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Environments during the spread of anatomically modern humans across Northern Asia 50–10 cal kyr BP: What do we know and what would we like to know?

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ABSTRACT

Northern Asia (here, the Russian Federation east of the Urals) played a key role in the spread of anatomically modern humans (AMH) across the Eurasian continent during the Upper Palaeolithic (UP). This time interval witnessed the climatically harshest and most variable part of the last glacial epoch when AMH spread to all continents, with the exception of ice-covered Antarctica, thus raising questions about how humans and environments interacted. Our review of available proxy records shows that the study region was largely dominated by productive steppe and tundra plant communities, which promoted a diverse small- to mega-scale fauna throughout the UP. While this rich fauna was an ideal food resource for AMH populations, its possible influence on the growth of woody plants through grazing is less well resolved. Another non-climatic factor that may have impacted on the spread of woody taxa are human activities (e.g. setting fires to facilitate hunting). Evidence that small populations of woody taxa were distributed in climatically favourable habitats comes from plant macro-remains from sediment sequences and archaeological sites and from aDNA data. Contrary to the long-standing view of a generally colder-than-present last glacial climate, these proxy records reveal evidence that summers were warmer than today by several degrees Celsius, providing additional advantages for human activities. Another benefit for large herbivores, and thus human subsistence, were the generally low winter precipitation levels (similar to those of the modern steppe regions of Mongolia), which sustained year-round grazing grounds. These factors apparently outweighed the harsh colder-than-present winter conditions and promoted habitation of AMH in Northern Asia even during the Last Glacial Maximum (LGM) ca. 30–18 cal kyr BP. While our understanding of qualitative climate trends, mainly based on fossil pollen records, has substantially improved, quantification of climate parameters is still a challenging task. For the last glacial interval in Northern Asia, plant macroremains, chironomids, diatoms and ostracods may provide suitable alternative proxies.

1. Introduction

Various research projects with a focus on anatomically modern humans (AMH), their dispersal, subsistence strategies, technological innovations and interactions with environments during the Pleistocene benefit from expanding knowledge of Late Quaternary vegetation and climate variability at regional to local scales (e.g. Chlachula, 2017; Hosfield and Cole, 2019; Leipe et al., 2018; Liu et al., 2015; Nishiaki and Akazawa, 2018). The Upper Palaeolithic (UP) period, broadly dated to between 50,000 and 10,000 years ago, is of particular interest (e.g. van Andel and Davies, 2003; Buvit et al., 2016; Straus et al., 2016) as it witnessed the climatically harshest and most variable part of the last glacial epoch (Svensson et al., 2008) when AMH spread to all continents, with the exception of ice-covered Antarctica.

It has been suggested that climate change and its effects on ecosystems may have played a key role in the evolution of the human species (deMenocal, 2011). However, in which way(s) did past changes in climate and environments influence hunter-gatherer population dynamics, cultural traditions, prosperity, continuous existence and collapses? Can we see major differences or similarities between large regions? These and other questions were raised in both archaeological and palaeoenvironmental studies published elsewhere (e.g. Beach,

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2016; Wagner et al., 2014; Weber et al., 2013). Substantial progress has been made in archaeological and environmental sciences during the past two decades, not least due to the implementation of Earth systems and human population models (e.g. Timmermann and Friedrich, 2016), ancient DNA research (e.g. Willerslev et al., 2014), more accurate dating and radiocarbon (^{14}C) age calibration (e.g. Bronk Ramsey et al., 2012; Reimer et al., 2013) and quantitative vegetation (e.g. Cao et al., 2019; Tarasov et al., 2000; Williams et al., 2011) and climate reconstruction techniques (e.g. Melles et al., 2012; Tarasov et al., 1999, 2005). However, the list of questions has not become shorter and the gap between "what do we know and what would we like to know" is far from being closed.

The vast areas of Northern Asia, including Siberia and the Russian Far East (Fig. 1), offer a wealth of archaeological data (e.g. Derevianko et al., 2014; Dolukhanov et al., 2002; Chlachula, 2017; Ineshin and Teten'kin, 2017; Krivoshapkin et al., 2018; Kuzmin and Keates, 2005; Lbova, 2014; Vasil'ev et al., 2002; Weber et al., 2010) and environmental information stored in sedimentary archives (e.g. Bezrukova et al., 2010; Binney et al., 2017; Karabanov et al., 2004; Kienast et al., 2005; Müller et al., 2010; Prokopenko et al., 2001; Shchetnikov et al., 2016; Shichi et al., 2009), providing great opportunities for multidisciplinary research. Furthermore, "our understanding of the Palaeolithic settlement of Siberia can provide a critical perspective on the timing, origins, and routes of founding migrations to the Americas, as well as a "reality check" on competing models and conflicting archaeological, linguistic and genetic evidence" (Goebel, 1999: 208). The ongoing Baikal Archaeology Project (BAP: https://baikalproject.artsrn.ualberta.ca/), Cultural History of PaleoAsia Project (http://paleoasia.jp/en/) and international research projects carried out in the Altai Mountains region (e.g. Jacobs et al., 2019; Douka et al., 2019) are good examples. By uniting interdisciplinary and international teams of researchers, these and other geo-archaeological projects pave the way to gain new knowledge, generate working hypotheses and verify conventional theories. The hypothesis developed by Timmermann and Friedrich (2016) on the basis of fossil and archaeological data suggests that the migration of AMH out of Africa and into Eurasia occurred in several episodes – the so-called Human Dispersal Windows. However, testing this hypothesis and assessing the role that orbital-scale global climate swings and millennial-scale climate changes played in shaping Late Pleistocene environments and human population distributions across Eurasia requires in-depth archaeological and environmental research in key regions (Timmermann and Friedrich, 2016).

Another important problem to be addressed is the controversy between pollen- and plant macrofossil-based reconstructions and climate-vegetation model simulations. While published proxy data indicate that most of ice-free Northern Eurasia was covered by open vegetation, climate-vegetation model simulations consistently suggest that (at least) broad areas of Europe would have been suitable for tree growth (Kaplan et al., 2016). To resolve this controversy, Kaplan et al. (2016) argue for highly mobile groups of hunter-gatherers that inhabited Europe during the last glacial and substantially reduced forest cover through deliberate burning. Despite the apparently harsh glacial climate suggested by the model simulations and proxy-based climate reconstructions (e.g. Ganopolski et al., 2010; Kageyama et al., 2001; Ray and Adams, 2001; Shichi et al., 2009), chronological and archaeological data from UP sites in Northern Asia do not confirm dramatic depopulation of the area during the last glacial (Dolukhanov et al., 2002). Quite the opposite: another regional study (Kuzmin and Keates, 2005) even suggests a gradual increase in archaeological site numbers between ca. 41 and 19 cal kyr BP. This lack of correspondence with the archaeological data from the Mediterranean region, where a significant reduction of human population and a near-complete breakdown of settlement patterns during the coldest and driest episodes of the last glacial period was attested (e.g. Davies et al., 2003a, 2003b; Schmidt et al., 2012), deserves more thorough investigation.

Were the last glacial environments in Siberia less hostile to UP hunter-gatherers than those in the Mediterranean region? If so, in which way? Were the last glacial landscapes of Siberia treeless and sparsely vegetated and the climate colder all year round than at present, as suggested by some key reconstructions (e.g. Frenzel et al., 1992; Ray and Adams, 2001) and climate model simulations (e.g. Kageyama et al., 2001; Andreev et al., 2011), or do these conventional views require adjustment and revision? High-resolution environmental proxies (pollen, diatoms, chironomids, stable isotopes, etc.) archived in lake

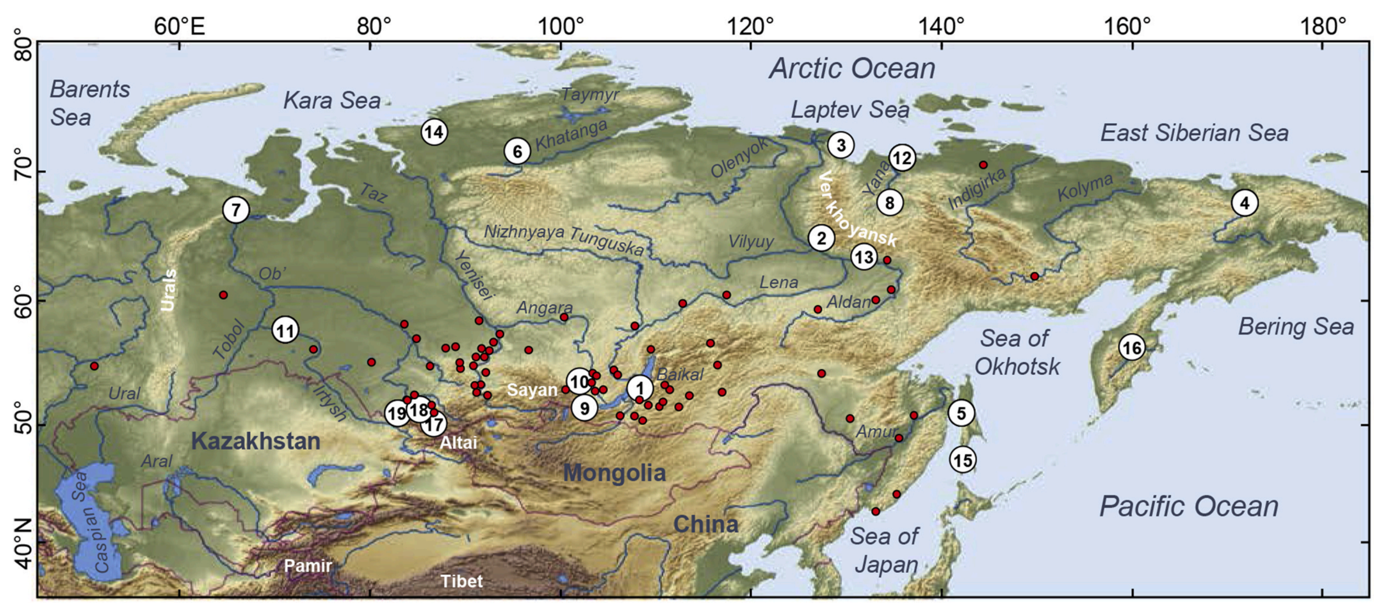


Fig. 1. Topographic map of Northern Asia showing major rivers and lakes and location of key sites (white circles with numbers) with palaeoenvironmental (sites 1–10) and archaeological records (sites 10–19) discussed in the text: 1 – Kotokel, 2 – Billyakh, 3 – Bykovsky/Mamontovy Khayata, 4 – El'gygytgyn, 5 – Khoe, 6 – Levinson-Lessing, 7 – Gerditzy, 8 – Batagay, 9 – Tunka, 10 – Mal'ta, 11 – Ust'-Ishim, 12 – Ikhine, 13 – Yana, 14 – Tarachikha, 15 – Ogonki-5, 16 – Ushki, 17 – Kara-Bom, 18 – Denisova Cave, 19 – Strashnaya Cave. Red dots indicate locations of ^{14}C-dated Upper Palaeolithic sites in Northern Asia (Dolukhanov et al., 2002). Topography is based on Global 30 Arc-Second Elevation (GTOPO30) data (Earth Resources Observation and Science Center, 1997). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

sediments and recently developed methodological approaches are helpful for addressing these questions and for better understanding past changes in vegetation and climate, their timing and driving mechanisms (e.g. Litt and Anselmetti, 2014; Melles et al., 2012; Nakagawa et al., 2012; Tarasov et al., 2019).

This review paper is based on a lecture presented by the authors at the International Workshop on the Cultural History of PaleoAsia, which was held at the Research Institute for Humanity and Nature in Kyoto (Japan) on December 15–18, 2018. It summarizes and discusses the published information on vegetation, animal, climate and human population dynamics in Northern Asia with a focus on archives from Siberia with robust chronologies. The focus time interval of the current article (ca. 50,000–10,000 years ago) covers the entire UP. Unless otherwise indicated, all dates are given in ^{14}C-based calendar-equivalent (calibrated) kilo-years before present (cal kyr BP), where the year 1950 CE is conventionally taken as "present".

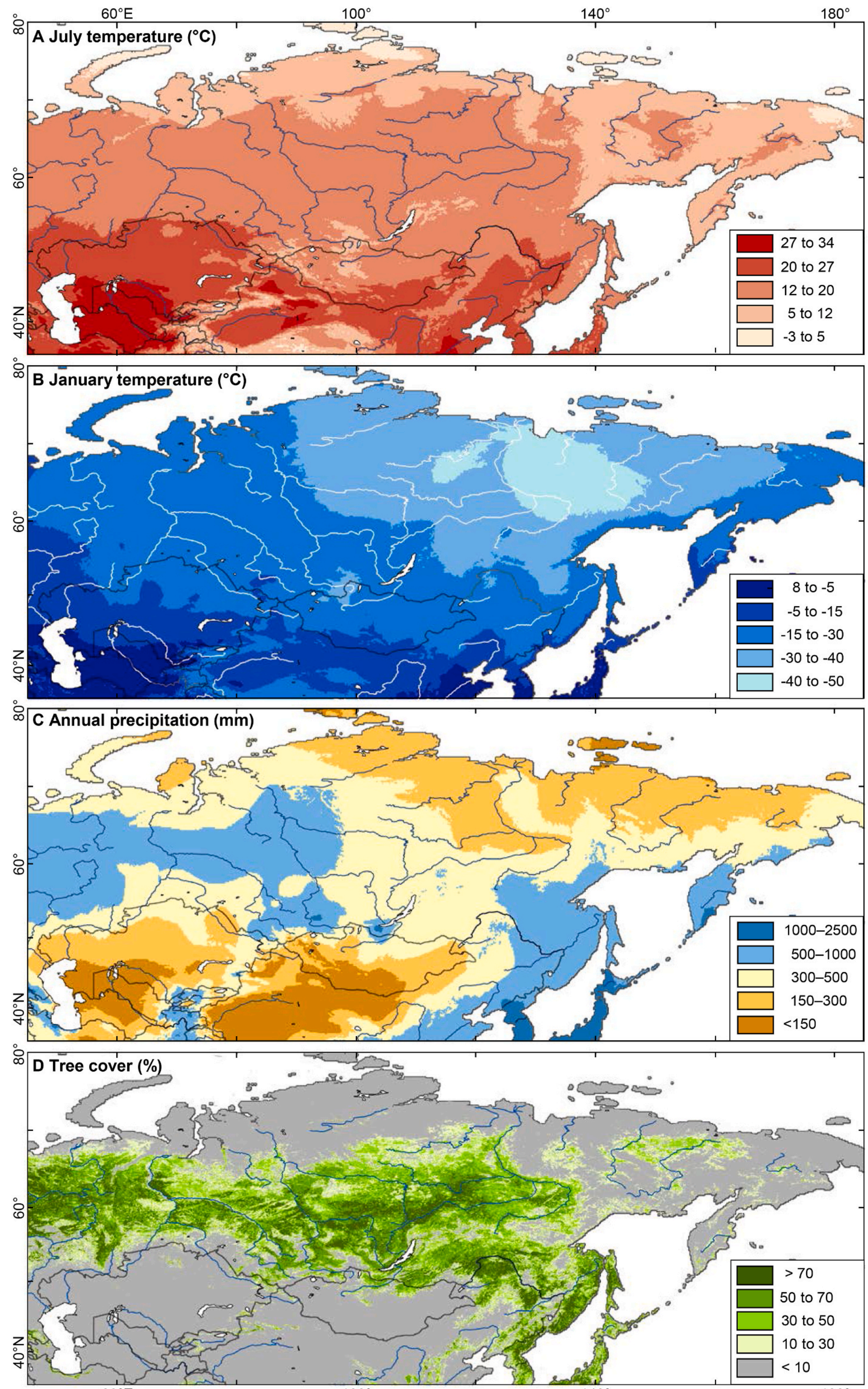


Fig. 2. Maps showing modern distribution patterns of (A) mean July temperature, (B) mean January temperature, (C) mean annual precipitation (New et al., 2002), and (D) AVHRR-derived tree cover (DeFries et al., 2000) in Northern Asia.

2. Modern environments

Here, the regional environments of Northern Asia are briefly introduced with a focus on topography, climate, water resources and vegetation, i.e. those factors, which play an important role in the lifestyle and subsistence strategies of prehistoric hunter-gatherers (Kobe et al., 2020). Northern Asia is an extensive geographical region spanning much of Eurasia between the Ural Mountains (ca. 500–1895 m a.s.l.) in the west and the Pacific Ocean in the east (Fig. 1; Alpat'ev et al., 1976). It extends ca. 3000 km from north to south and includes a wide variety of landscapes and several climatic and vegetation zones. In the north, it is surrounded by the shallow continental seas of the Arctic Ocean and the southern boundary corresponds to the state border of Russia with Kazakhstan, Mongolia and China at ca. 50°N. The topography of the region is rather complex. The territory of western Siberia (ca. 60–90°E) between the Ural Mountains and the Yenisei River is relatively flat. It is occupied by the West Siberian Lowland (0–200 m a.s.l.) and drained by the Ob' River and its tributaries. East of 90°E, low-elevated plains occupy a 50 to 600-km-wide band along the Arctic Ocean coast and the broad valleys of the Lena River and its major tributaries north of ca. 62°N, while elevated plateaus and mountain ranges with altitudes generally exceeding 1000 m a.s.l. predominate south of 70°N. The most prominent of them are the Central Siberian Plateau and the mountain ranges of southern Siberia with the highest points in the Altai (4506 m a.s.l.) and in the Sayan Mountains (3492 m a.s.l.).

The climate of the entire region is extremely continental with pronounced seasonality (Alpat'ev et al., 1976; Tarasov et al., 2007). The mean July (warmest month) temperatures decrease northward from ca. 20 °C to less than 5 °C (Fig. 2A). The absolute temperature minimum and maximum registered in Yakutsk are −64 °C and +38 °C, respectively (Alpat'ev et al., 1976; Müller et al., 2010). A strong Siberian anticyclone controls the winter weather. The mean January (coldest month) temperatures vary from ca. −16 °C in the south, for example at the coast of Lake Baikal (Galaziy, 1993), to ca. −50 °C in the interior regions east of the Lena River (Fig. 2B). More than 65% of the annual precipitation falls during the warm season (Leemans and Cramer, 1991; Tarasov et al., 2007). The westerly flow from the Atlantic Ocean is a major source of precipitation in the area west of Lake Baikal (e.g. Kostrova et al., 2020), while the Asian monsoon circulation brings moisture from the Pacific Ocean in the east. Annual precipitation is highest in the south-eastern part of the region affected by Pacific air masses (Fig. 2C). Central parts of western Siberia and the high mountain ranges around Lake Baikal also receive high precipitation (Fig. 2C), mainly associated with Atlantic cyclones (Galaziy, 1993; Kleinen et al., 2011). The lowest precipitation values are recorded in the central parts of Northern Asia, situated far away from Atlantic and Pacific influence, and in the northern coastal plains, which are controlled by the cold and dry air masses from the Arctic Ocean (Fig. 2C). The lowest values below 200 mm/yr are registered in central Yakutia (Müller et al., 2010), at the Olkhon Island of Lake Baikal and in the isolated depressions and river valleys of southern Siberia (Galaziy, 1993).

Low summer temperatures and low evaporation rates together with high amounts of atmospheric precipitation received by the mountains support a well-developed river network in western and eastern Siberia (Fig. 1). This network of longitudinally and transversely oriented rivers and wide valleys further complicates the topography of the region, but offers the most suitable migration and transport routes that connect north and south, east and west (Kobe et al., 2020).

The spatial distribution of major vegetation types or biomes is determined by the features of the Northern Asian climate (Alpat'ev et al., 1976; Tarasov et al., 2007). Climatic variables used to explain natural biome distribution include temperatures of the coldest and warmest months, length of the growing season and a moisture index calculated as the ratio of actual to potential evapotranspiration (Prentice et al., 1992, 1996). The climate-derived biome distribution in Northern Asia simulated with the BIOME1 model (Prentice et al., 1992) reveals a primarily latitudinal pattern, which is modified by altitude and slope aspect in the mountain regions and very similar to the patterns established in regional botanical studies (Tarasov et al., 2007). The arctic lowlands and the elevated parts of the plateaus reveal treeless vegetation (Fig. 2D) represented by various moss, grass, sedge, dwarf shrub and shrub tundra types (Alpat'ev et al., 1976; Gerasimov, 1964; Müller et al., 2010). Southward, the tundra zone is gradually replaced by boreal cold deciduous forest dominated by larch (*Larix*), birch (*Betula*) and aspen (*Populus*) species and further south by the evergreen conifer forest (boreal taiga) biome represented by Siberian spruce (*Picea obovata*), Siberian pine (*Pinus sibirica*), Scots pine (*Pinus sylvestris*) and fir (*Abies sibirica*) mixed with cold deciduous forest species (Andreev and Tarasov, 2013). Shrubby forms of birch (*Betula* sect. *Nanae* and *B.* sect. *Fruticosae*), alder (*Alnus fruticosa*), willow (*Salix*) and various members of the heath family (Ericales) are common in the arctic and alpine shrub tundra associations, but also on the surface of peat bogs and beneath the forest canopy (Müller et al., 2010; Kobe et al., 2020). The boreal forest belt, which extends for over 1500 km south of ca. 65°N (Fig. 2D), is the most prominent feature of the Northern Asian vegetation during the Holocene interglacial. Landscapes become gradually open again to the south of Lake Baikal and in Central Asia (Fig. 2D) in response to increasing summer temperatures (Fig. 2A) and decreasing precipitation values (Fig. 2C). Cold steppe and meadow steppe vegetation associations in the region are dominated by species of grasses (Poaceae), *Artemisia* and various mesophyllous herbs and shrubs (Tarasov et al., 2012), while desert vegetation further south reveals high proportions of chenopods (Chenopodiaceae), *Artemisia* and *Ephedra* (Gerasimov, 1964; Tarasov et al., 1998).

3. Data and methods

3.1. ^{14}C-dated archaeological records of human habitation

Dolukhanov et al. (2002) made one of the first attempts to discuss the dispersal pattern of AMH in Northern Asia using a representative dataset of conventional and AMS ^{14}C dates from UP sites in Siberia and the Russian Far East. The original ^{14}C dates were screened using quality control procedures (see Dolukhanov et al., 2002 for details and references) and all dates without clear archaeological context, as well controversial dates or single dates strongly deviating from a series of close-by dates from the same site/layer, were excluded from the analysis. For the purpose of this study, and in order to facilitate comparison with the robustly-dated environmental and climate archives, we calibrated all ^{14}C dates compiled by Dolukhanov et al. (2002) to calendar ages using OxCal v4.3 (https://c14.arch.ox.ac.uk/oxcal.htmlBronk; Bronk Ramsey, 1995) and the IntCal13 curve (Reimer et al., 2013). The spatial distribution of the ^{14}C-dated archaeological sites is shown in Fig. 1.

More recently, Lbova (2014) presented a review of the UP of Northern Asia. In this paper the most representative archaeological sites are grouped into three stages: the Early UP (EUP: 45–30 cal kyr BP), the Middle UP (MUP: 28/25–19/18 cal kyr BP) and the Final UP (FUP: 17–11 cal kyr BP). The number of sites from Siberia and the Russian Far East, shown in the corresponding maps, increases through time from 24 to 37 and to 55, respectively. In the data synthesis (Lbova, 2014), the mapped sites are not provided with coordinates and ^{14}C age determinations, however their spatial distribution patterns generally repeat that shown in Dolukhanov et al. (2002 and Fig. 1).

Dating and establishing robust chronologies for UP sites remain among the major challenges for archaeological research in Northern Asia (Goebel, 1999; Graf, 2009; Lbova, 2014). However, with the introduction of AMS dating to archaeological research, the situation is constantly improving and numerical analysis of series of ^{14}C dates is becoming a generally accepted approach when discussing the occupation dates and spatiotemporal dynamics of archaeological sites (e.g. Dolukhanov et al., 2002; Fiedel and Kuzmin, 2007; Kuzmin, 2009).

Another methodological problem for such studies, as discussed by Kuzmin and Keates (2005), is how to convert individual ^{14}C dates from different sites into frequencies of human occupation for comparison with continuous records of past environments and climate. Fiedel and Kuzmin (2007), using the published ^{14}C data, addressed this problem by converting ^{14}C date frequency into an index of intensity of the UP occupation of Siberia between ca. 42 and 14 cal kyr BP. These results, together with recently published information from key archaeological sites (see Fig. 1 for site names and locations), are used in the discussion section along with the proxy records of past climate and vegetation.

3.2. Sedimentary records of past climate and vegetation

Robustly dated continuous (or even semi-continuous) terrestrial proxy records, which represent environmental and climatic conditions of Northern Asia ca. 50–10 cal kyr BP, are rare. Among them, long pollen records obtained from lake sediment cores are a particularly important source of information that is needed to discuss regional and local responses of the UP humans and environments to large-scale climate changes (e.g. Bezrukova et al., 2010; Brauer et al., 2014; Litt and Anselmetti, 2014; Rach et al., 2014; Stebich et al., 2015). The problems of generating such records, however, are manifold, including chronological control (e.g. Colman et al., 1996; Bronk Ramsey et al., 2012), significant technical challenges, financial considerations, labour and time investments necessary for sediment core recovery and detailed analyses (e.g. Melles et al., 2012; Nakagawa et al., 2012).

In this paper, we use records of vegetation and climate from robustly dated lake sedimentary archives from Northern Asia that were published over the past decade (see Fig. 1 for record names and locations) for discussion and comparison with the internationally known conventional scenario of the last glacial environments (Ray and Adams, 2001) based on a range of literature and cartographic sources and presented as a series of GIS-based maps that show the regional and global distribution of vegetation during the Last Glacial Maximum interval (LGM) ca. 25–15 ^{14}C kyr BP (i.e. ca. 30–18 cal kyr BP; Lambeck et al., 2014). The work of Ray and Adams (2001) has been selected as it was developed for use by archaeologists and anthropologists.

To strengthen and facilitate the following discussion and comparison with the existing records and environmental reconstructions, we selected two long pollen records and presented them in more details in the Results and Discussion section. Lake Kotokel (site 1 in Fig. 1) situated in the Trans-Baikal region provides a reference record of vegetation and climate history in the southern part of Siberia from ca. 47 cal kyr BP (Bezrukova et al., 2010; Tarasov et al., 2017, 2019). Lake Billyakh (site 2 in Fig. 1) in the upper reaches of the Lena River provides a reference record of vegetation and climate history in the northern part of Siberia over the past ca. 50 cal kyr BP (Müller et al., 2010; Tarasov et al., 2013b). For detailed information on lake setting, coring equipment, data analyses and reconstruction methods, readers are referred to the original publications. For the purposes of this study, simplified pollen diagrams, covering the focus interval between ca. 50 and 10 cal kyr BP, were created using the Tilia software package (Grimm, 1993, 2004).

3.3. Animal records

Before the introduction of plant cultivation and animal husbandry during the past ca. 10 cal kyr BP, human populations in Northern Asia wholly relied on wild resources. Therefore, a detailed reconstruction of plant and animal communities and their accurate dating are important for understanding the nutritional characteristics and survival strategies of ancient human populations on a local and regional scale. This research field has also benefited greatly from enhanced international collaboration and the introduction of the AMS dating method in the routine work of palaeontologists and zooarchaeologists over the past decade (e.g. Kuznetsova et al., 2019; Markova et al., 2015; Puzachenko et al., 2017). The recently published syntheses used in the following discussion present rich and directly dated information on changes in the geographical distribution of large mammals, such as the musk ox, steppe bison (Markova et al., 2015) and Eurasian mammoth (Puzachenko et al., 2017) in Northern Eurasia since ca. 50 cal kyr BP. Kuznetsova et al. (2019) focused on the changes in palaeozoological assemblages of the late Pleistocene and Holocene deposits of the Bykovsky Peninsula (site 3 in Fig. 1) in the Lena River delta region and offered insight in the animal history of the northernmost part of eastern Siberia over the past 50 cal kyr BP.

4. Results and Discussion

This section turns to the central questions posed in the title of this paper: What do we know and what would we like to know about environments of Northern Asia during the UP period and how these palaeoenvironments are linked to human occupation and dispersal?

4.1. Chronology of the UP in Siberia

Accurate chronology is crucial when discussing human-environmental interactions and possible impacts (including leads and lags) of climatic shifts on humans and regional environments (e.g. Fiedel and Kuzmin, 2007; Kobe et al., 2020; Weber et al., 2013, 2016). The spatiotemporal range of the Upper Palaeolithic defined on the basis of changes in material complexes and absolute dating varies between different authors and publications. More systematic applications of direct AMS dating and Bayesian modelling have led to progress in solving this issue (e.g. Douka et al., 2013). The authors of the latter work stated that significant changes in human behaviour, cognition and innovation became obvious in the archaeological record of Eurasia about 45 cal kyr BP and suggested this date as the onset of the UP period. This age is in general agreement with the emergence of the EUP in Siberia defined by Kuzmin (2009). He dated the onset of the UP to ca. 43 ^{14}C kyr BP (ca. 48–45 cal kyr BP) in the Altai Mountains and to ca. 38 ^{14}C kyr BP (ca. 44–42 cal kyr BP) in the Trans-Baikal region, but assumed coexistence of Middle Palaeolithic and EUP complexes during the following millennia (Kuzmin, 2009). Further support for the very early onset of the UP in Siberia came from the first genetic identification of the AMH remains found in western Siberia, near the village of Ust'-Ishim (site 11 in Fig. 1). The remains were dated to ca. 45 cal kyr BP (i.e. 46,880–43,210 cal yr BP at 95.4% probability), making the Ust'-Ishim man the oldest directly ^{14}C-dated AMH found outside Africa and the Middle East (Fu et al., 2014). The radiocarbon ages for the oldest pendants and the bone points found at Denisova Cave (site 18 in Fig. 1; 51°23′51.3″ N, 84°40′34.3″E; 670 m a.s.l.) overlap with the directly dated AMH remains from Ust'-Ishim, thus raising the possibility of a connection between the spread of modern humans and the emergence of innovative technologies and symbolic artefacts in this region as early as 48 cal kyr BP (Douka et al., 2019). However, no skeletal or genetic remains of modern humans of that age have yet been recovered (Jacobs et al., 2019). The ongoing multi-disciplinary investigations at Strashnaya Cave (site 19 in Fig. 1; 51°10′26.0″N, 83°01′42.6″E; ca. 510 m a.s.l.) have contributed new information concerning Middle and Upper Palaeolithic cultural variability in the Altai Mountains and provided the first regional evidence for the presence of AMH during the LGM (Krivoshapkin et al., 2016, 2018).

The upper boundary of the UP in Northern Asia is rather controversial and subjectively drawn. This is related to the particularities of regional cultural developments and definition of the onset of the Mesolithic and Neolithic in different regions. The conventional date of ca. 10 cal kyr BP is still accepted as the boundary between the Palaeolithic and Mesolithic in the Baikal region (e.g. Kobe et al., 2020) and in Northern China (e.g. Sun et al., 2014). Lbova (2014), discussing the UP developments in the larger region of Northern Asia, pushed it to ca. 12/11 cal kyr BP, which represents the Late Pleistocene–Holocene climatic transition, while Tabarev (2014) placed the Palaeolithic/Neolithic boundary at ca. 13 cal kyr BP, which broadly corresponds to the appearance of early pottery in the Russian Far East and the beginning of the Allerød interstadial. Fiedel and Kuzmin (2007) selected ca. 14 cal kyr BP, which slightly postdates the abrupt Lateglacial climate warming (i.e. Bølling interstadial) dated to 14.7 cal kyr BP. Long et al. (2017), using an extensive ^{14}C dataset from Neolithic and Early Bronze Age sites in the Haidai region of East China and a Bayesian modelling approach, demonstrated the existence of systematic overlaps between the cultural periods, which likely indicate the coexistence of different cultural groups and higher cultural diversity in this topographically and climatically complex region in contrast to conventional chronologies which suggest clear-cut separations between different cultural periods. The same features should be expected in the much larger and environmentally complex Northern Asia (e.g. Kuzmin, 2009). An in-depth discussion of the chronological boundaries of the UP archaeological cultures is beyond the scope of our paper. Therefore, the environmental records presented in the following sections cover (if available) the entire interval from ca. 50 to 10 cal kyr BP.

4.2. *Vegetation cover: desert or not?*

There were numerous attempts to reconstruct last glacial vegetation cover of Northern Asia at local and regional scales. The published summaries (e.g. Frenzel et al., 1992; Velichko, 2009) mainly rely on poorly dated and discontinuous results of pollen analysis of terrestrial sequences supplemented by results obtained from archaeological layers and the stomachs of large herbivores preserved in the permafrost. Ray and Adams (2001) presented a GIS-based map that shows the distribution of major vegetation types in Asia during the LGM between ca. 30 and 18 cal kyr BP. Here, we use the part of this map, which represents Northern Asia (Fig. 3) for discussion and comparison with recent studies.

According to the LGM vegetation map by Ray and Adams (2001), much of Siberia and Central Asia was desert-like (areas indicated by categories 15 and 16 in Fig. 3) with less than 2% ground cover by any species of vascular plants, while most parts of the remaining area were covered by scarce steppe-tundra vegetation resembling semi-desert (category 14 in Fig. 3) or year-round ice or snow (category 26 in Fig. 3). An open boreal woodland vegetation cover (category 11 in Fig. 3) is reconstructed in the northern part of Honshu, Japan. This reconstruction shows hostile environments that are unsuitable for large herbivores, but also for human habitation during the entire MUP and, thus, contradicts the recent archaeological site data for this interval (e.g. Fig. 3; Dolukhanov et al., 2002; Lbova, 2014). Today, there is sufficient new information that helps to resolve this apparent contradiction. Here we selected the environmental records of lakes Kotokel and Billyakh, representing the northern and southern parts of the vast zone, for which Ray and Adams (2001) reconstructed polar and alpine desert vegetation and year-round cold LGM climate.

The pollen record (Fig. 4) of Lake Kotokel (52.78°N, 108.12°E; 458 m a.s.l.) demonstrates changes in the percentages of main pollen/plant taxa, which reflect changes in local and regional vegetation during the entire UP (Bezrukova et al., 2010; Tarasov et al., 2017, 2019). From ca. 47 to 30 cal kyr BP (i.e. during the EUP phase) the pollen composition demonstrates high percentages of *Artemisia* (30–50%) and *Betula* sect. *Nanae/Fruticosae* (up to 40%). Arboreal pollen (AP) taxa, mainly represented by *Picea*, *Larix* and *Pinus*, contribute 10–30% in this zone (Fig. 4). These data suggest predominantly open landscapes around the lake and vegetation consisting of cold steppe and tundra communities with scattered trees (or isolated forest stands) occupying locally wetter habitats (Tarasov et al., 2017).

The interval between ca. 30 and 18 cal kyr BP, which corresponds to the MUP (Lbova, 2014) and LGM represented by the vegetation map (Fig. 3), reveals the highest percentages of *Artemisia* (up to 80%) and Poaceae (25–40%) and very low pollen contribution of boreal trees and

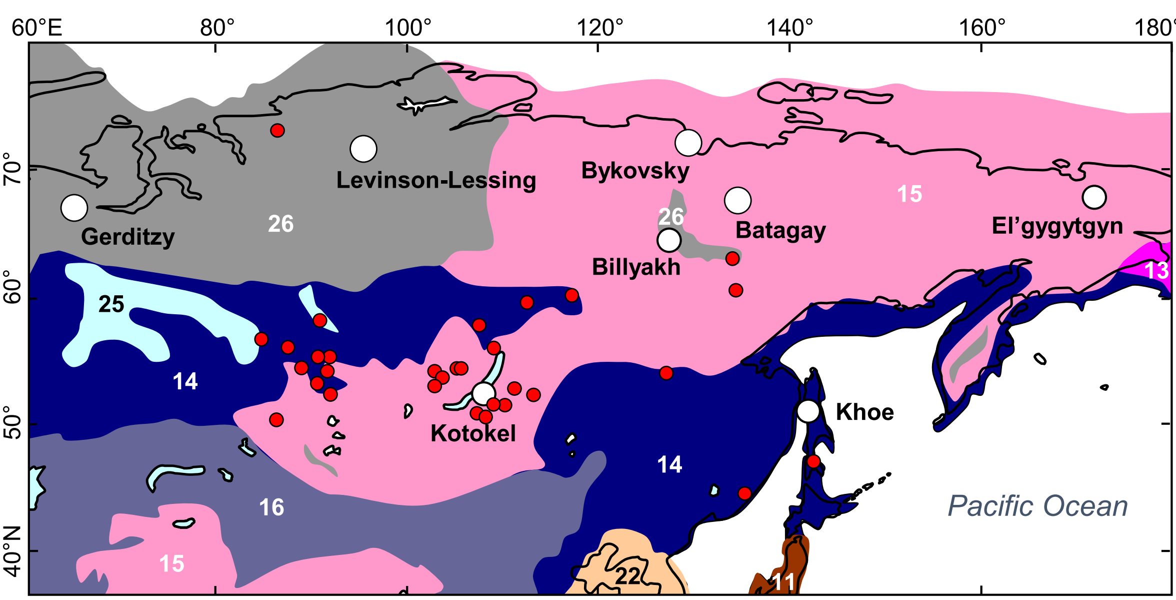


Fig. 3. Reconstruction of vegetation and land cover in Northern Asia during the Last Glacial Maximum (ca. 30–18 cal kyr BP) proposed by Ray and Adams (2001) and assessed in the current study. The present-day coast line is shown for orientation. Red dots indicate the location of archaeological sites (Dolukhanov et al., 2002) assigned to the same time interval. Numbers of land cover categories (from Ray and Adams, 2001): 11 – open boreal woodlands (less than 60% canopy cover); 13 – tundra (greater than 2% cover by low shrubs or grasses); 14 – steppe-tundra (plant cover around 50%, bare ground abundant); 15 – polar and alpine desert (less than 2% ground cover by vascular plants); 16 – temperate desert (less than 2% ground cover); 22 – dry steppe (greater than 20% vegetation cover, mainly grasses); 25 – lakes and open water bodies; 26 – ice sheet and other permanent ice. To avoid confusion with the land cover category numbers, full names of the palaeoenvironmental records (white circles) are given (see also Fig. 1). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

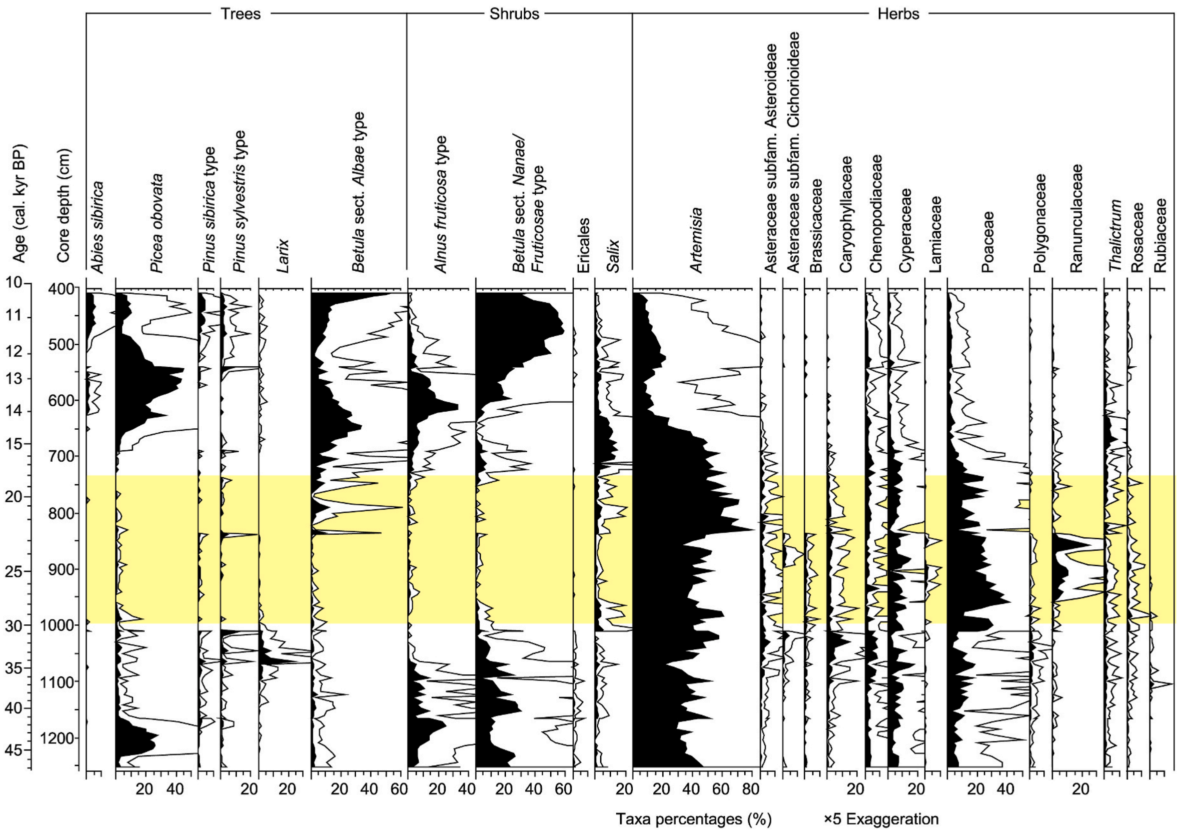


Fig. 4. Percentage diagram of the Lake Kotokel pollen record for the interval 47–10 cal kyr BP (after Bezrukova et al., 2010). Yellow band indicates the Last Glacial Maximum interval (ca. 30–18 cal kyr BP). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

shrubs, suggesting that cold steppe predominated in the region. However, the limited presence of boreal trees and shrubs indicates that these drought-tolerant and cold-resistant taxa could survive the LGM in locally moist habitats (Tarasov et al., 2017). In addition, the moderately high values of sedge and grass pollen, the absence of *Ephedra* (a typical desert plant) pollen, as well as a very low percentage of Chenopodiaceae (Fig. 4) neither support sparse nor desert vegetation in this area throughout the entire LGM (Bezrukova et al., 2010; Müller et al., 2014).

The final stage of the UP in the Lake Kotokel record reveals noticeable changes in the pollen assemblage composition (Fig. 4). An increase in *Picea* up to 20–50% along with an increase in *Betul*a sect. *Nanae/ Fruticosae* and *Alnus fruticosa* shrubs pollen up to 40% occurs between ca. 14.5–12.7 cal kyr BP. These changes indicate a rather quick spread of the boreal woodland and shrub tundra vegetation with a significant contribution of spruce, fir and larch and shrubs of alder, birch and willow (Bezrukova et al., 2010; Tarasov et al., 2017). A sharp decrease in AP percentages accompanied with high values of shrubby birch (40–55%) and herbaceous pollen (up to 35%) between ca. 12.7 and 11.7 cal kyr BP suggest a retreat of trees and spread of tundra and steppe vegetation in the area. The initial phase of the Holocene interglacial again reveals the predominance of AP taxa including birch, spruce, fir and larch in the pollen assemblages and decrease in *Artemisia* to below 10%. The pollen spectra suggest a quick recovery of forest vegetation and spread of boreal woodland in the area around the lake (Bezrukova et al., 2010; Tarasov et al., 2017).

The pollen record of Lake Billyakh (65.28°N, 126.78°E; 340 m a.s.l.) situated in the western foreland of the Verkhoyansk Mountains, about 140 km south of the Arctic Circle (Müller et al., 2010; Tarasov et al., 2013b), is presented in Fig. 5. The pollen assemblages dated to ca. 50–30 cal kyr BP show the predominance of herbaceous taxa, mainly grasses and sedges. *Artemisia* pollen percentages are low prior to 40 cal kyr BP, but reach 10–20% after this date. Several times during this interval, the total percentages of shrub pollen (mainly birches and alder) increase to above 20%. The pollen grains of larch and birch trees are rare but constantly present in the sediment. Such pollen assemblage composition indicates the widespread distribution of herbaceous tundra communities in the landscape, while frost-resistant boreal shrubs and trees likely occupied isolated locations with the most favourable microclimate. The cold steppe associations with wormwood and other herbs occupied drier habitats (Müller et al., 2010; Tarasov et al., 2013b).

The interval between ca. 30 and 18 cal kyr BP shows the absolute dominance of herbaceous taxa, mainly sedges, grasses and wormwood, but also members of Caryophyllaceae, Ranunculaceae and Asteraceae. The percentage of shrub taxa never exceeds 20% and pollen of larch almost disappear during this phase (Fig. 5). Müller et al. (2010) reconstructed a vegetation mosaic of steppe and tundra communities in the area around the lake, but did not find palynological evidence for extreme aridity, an arctic desert environment, or sparse vegetation. Although contributions of AP taxa are the lowest for the entire period, especially from 27 to 17 cal kyr BP, continuous presence of larch and birch trees in the region is remarkable. It was suggested that the western and southern forelands of the Verkhoyansk Mountains provided enough moisture and warm microhabitats to buffer larch specimens against climatic extremes even during the globally colder- and drier-than-present LGM (Tarasov et al., 2007; Müller et al., 2010). Indeed, living trees of *Larix dahurica* were found ca. 750 km north of Lake Billyakh within the arctic tundra-dominated landscape with a mean July temperature of about 8 °C and annual precipitation below 300 mm (Pisaric et al., 2001). Another important feature of larch and other boreal trees in Siberia is their ability to survive unfavourable times as a prostrate shrub. This life form is particularly resistant against strong winds, low temperatures and thin snow cover and has been found as far north as ca. 74.5°N (Andreev et al., 2003; Tarasov et al., 2013b).

During the final stage of the UP, the pollen assemblages change

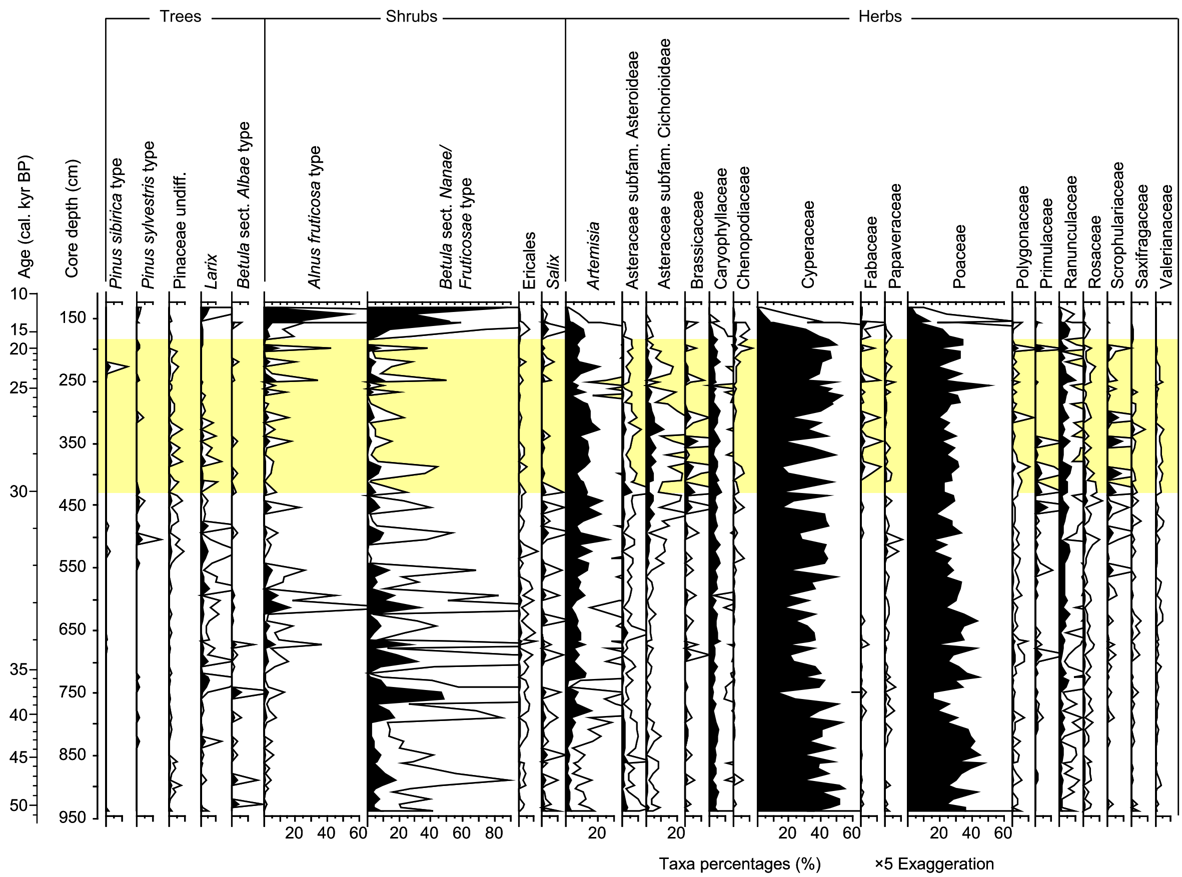


Fig. 5. Percentage diagram of the Lake Billyakh pollen record for the interval 50–10 cal kyr BP (after Müller et al., 2010). Yellow band indicates the Last Glacial Maximum interval (ca. 30–18 cal kyr BP). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

pronouncedly (Fig. 5). An increase in the percentages of larch, birch and alder shrubs accompanied by a sharp decrease in the percentages of all major herbaceous taxa indicate a fairly rapid spread of shrub tundra and boreal woodland around Lake Billyakh. A pollen-based wood cover reconstruction (Tarasov et al., 2013b) shows a shift from very low values during the LGM to 10% at ca. 13.5 cal kyr BP, a slight decrease to 8% during the Younger Dryas and a subsequent increase in wood cover up to 25% at about 10.5 cal kyr BP.

The two representative pollen records from Kotokel and Billyakh demonstrate a very similar pattern of vegetation changes between ca. 50 and 10 cal kyr BP. Although both records indicate an almost complete disappearance of forest vegetation (although leaving room for individual tree specimens, possibly in the form of prostrate shrubs, in the most favourable habitats), there is no evidence supporting reconstructions of polar or temperate desert and extensive areas of bare land with limited plant cover. Comparison with other vegetation records from different parts of Northern Asia helps to evaluate the validity of this conclusion across space and time.

A well-dated continuous pollen record from Lake El'gygytgyn (site 4 in Fig. 1; 67.5°N, 172.0°E; 492 m a.s.l.) located 100 km to the north of the Arctic Circle within the treeless tundra of the Chukotka Peninsula also demonstrates absolute predominance of herbaceous pollen between ca. 50 and 15 cal kyr BP, with Poaceae pollen contributing ca. 45–75% to the total pollen sum followed by *Artemisia*, Cyperaceae, Caryophyllaceae and Papaveraceae (Lozhkin et al., 2007; Matrosova, 2009). This pollen composition has been interpreted as representing the herb-dominated tundra vegetation near the lake, similar to that found in some areas of Chukotka and on Wrangel Island today. The quantitative method of biome reconstruction (Prentice et al., 1996) applied to the El'gygytgyn pollen record (Melles et al., 2012) resulted in recognition that the cold steppe biome was the dominant vegetation type, which, by ca. 14.9 cal kyr BP, was replaced by the tundra biome (Tarasov et al., 2013a). Lozhkin et al. (2007) suggested a largely barren LGM landscape around the lake, based on lower-than-present pollen concentrations in the analysed sediment samples. However, the relative decrease in pollen concentration can also be explained by other factors, for example, by generally lower pollen productivity of herbaceous vegetation compared to modern shrub-tundra or forest-dominated landscapes, as proved by a study of modern surface pollen spectra from eastern Siberia by Müller et al. (2010). The minimal presence of *Salix* and other shrub taxa (e.g. *Betula*, *Alnus* and *Pinus pumila*), likely representing the dispersed populations of these plants in the region, and the very rapid spread of shrub tundra vegetation around the lake soon after 14.9 cal kyr BP, also speak against an arctic desert environment around Lake El'gygytgyn between ca. 50 and 15 cal kyr BP.

The pollen record from the Khoe sedimentary sequence (site 5 in Fig. 1; 51.34°N, 142.14°E, 15 m a.s.l.), located on the western coast of Sakhalin Island, reveals the vegetation history in the easternmost part of the Asian taiga zone during the last ca. 43,700 years (Leipe et al., 2015). In the pollen assemblage, spruce, pine, larch and birch pollen predominate over fir, indicating that boreal conifer forest grew around the study site during the represented period (Igarashi and Zharov, 2011). Pollen-based reconstruction of wood cover shows lower than present, but still reasonably high values (i.e. 40–52%), indicating a forested landscape between ca. 43.7 and 30 cal kyr BP (Leipe et al., 2015). During ca. 30–15 cal kyr BP, the tree cover reconstruction shows a decrease to ca. 30–40%, though boreal woody plants (pine, larch and spruce) still occupied large parts of the landscape.

The entire mid-latitudinal belt between Lake Baikal and the Ural Mountains in the west and the Pacific coast in the east is lacking vegetation records spanning the 50–10 cal kyr BP interval (Binney et al., 2017). However, valuable information comes from the arctic regions. The pollen record from Levinson-Lessing Lake (site 6 in Fig. 1; 74.47°N, 98.63°E; 47 m a.s.l.) reveals vegetation changes on the northern Taymyr Peninsula during the last ca. 34,000 years (Andreev et al., 2003). The pollen assemblage composition, similar to that of Lake El'gygytgyn, confirms that steppe-like vegetation with Poaceae, *Artemisia* and Cyperaceae predominated ca. 28–14.8 cal kyr BP, while tundra-like vegetation communities with *Oxyria*, Ranunculaceae and Caryophyllaceae grew in locally wetter habitats (Andreev et al., 2003). A change from the herb-dominated vegetation to shrubby tundra with birch, alder and willow species is registered after 14.8 cal kyr BP.

Further west, Svendsen et al. (2014) reconstructed the glacial vegetation history using the pollen record from Lake Gerditzy (site 7 in Fig. 1; 66.83°N, 66.0°E, 213 m a.s.l.), which is situated in the Polar Urals. Their record reflects a herbaceous tundra and steppe-like vegetation throughout 60–11.7 cal kyr BP, but a first significant increase of dwarf-shrub willow and birch communities occurred at around 15 cal kyr BP or shortly after, which is similar to the records from the regions in the east. Forests of birch and spruce established in the area very quickly, just a few hundred years after the Holocene transition (Svendsen et al., 2014).

The great value of the pollen analysis for environmental reconstructions and archaeology is widely acknowledged (e.g. Bryant and Holloway, 1983; Faegri and Iversen, 1989), however, pollen-based reconstructions may be ambiguous when representing open herb-dominated vegetation types (e.g. Prentice et al., 1996; Peyron et al., 1998; Tarasov et al., 1998, 1999). The most frequently mentioned reasons for this are the insufficiently high taxonomic level of identification (i.e. genus or family for most of the taxa), great differences in pollen productivity, preservation and dispersion between different plants and the possibility of contamination by wind-transported pollen or pollen grains reworked from older sediments (e.g. Faegri and Iversen, 1989). Plant macrofossil records, although rare and seldom continuous, provide much more detailed information about past vegetation assemblages and can be securely dated with the AMS ^{14}C dating technique (e.g. Kienast et al., 2005; Werner et al., 2010). Northern Asia, with its cold climate and widely-spread permafrost, provides excellent environments for plant macrofossil preservation, thus allowing verification of pollen-based interpretations.

Recently published results obtained from the Batagay permafrost sequence (site 8 in Fig. 1; 67.58°N, 134.76°E, 240–300 m a.s.l.) in the Yana Highlands east of the Verkhoyansk Mountains provide a first insight into the environmental history of the coldest region of Eurasia during the LGM and throughout Marine Isotope Stages (MIS) 6 to 2 (Ashastina et al., 2018). The exceptionally rich plant macrofossil assemblages undoubtedly point to meadow steppe (analogous to modern communities dominated by grasses and forbs), which formed the primary vegetation in the region during the cold stages of the Late Pleistocene, being replaced by larch-dominated open woodland during the interglacial periods. In contrast to the conventional reconstructions of LGM vegetation cover in the region, suggesting a sparsely vegetated arctic desert or species-poor arctic tundra (e.g. Ray and Adams, 2001), the Batagay palaeobotanical records suggest meadow steppe vegetation with largely open grounds, scattered larch stands, and ephemeral ponds or puddles ca. 29–14 cal kyr BP and similar vegetation with tundra-steppe inclusions and small woods during ca. 50–29 cal kyr BP in this area north of the Arctic Circle (Ashastina et al., 2018). Plant macrofossils from the Mamontovy Khayata permafrost section (site 3 in Fig. 1; 71.75°N, 129.42°E; ca. 40 m s.l.) on the Bykovsky Peninsula in the southern Lena River delta also reflect a mosaic vegetation during the last glacial period composed of arctic, aquatic, littoral, meadow and steppe taxa similar to modern vegetation mosaics described for the central Yakutian relict steppe areas (Kienast et al., 2005).

A virtual absence of woody plant remains in the sedimentary records from Northern Asia assigned to the last glacial interval is commonly taken as proof of extremely cold environments (i.e. arctic desert or arctic herbaceous tundra) and a poor vegetation cover. Those cases in which arboreal pollen has been identified (e.g. Bezrukova et al., 2010; Müller et al., 2010) are generally met with scepticism and explained by long-distance transport. However, a growing body of evidence based on ^{14}C-dated pollen and plant macrofossil records (e.g. Binney et al., 2009, 2017; Müller et al., 2010; Werner et al., 2010) argues against such interpretations. Tarasov et al. (2007) performed a satellite- and pollen-based quantitative woody cover and biome reconstruction using extensive surface pollen reference data and LGM pollen spectra dated to ca. 24–18 cal kyr BP. Their results confirm that large areas of Northern Asia presently occupied by boreal forests (Fig. 2D) were much more open. However, this work also suggested that boreal broadleaved and needleleaved trees and shrubs likely grew at all analysed sites located within 52–66°N. This may explain the rather quick spread of tree and shrub vegetation across the entire region after 15 cal kyr BP, as indicated by the pollen and plant macrofossil records from Northern Asia cited above.

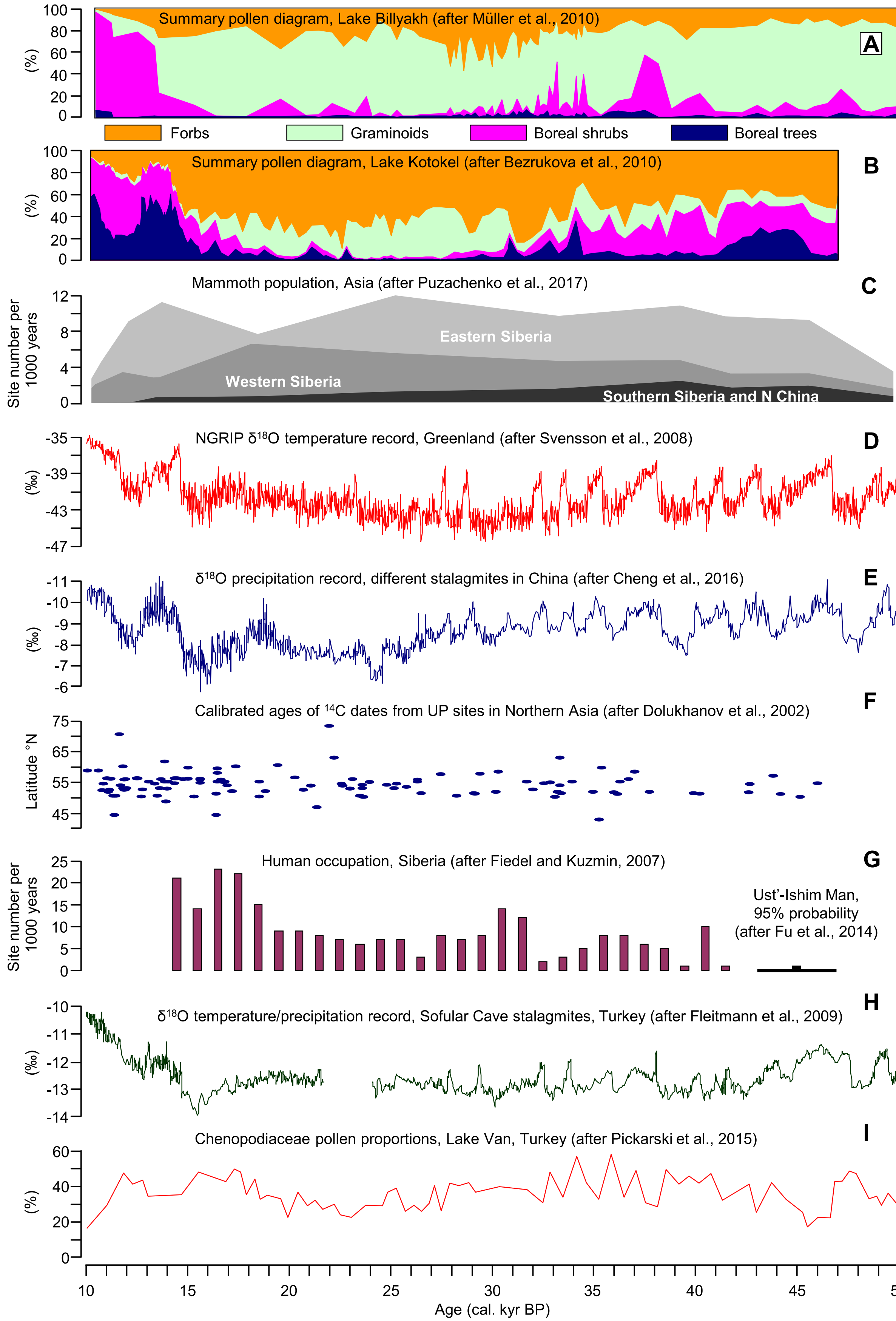
Brubaker et al. (2005), by re-analysing extensive pollen datasets from the north-eastern part of Siberia and Alaska, also concluded that small populations of boreal trees and shrubs were capable of surviving long periods of harsh glacial climate and expanded as climate became warmer. Even more solid proof comes from the ^{14}C database of the Siberian Palaeolithic (Vasil'ev et al., 2002), which reports conventional and AMS dates on wood and charcoal remains from 16 archaeological sites in Siberia and the Russian Far East between 47 and 62°N. It reveals a co-occurrence of woody plants and human populations during the LGM (Tarasov et al., 2007).

The controversy between the virtually treeless LGM landscapes in the ice-free parts of Europe suggested by the pollen-based reconstructions and the climate-based vegetation model simulations which suggest that broad areas of Europe were suitable for trees at that time, has been addressed by Kaplan et al. (2016). Their study hypothesizes that hunting-facilitating fires set by the very mobile UP hunter-gatherer groups could have substantially reduced tree cover there. This raises the intriguing question of to which extent the UP human populations of Northern Asia could have been responsible for the reduction of forest cover during the last glacial period.

4.3. Productive vegetation and glacial fauna

The vegetation records discussed in the previous section advocate that productive meadow and steppe communities consisting of diverse herbs, forbs and grasses played an important role across Northern Asia from the upper reaches of the Lena River to the plains of the Trans-Baikal Region and from the Chukotka Peninsula to the Ural Mountains and could have served as food resources for large populations of herbivores (e.g. Kienast et al., 2005; Müller et al., 2010; Tarasov et al., 2019). These conclusions, initially made on the basis of pollen and plant macrofossil analyses, recently received strong support from a large-scale ancient DNA (aDNA) study by Willerslev et al. (2014), which presented a 50-kyr record of Arctic vegetation history derived from 242 sediment samples from 21 sites across the non-glaciated parts of Eurasia and North America. For the period between 50 and 10 cal kyr BP, the aDNA analysis suggests steppe-tundra vegetation dominated by forbs and graminoids, which remained dominant also during the coldest phase ca. 25–15 kyr BP. Furthermore, genetically analysed stomach contents and coprolites of woolly mammoth, woolly rhinoceros, bison and horse specimens from Siberia and Alaska dating 55–21 cal kyr BP prove that diets of these large herbivores were based primarily on high-protein forbs and grasses, though trees and shrubs aDNA were also identified (Willerslev et al., 2014), thus supporting our conclusions derived from the results of palaeobotanical investigations (Fig. 6A and B).

During the past decade, intensive studies of zoological remains provided rich information about spatiotemporal patterns of glacial fauna in Northern Asia. Puzachenko et al. (2017) performed a



(caption on next page)

Fig. 6. Summary chart showing selected environmental and climate records used in the discussion: summary pollen diagram of (A) Lake Billyakh (after Müller et al., 2010) and (B) Lake Kotokel (after Bezrukova et al., 2010); (C) mammoth population dynamics in Northern Asia (after Puzachenko et al., 2017); (D) the $\delta^{18}O$ ice core records from Greenland, as indicator of the Northern Hemisphere air temperature (after Svensson et al., 2008); (E) the stacked $\delta^{18}O$ record from Chinese stalagmites as a proxy for Asian summer monsoon intensity (after Cheng et al., 2016); (F) distribution of calibrated ages of ^{14}C dates from Upper Palaeolithic archaeological sites in Northern Asia (after Dolukhanov et al., 2002) plotted along latitude; (G) frequencies of calibrated ages of occupation "centroids" for the Siberian Palaeolithic (after Fiedel and Kuzmin, 2007); (H) the $\delta^{18}O$ record of Sofular cave stalagmites, indicating temperature and precipitation changes (after Fleitmann et al., 2009); and (I) Chenopodiaceae pollen percentages in the Lake Van sedimentary record (after Pickarski et al., 2015).

comprehensive analysis of the regional aspects in the Eurasian mammoth distribution during the past 50 cal kyr BP. Their analysis demonstrates some distinct variations in the absolute number and concentration of localities with dated mammoth finds in the large regions of Northern Asia (Fig. 6C). The highest concentration of mammoth localities per 1000 years is recorded in eastern Siberia, which indicates a rather stable mammoth habitation between ca. 46 and 13 cal kyr BP, with a maximum concentration recorded during the LGM (Fig. 6C) and a maximum density of localities and the broadest range during the Denekamp interstadial ca. 38–29 cal kyr BP (Puzachenko et al., 2017). In western Siberia, concentration and density values are relatively high between 41 and 15 cal kyr BP, reaching a maximum ca. 22–15 cal kyr BP. In southern Siberia, finds are less numerous and maximum concentrations occurred ca. 41–38 cal kyr BP (Fig. 6C). All three regions show a drastic reduction in sites and distribution area after 15 cal kyr BP and the last remains of the mammoth population survived only north of 70°N (Puzachenko et al., 2017).

Another study, focusing on changes in the distribution of the extinct bison (*Bison priscus*), revealed a broad distribution range of this species in Siberia from the coastal plains in the Asian Arctic to the Trans-Baikal region between ca. 50 and 15 cal kyr BP (Markova et al., 2015), which is in line with the reconstructed productive meadow steppe vegetation of that time. In contrast to the mammoth, the steppe bison distribution area contracted from the north after ca. 15 cal kyr BP with the last remnants surviving in the southern parts of Siberia, while the northern regions hosted the remains of the musk ox (*Ovibos moschatus*), which shared a great part of its distribution area with the bison during the last glacial interval (Markova et al., 2015).

Detailed on-site palaeontological investigations and intensive ^{14}C dating of bone material show an abundant and diverse assemblage of large and small herbivorous and carnivorous animals in different regions of Siberia during the entire 50–10 cal kyr BP interval. Kuznetsova et al. (2019) reported palaeozoological results from permafrost deposits of the Bykovsky Peninsula (site 3 in Fig. 1) on the Laptev Sea coast, supported by 90 ^{14}C dates of animal bones. The obtained results together with numerous dates on terrestrial plant macrofossils (Kienast et al., 2005) indicate that the steppe-like environments of the Late Pleistocene were most favourable for mammoths and ungulates, including horse, reindeer and steppe bison, in the northern parts of eastern Siberia (Kuznetsova et al., 2019).

Studies from the southern part of eastern Siberia also demonstrate abundant remains of large herbivores in sediment layers dated to the LGM (e.g. Kuzmin, 2009; Lbova, 2009). The fossil bone assemblage from the Tunka Valley (site 9 in Fig. 1) west of Lake Baikal dated to ca. 42–30 cal kyr BP revealed remains of wholly rhinoceros, twisted-horned antelope, red deer, horse and Mongolian gazelle, but also a number of small mammals such as long-tailed ground squirrel, steppe vole and narrow-headed vole (Kozyrev et al., 2014; Shchetnikov et al., 2015, 2019), which are typical representatives of the productive steppe, meadow and tundra landscapes, inhabiting this area during the last glacial period. Future investigations in the central parts of Siberia must fill the gap in our current knowledge about plant cover and animal communities during the last glacial. However, the fossil animal records from the northern and southern regions are in line with the botanical and aDNA records in not supporting desert environments in Northern Asia between 50 and 10 cal kyr BP, not even during the LGM.

4.4. Climate of the UP

The climate of the Northern Hemisphere between ca. 50 and 10 cal kyr BP was affected by extensive ice sheets, which covered large parts of Europe and North America and caused lower-than-present annual temperature, atmospheric precipitation and global sea level that reached the lowest levels during the LGM and steadily increased towards the Early Holocene (e.g. Cheng et al., 2016; Miller et al., 2010; Wolff et al., 2010). Although scientists basically agree upon these general features and trends, the spatiotemporal climate dynamics and their implications for the regional environments as well as inter-annual climate variability and absolute values of reconstructed variables remain highly debated topics. In Northern Asia such debates are particularly intense and include all aspects of the last glacial environments. This is to some extent related to its huge area, poor accessibility of remote and scarcely populated regions, and high costs for organizing and running field research. The past 20 years has witnessed substantial progress in the research on Late Pleistocene environments, which allows reconsideration of earlier reconstructions. In particular, the hypothesis of a pan-Eurasian ice sheet covering the Arctic and Pacific regions of Siberia (Grosswald, 1998), that biased earlier climate model simulations (e.g. Kageyama et al., 2001) and proxy-based reconstructions (e.g. Ray and Adams, 2001), has undergone a major revision (e.g. Andreev et al., 2011; Melles et al., 2012; Svendsen et al., 2004, 2014). This revision corroborates the geomorphological and palaeontological data, indicating that the vast areas of Northern Asia outside high mountain ranges were ice-free and well-vegetated, providing continuously hospitable environments and enough food for a large population of herbivores and predators, the so-called "mammoth fauna", over many thousands of years (e.g. Willerslev et al., 2014). The existence of such environments in Siberia, particularly in its coldest northern regions, during the UP cannot be adequately explained by the still widely accepted "year-round colder-than-present climate scenario". The $\delta^{18}O$ data from Greenland ice cores (e.g. Svensson et al., 2008), commonly considered as a high-resolution record of Northern Hemisphere climate (Fig. 6D), reflect fluctuations in mean annual temperature between 50 and 10 cal kyr BP. Although some of the major identified fluctuations can be traced in the isotope and pollen records from the different parts of Northern Asia (e.g. Bezrukova et al., 2010; Leipe et al., 2015; Müller et al., 2010; Tarasov et al., 2019), a number of questions remain unresolved. For example, were these thermal fluctuations of the same amplitude (i.e. up to ca. 20 °C, regarding mean annual temperature) as reconstructed for Greenland (Alley, 2000; Cuffey and Clow, 1997) and how did they impact the summer and winter seasons?

Quantitative reconstructions of the last glacial climate in Northern Asia have been mainly obtained from pollen records (e.g. Frenzel et al., 1992; Leipe et al., 2015; Müller et al., 2010; Stebich et al., 2015; Tarasov et al., 1999, Tarasov et al., 2013a, 2017). However, pollen-based temperature reconstructions for the glacial period are inconclusive, since herbaceous pollen taxa identified at the genus or family level have very broad bioclimatic tolerances and can be found in cold and warm climates (Tarasov et al., 1998). Therefore, pollen-derived summer and winter temperature reconstructions have very large probability ranges (Leipe et al., 2015; Tarasov et al., 1999). Conventionally, warmer-than-present summer temperatures were considered implausible in most publications. The first more accurate evidence of warm glacial summers in the Siberian Arctic was obtained from a plant macrofossil record, which allowed precise taxonomic identification of plant remains. The composition of seeds and other plant macrofossils from the Mamontovy Khayata permafrost sequence on the Bykovsky Peninsula (Kienast et al., 2005) reflects an extremely continental, relatively dry climate with winters colder and summers distinctly warmer than at present in the eastern Siberian Arctic during the last cold stage. This contradicts earlier reconstructions of very low summer temperatures (i.e. close to 0 °C) during the last cold stage across the northern Siberian lowlands (e.g. Frenzel et al., 1992; Velichko, 2009). Using an indicator-species approach, Kienast et al. (2005) reconstructed mean July temperatures above 12 °C for most of the last cold stage in the study area, where modern mean July temperatures are about 7 °C.

The temperature reconstruction derived from the chironomid record of Lake Kotokel (Tarasov et al., 2019) suggests at least 3.5 °C higher-than-present summer temperatures during the LGM in the southern part of eastern Siberia. Overall, it appears that environments in central Eurasia during the LGM were affected by much colder-than-present winter temperatures, but similar or higher-than-present summer temperatures, although the effects of temperature oscillations on vegetation were enhanced by changes in humidity (Tarasov et al., 2019). Newly obtained robustly dated palaeovegetation records and proxy-based precipitation reconstructions from sites in Northern Asia (e.g. Kobe et al., 2020; Tarasov et al., 2013a, Tarasov et al., 2013b, 2017) suggest that lower-than-present annual precipitation and severe winters coupled with thin snow cover and low atmospheric CO_2 concentrations were the main factors responsible for the extensive spread of steppe and herbaceous tundra and the virtual absence of trees in the last glacial landscape of Siberia. Wildfires associated with warm and relatively dry summers and with grazing pressure of rich herbivorous megafauna could have played an additional role in the poor representation of woody plants in the vegetation cover.

4.5. Humans: why go, why stay?

In the unceasing discussion on the spread of AMH populations out of Africa and across the world the frequently asked questions are about timing and driving forces of these human migrations. The available archaeological data from Northern Asia proves that modern humans were present at Ust'-Ishim in the Irtysh River valley, western Siberia (site 11 in Fig. 1) already ca. 46.9–43.2 cal kyr BP (Fu et al., 2014). Since this site is situated at ca. 57.7°N, i.e. relatively far north, it is plausible that AMH were present in the Altai region of southern Siberia even earlier, i.e. ca. 48–45 cal kyr BP, as suggested by Kuzmin (2009) and Douka et al. (2019). These earlier dates fall within one of the Human Dispersal Windows hypothesized by Timmermann and Friedrich (2016). The foothills of the Altai Mountains were assumed to be the first region occupied by AMH in Siberia (Derevianko et al., 2014; Jacobs et al., 2019; Kuzmin et al., 2009). From there they spread further north and east reaching the Lake Baikal region ca. 44–42 cal kyr BP and Mongolia and Northern China ca. 40 cal kyr BP (Lbova, 2014 and references therein). The archaeological sites of the EUP in Siberia are mainly associated with the valleys of the Irtysh, Angara, Lena and Selenga rivers and their tributaries (Lbova, 2014). The Yana site (site 13 in Fig. 1; 70.72°N, 135.42°E) dated to around 31 cal kyr BP clearly demonstrates that AMH explored very remote areas in the north-eastern part of Siberia already in the EUP and before the LGM (Pitulko et al., 2004; Nikolskiy and Pitulko, 2013). The MUP experienced an increase in site numbers (Fig. 6G). More sites have been found in the arctic regions north of 60°N, including Ikhine (site 12 in Fig. 1; ca. 63°N) at the Aldan River in the central part of eastern Siberia (Lbova, 2014) and Tarachikha (site 14 in Fig. 1; 73.07°N, 86.83°E) on the Taymyr Peninsula (Dolukhanov et al., 2002). Numerous sites are also documented along the Yenisei River ca. 51–56°N (Lbova, 2014). The multi-layered MUP site Ogonki-5 (site 15 in Fig. 1; 46.78°N, 142.48 E) on Sakhalin Island is dated to 23–21 cal kyr BP (Rudaya et al., 2013). During the FUP stage (ca. 16–13 cal kyr BP), archaeological sites are found in the easternmost part of Northern Asia, e.g. Ushki (site 16 in Fig. 1) on the Kamchatka Peninsula (Dolukhanov et al., 2002). The in-depth discussion of archaeological evidence is beyond the scope of our paper. However, studies focused on the discovery and direct dating of human remains will provide new facts on spatiotemporal patterns of the UP human occupation of Northern Asia (e.g. Douka et al., 2013; Krivoshapkin et al., 2018; Shchetnikov et al., 2019).

Direct dates from archaeological sites (Dolukhanov et al., 2002; Fiedel and Kuzmin, 2007, Fu et al., 2014) prove that there was a constant human presence in the Siberian mid-latitudes (ca. 50–60°N) during the entire UP (Fig. 6F). The Altai variant of the Middle to Upper Palaeolithic transition (e.g. Kara-Bom, site 17 in Fig. 1) shows both typological and chronological similarities with the Near East (Lbova, 2014), for example, with the Boker Tachtit site in Israel (e.g. Stepka et al., 2018) dated to ca. 50.4–46.4 cal kyr BP (Kuzmin, 2009). This, and the early date of the AMH from Ust'-Ishim (Fig. 6G; Fu et al., 2014), may indicate the very quick spread of humans and their technologies from the Levant region to Siberia (see Jacobs et al., 2019; Kuzmin, 2009; Lbova, 2014 for discussion and references).

The "quick migration" hypothesis raises two intriguing questions relevant to our study: Why AMH came to this area and why they decided to stay? The answer on the first question is difficult and requires much more careful investigation. What may push and pull people to migrate: the search for a better life, climate change, limited food resources, the wish to exploit new territories? Alterations of climate and environments are often regarded as a trigger for human evolution and dispersal, however, the causality is very difficult to prove (see Blockley et al., 2012 for detailed discussion and references). In the Near East, the important archives, which provide high-resolution and robustly dated records of past environments, are speleothems from the Sofular Cave (41.42°N, 31.93°E) and the Lake Van (38.60°N, 42.90°E) sediments, both located in Turkey. The $\delta^{18}O$ record from the Sofular stalagmites (Fig. 6H; Fleitmann et al., 2009) shows a rapid and sensitive response of the Eastern Mediterranean climate and ecosystem to the hemispheric-scale changes in temperature (Fig. 6D) and precipitation (Fig. 6E). All three records reveal a pronounced climate cooling episode between ca. 49 and 47.7 cal kyr BP. Sedimentary, geochemical and mineralogical analyses of the ICDP cores recovered from the Northern Basin of Lake Van provide evidence of lake level and climatic changes related to orbital forcing and North Atlantic climate change over the last 90 ka (Çağatay et al., 2014). They report a drop in lake level to ca. 50 m below the modern one around ca. 50–48 cal kyr BP followed by a phase of relatively high lake level ca. +10 m above the modern level, suggesting highly unstable climate and weather conditions. The detailed pollen record from Lake Van (Litt et al., 2014; Pickarski et al., 2015), covering the entire last glacial, also shows a ca. 15% increase in Chenopodiaceae pollen to almost 50% of the total pollen sum (Fig. 6I) and virtual disappearance of arboreal pollen around 48 cal kyr BP, suggesting very arid climate conditions in the region. These and other environmental records from the Eastern Mediterranean demonstrate that the climate of the last glacial was cold and dry (Litt et al., 2014; Pickarski et al., 2015). The episode of further cooling and drying of the regional climate ca. 49–47.7 cal kyr BP (Fleitmann et al., 2009) could have been a potential factor that triggered the movement of a part of the AMH population north-eastwards. However, this remains hypothetical and many other factors (e.g. Behrensmeyer, 2006) could have played a role.

Answering the second question – why did they stay? – seems to be easier, particularly when considering the environmental conditions that newcomers found in Siberia ca. 48–45 cal kyr BP. Fu et al. (2014) reported that the diet of the Ust'-Ishim individual reconstructed using carbon and nitrogen isotope ratios was based on terrestrial C_3 plants and animals that consumed them, but also on aquatic foods, such as freshwater fish, which is in line with the reconstructions made for EUP human groups from Europe (e.g. Richards and Trinkaus, 2009). The broad evidence presented and discussed in the previous sections demonstrates that these types of food were available in amounts greatly exceeding the needs of the sparse hunter-gatherer population. River valleys, where most of the archaeological sites are located, would have been a permanent source of fresh water and aquatic foods, but also important routes for seasonal animal migrations. Large herbivores were an important year-round source of protein and also provided all materials necessary for making clothes, tents, weapons and fire. Even wood was available, as suggested by the results of pollen and plant macrofossil investigations (e.g. Ashastina et al., 2018; Tarasov et al., 2007). New investigations performed in the area around the famous site of Mal'ta (site 10 in Fig. 1; ca. 52.85°N, 103.53°E) in the Cis-Baikal region provide a very detailed insight into faunal resources that were available to the UP people, including molluscs, fish and bird species, diverse rodents and 14 species of big mammals, among them hare, wolf, red fox, Arctic fox, wolverine, brown bear, Eurasian cave lion, woolly rhinoceros, Siberian bighorn sheep, horse, red deer, reindeer, steppe bison and mammoth (Khenzykhenova et al., 2019).

Fiedel and Kuzmin (2007) noted that the challenges and opportunities that cold climates posed to anatomically and behaviourally modern humans have been grossly misjudged and Northern Asia did not experience depopulation even during the coldest phase of the last glacial (Fig. 6G). This phenomenon can be explained by the specific Late Pleistocene environments of Siberia that offered some important advantages to UP hunter-gatherers that compensated low winter temperatures. These include productive steppe vegetation and very thin snow cover, which secured year-round grazing grounds for large herbivores and a stable source of food for people (Tarasov et al., 2017; Kobe et al., 2020). Furthermore, warm and relatively dry summers allowed (at least seasonal) habitation even in the northernmost parts of Siberia (e.g. Lbova, 2014; Pitulko et al., 2004; Svendsen et al., 2014). The human diet based on meat and fish was supplemented by wild berries and other plant foods. Absence of extensive mires and boreal forests (the main features of the Holocene environments) and a very thin snow cover facilitated movement and hunting. Although experiencing modifications and innovations during the Mesolithic and Early Neolithic, this life style could persist into the Early Holocene in the Lake Baikal region (Tarasov et al., 2017; Weber et al., 2013) and only collapsed with the extinction of the mammoth fauna, the development of the coniferous taiga belt, separating tundra and steppe zones of Northern Asia, and the major increase in winter precipitation (Kobe et al., 2020).

Assessment of a possible vulnerability of the UP human population in Northern Asia to Late Pleistocene climate variability remains a highly debated topic and subject of future research. Re-evaluating the radiocarbon chronology of the middle and late UP in the Yenisei River valley on a site-by-site and date-by-date basis, Graf (2009) reported at least seven cultural occupations during 31–24.8 cal kyr BP, but no securely dated human occupations between 24.8 and 20.7 cal kyr BP. A drop in the frequency of dated occupations during the coldest phase of the last ice age was also suggested in several other regions of Siberia as a result of harsh climatic conditions (Goebel, 1999, 2002; Goebel et al., 2000). The opposite scenario was proposed by Fiedel and Kuzmin (2007). Using ^{14}C-dated archaeological material (Fig. 6G) and a Northern Hemisphere temperature record (Fig. 6D), they concluded that climate change was not a substantial challenge. However, comparing Fig. 6D, E, 6G, 6H and 6I, one can see that all of the minima in the site occupation data around 39.5, 33, 26.5 and 15.5 cal kyr BP find their contemporary cold and dry oscillations in the climate records from Eurasia. On the other hand, this rule does not work for other oscillations towards dry and cold climates, leaving the question about causality open.

5. Conclusions

The growing body of palaeoenvironmental and palaeoclimate studies from Northern Asia has modified and refined our view of the last glacial landscapes of this vast and supposedly harsh climatic region. The main focus of the current paper is on the character and, in particular, the productivity of vegetation sustaining megafauna and their human predators as well as the climate characteristics generating these productive ecosystems at the time of (rapid) dispersal and occupation by AMH. Existing proxy records suggest that vegetation was generally more abundant than has long been believed and that even during the LGM regional landscapes were not dominated by semi-desert or desert. In most areas, including the coldest regions in the Siberian Arctic, last glacial vegetation was mainly characterized by a steppe and dry tundra mosaic with diverse communities of herbs, forbs and grasses. Within this landscape there were limited stands of woody plants in favourable microhabitats even during the coldest phases of the LGM. That the pollen-based evidence for the existence of woody plants is valid, and not solely the result of long-distance transport, has been verified by records of plant macroremains from sediment sequences, aDNA from food remains of large mammals, and wood and charcoal remains from archaeological sites. We see further evidence for small woody plant populations throughout the LGM in the rapid spread of boreal trees and shrubs at the onset of warmer and wetter Lateglacial climate ca. 15 cal kyr BP, as recorded in fossil pollen and macrofossil records from various regions of Northern Asia.

Although long regarded implausible, the now available palaeoclimate reconstructions suggest that summer temperatures in Northern Asia between 50 and 15 cal kyr BP were above modern averages, in some regions probably even by several degrees Celsius. The determining climate parameters for vegetation distribution were the extreme cold winter season and the generally low moisture availability, which strongly limited the growth of woody taxa. To unequivocally identify the controlling factors of the last glacial environments, future studies focusing on quantitative reconstruction of climate parameters and seasonality are needed. In addition to fossil pollen records, we regard studies of plant macroremains, chironomids, diatoms, ostracods and aDNA as the most promising potential approaches.

The last glacial environments dominated by productive steppe, meadows and tundra, as reconstructed by the numerous studies discussed above, would have provided ideal habitats for a diverse fauna ranging from small to mega species of herbivores and carnivores. It is thus not surprising that AMH, after their arrival to the southern part of Northern Asia currently dated to between ca. 50 and 45 cal kyr BP, spread even to very remote areas in the north-eastern part of the region. The rich hunting grounds and herbaceous vegetation provided inexhaustible resources of food and explains the continuous presence of humans even during the entire LGM. While the advantages of the glacial landscapes for humans seems relatively clear, we know little about how human activities affected the natural environment. This is especially important to better understand the potential natural distribution of woody plants during the last glacial. While we see evidence that herbivores were likely to have influenced the growth and regeneration of arboreal taxa, it remains unresolved to what extent this could have been caused by human activities, such as setting fires for hunting.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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