discharge of freshwater into the Arctic Ocean (Murton et al., 2010) and Pacific Ocean (Praetorius et al., 2020) winter sea-ice is hypothesised to have persisted later into the spring/summer months during the Younger Dryas, but recent developments in sea-ice proxies indicate complex extent and timing dynamics that require further investigation (Méheust et al., 2018; Mann and Gaglioti, 2024).

4. Looking forward

Current and future planetary warming promises drastic changes in northern landscapes and ecosystems, and understanding past changes has never been more relevant to how we anticipate what may happen in the future. Lessons from the past can be used as analogues for expected future change, or to illustrate environmental changes that lie outside the envelope of recent experience. Furthermore, down-scalable transient climate simulations (e.g., TRACE21, Liu et al., 2021; Karger et al., 2023) form the basis for a range of modelling exercises over the past 21,000 yr. So, what are some of the key topics for future research?

4.1. *Biomass estimates and carrying capacity of the steppe tundra biome*

With increasing interest in Pleistocene rewilding (e.g., Zimov et al., 2005), accurately estimating the biomass of both plants and animals in the steppe-tundra is key to understanding its functionality and whether or not it has any bearing on contemporary efforts to retain soil carbon (section 3.2.6). Currently, there are no convincing estimates of plant or animal biomass from this extinct ecosystem. Approaches using pollen influx, dated fossil frequencies or aDNA can only yield relative data. Modelling of steppe-tundra productivity, and hence carrying capacity, under conditions of late Wisconsin climate, atmospheric CO2 and disturbance regime (fire, as well as trampling) would be a welcome development.

4.2. *The post-glacial expansion of woody taxa*

Range extensions of trees and shrubs are expected—and indeed already observed—due to strong warming of the high latitudes. Bioclimatic niche modelling can take us only so far in projecting future afforestation rates and patterns, as the leading edge of a population is subject to other controls that are not always considered, and expected rates of spread may not be achieved (see section 3.4.4). Frustratingly, it remains unclear whether *Picea* survived in refugia in Beringia and if refugial populations gave rise to the major expansion at ca. 10,000 cal yr BP. If spruce was functionally extirpated during full-glacial time and re-entered eastern Beringia, then its east-west migration comprised different rates of spread over millennia (Ritchie, 1984); conceivably, the observed patterns reflect both processes (Edwards et al., 2014). What are the likely locations where datable late Wisconsin macrofossils can be found? Places to start are known middle Wisconsin *Picea* localities and along major river systems, which may have been relatively favourable habitats as well as dispersal corridors. Furthermore, major insights of past geography may be gained from more genetic studies of both modern and ancient populations, the latter now becoming feasible via shotgun metagenomics.

4.3. *The importance of fire*

Fire is a top-down control over forest and tundra vegetation that is becoming increasingly important today (Kasischke et al., 2010; French et al., 2015). The link between fire and the deglacial transition from predominantly herbaceous tundra to woody vegetation (*Betula*, *Salix*) provides a partial analogue for “Arctic greening” (Higuera et al., 2009), the shrub (and eventually forest) invasion of tundra linked with Arctic warming (Sturm et al., 2001; Myers-Smith et al., 2011; Dial et al., 2022; see section 3.4.4). In the boreal forest, increased fire frequency today may drive a switch towards hardwoods (Mack et al., 2021), which also dominated in the late Pleistocene (Edwards et al., 2005). While differences between past and future conditions must be considered, complementary studies of past and present fire dynamics across Alaska, together with fire modelling, would aid our understanding of potential future trajectories.

4.4. *Terrestrial-ocean interactions*

How sensitive is eastern Beringia to abrupt ocean reorganizations? During the middle Wisconsin (MIS3), rapid climate shifts are observed in the North Atlantic region (Dansgaard et al., 1993; Rasmussen et al., 2014), while in the North Pacific large ice-rafting events may also have affected regional climate (Walczak et al., 2020). To what extent were these events were expressed in eastern Beringia (see sect. 3.1.2) remains an open question. Our understanding of the regional expression of the last major climate reversal, the Younger Dryas, remains limited, as most proxies are sensitive to summer conditions, whereas winter saw greater change (see sect. 3.5). Can we find more localities that hold a record of high-frequency environmental change, whether lake-sediment or terrestrial deposits, that span the middle Wisconsin and new, informative proxies for the Younger Dryas? Such records could also be used to test hypotheses regarding the role of disequilibrial vegetation assemblages in supporting the megafauna within the steppe-tundra biome (Mann et al., 2019).

4.5. *Application of SedaDNA*

The lake-sediment and terrestrial permafrost deposits of eastern Beringia provide exceptional archives for *sed*aDNA (Shapiro and Cooper, 2003); however, so far this technique has been used at only a handful of regional sites (e.g., Haile et al., 2009; Wang et al., 2017; Murchie et al., 2021; Clarke et al., 2024). It is plausible that *sed*aDNA is preserved in deposits that span multiple glacial-interglacial cycles (Froese et al., 2008; Kjær et al., 2022) and can be dated by a secure tephrochronological framework (Froese et al., 2009). Within radiocarbon timescales, new data from *sed*aDNA studies promise to yield further detail on the still enigmatic steppe-tundra palaeoflora that sustained the megafauna (section 3.2). Identification of vertebrates beyond the limited landscape locations where fossil bones are found, along with information on other phyla and soil microbiota (e.g., Courtin et al., 2022), promise greater insight into the functioning of both the steppe-tundra biome and past warm stages (see below).

4.6. Previous warm stages

Understanding previous warm stages is relevant to modern concerns regarding climate change and its broader ecosystem impacts. For anticipated warm, moist, future conditions, the last interglaciation (MIS5) is the most accessible partial analogue. During MIS5, summer temperatures in eastern Beringia likely reached 2–4 °C above present (Hamilton and Brigham-Grette, 1991; CAPE Project Members, 2006; Otto-Bliesner et al., 2006), and recent simulations suggest that the Arctic Ocean may have been ice-free in summer (Guarino et al., 2020). Coniferous boreal forest extended further north than today (Hamilton and Brigham-Grette, 1991; Muhs et al., 2001; Miller et al., 2010). While it remains challenging to date MIS5 deposits directly, there are both stratigraphically constrained terrestrial deposits (e.g., by tephra beds; Reyes et al., 2010b) and lake-sediment records (see Supplementary text, S4) that cover this interval. New proxies may provide records of, for example, temperature, hydroclimate, fire dynamics, permafrost thaw, carbon dynamics, and the nature of plant and animal biotas. Such work requires coordination of field logistics and proxy expertise to deliver a coherent picture of eastern Beringian ecosystems under extremely warm conditions.

4.7. The nature of the central Bering land bridge

Eastern Beringia was connected to Eurasia via the Bering Land Bridge for long periods and is a region that we know little about. Several lines of palaeoecological (e.g. Guthrie, 2001) and climatological (e.g., Kaplan et al., 2003) evidence point to the land bridge being moister than the rest of Beringia, but these remain largely untested and important questions are unanswered: why did the land bridge pose a barrier to some megafauna (e.g., woolly rhinoceros; *Coelodonta antiquitatis*)? Did the land bridge provide refugia for spruce or even humans? Past and present efforts to core lake basins or wetlands that are now submerged under the Bering Sea promise to reveal more about this enigmatic landscape.

5. Conclusions

Quaternary deposits in eastern Beringia preserve evidence for past climatic and ecological change that has interested scientists for nearly a century. Recent advances in chronology and novel proxies have addressed previously unresolved questions regarding the nature of late Quaternary environments in eastern Beringia; however, many issues continue to prove perplexing. At the same time, these advances have raised new questions that can be framed in the context of the rapid climate changes affecting the northern high latitudes today.

The nature of the middle Wisconsin (57,000–30,000 cal yr BP) remains poorly understood, in part because of chronological limitations. Available palaeoecological evidence indicates that climate was cooler and drier than the Holocene, with widespread loess deposition. Environments and vegetation were diverse. In the interior, valley bottoms supported elements of gallery forest and herbaceous taxa. Further north, shrub tundra was widespread, however, with a lesser *Betula* component than the deglacial period (15,000–10,000 cal yr BP) shrub tundra. Many of the megafauna taxa more closely associated with steppe-tundra (e.g., steppe-bison and woolly mammoth) were abundant during this period, suggesting there is further complexity in Beringian vegetation-herbivore interactions to be understood. The transition towards cold-stage conditions took place between 35,000–30,000 cal yr BP and coincides with the emergence of the Bering Land Bridge.

The steppe-tundra (mammoth steppe) remains one of the most fascinating and contentious aspects of the late Quaternary, partly because of its association with the megafauna. Evidence from plant macrofossils and *sed*aDNA demonstrates diverse herbaceous plant assemblages, while the idea of a ubiquitous, highly productive prairie-like steppe does not fit well with available data. Evidence of top-down controls in maintaining the steppe-tundra is lacking. Whether spruce survived the cold, arid late Wisconsin (30,000–15,000 cal yr BP) in eastern Beringia remains an unresolved question.

The late Pleistocene deglaciation and floral/faunal turnover of eastern Beringia was caused by a range of drivers including summer isolation (65°N), atmospheric CO_2, sea-level change and atmospheric reorganisation as the Laurentide-Cordilleran ice-sheet complex collapsed. Hydrology emerges as a key control on late Pleistocene vegetation change that affected *Salix* and *Betula* differently; while *Salix* was sensitive to temperature *Betula* did not expand until regional moisture thresholds were crossed.

The Younger Dryas climate event was variably expressed in eastern Beringia; sites on the North Slope and in southern Alaska showed strong responses to the cooling, sites in the interior were mostly insensitive. The latter may reflect proxy bias, chronological ambiguity or the overriding effects of high summer insolation and continentality.

Author contributions

AJM, MEE and DF conceived the project. AJM and MEE wrote the manuscript with input from all authors. AJM designed the figures.

Declaration of competing interest

We confirm that none of this material has been published or is under consideration elsewhere, and all authors have approved submission. This manuscript has been through USGS internal review.

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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.2025.109527.

Data availability

No code is used in this review

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