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Research Article

Potential refugia on the Tibetan Plateau during the last glacial maximum

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Abstract

The prehistoric human habitation of the Tibetan Plateau (TP) is well evidenced by the archaeological record, but poorly constrained in time and space. To test the plausibility of in situ survival during the last glacial maximum (LGM) and the coldest periods of the Pleistocene, this paper gauges the effects of LGM conditions and varying local ice coverage on the climate. Three different climate model scenarios are generated, and their outputs are used to drive vegetation simulations. This allows us to evaluate 10 archaeological sites that show evidence of human activity either pre- or post-LGM as possible human refugia. The results show that the higher the level of ice coverage on the plateau, the colder and drier the climate becomes, and barren unproductive land extends farther south. However, there are sites that remain habitable in all scenarios, with the southern and northeastern plateau identified as the areas with the highest likelihood of refugia during the LGM, specifically at the locations of Baishiya Karst Cave and Siling Co. There is a high probability of the TP being habitable during the LGM, as even the scenario with the most ice yields some regions with favourable conditions that are within the habitability criteria.

Keywords: Tibetan Plateau; last glacial maximum; refugia; habitability; climate modelling; Archaeology

Introduction

The Tibetan Plateau (TP) is located in Asia, covering 25–45°N, 70–105°E, and is bordered by the Himalayan, the Pamir, and Karakoram mountain ranges (Aldenderfer and Zhang, 2004; Yanai and Wu, 2006). The plateau covers an area of 2.5 million km^2 and reaches altitudes of more than 5000 m above sea level (m asl) (Qi et al., 2013; D'Alpoim Guedes and Aldenderfer, 2019). The extent to which the TP was glaciated during the last glacial maximum (LGM) is highly debated, ranging from increased ice caps with extended mountain glaciers, to a plateau-wide ice sheet (Lehmkuhl et al., 1998; Kuhle, 2004). With varying ideas about the LGM ice coverage from 22 to 18 ka (thousands of years ago), palaeoclimate simulations are wide ranging (Madsen et al., 2006). Therefore, it is difficult to ascertain whether humans could have survived on the plateau in situ, without direct evidence in the archaeological record (D'Alpoim Guedes and Aldenderfer, 2019).

The archaeological data available at this time are sparse, leading to controversy around the date at which humans first permanently occupied the plateau and whether communities persisted through the LGM (Zhang, 2002; Miehe et al., 2021). Some researchers theorise that colonisation of the high elevations occurred during the Pleistocene with Palaeolithic humans, whereas others suggest it was later in the Holocene, with the introduction of agriculture by Neolithic people (Qi et al., 2013; Zhang et al., 2018; Miehe et al., 2021). Although there is archaeological evidence of humans on the TP during Palaeolithic times, whether it shows temporary encampments or permanent settlement must also be questioned (Chen et al., 2014). However, due to the extreme climate on the TP that humans had to face, DNA evidence can help identify when permanent settlement on the Plateau occurred (Jeong et al., 2014). For context, the highest settlement in Tibet currently is Tuiwa, which is situated at 5040 m above sea level (asl) (Hancco Zirena, 2021). Gene selection against hypoxia facilitated living at these high elevations and allowed population migration onto the TP, and the timing of this haplotype diversion can be traced back (Rhode, 2016). One theory is that this gene haplotype came from Denisovans, an archaic hominin that could have lived at high elevations as far back as 165 ka, and that *Homo sapiens* acquired it through admixture (Rhode, 2016; D'Alpoim Guedes and Aldenderfer, 2019). If this does offer evidence of pre-LGM settlement, there is still the question of whether Palaeolithic communities were able to survive on the TP during the LGM, when conditions were far from favourable (Qin et al., 2010).

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Glacial extent of LGM TP

In the present day, ice coverage on the plateau averages 50,000 km^2. There are varying hypotheses concerning the ice coverage over the TP during the LGM in Marine Isotope Stage 2 (MIS 2), but what is known is that the LGM in high-altitude Asia was slightly asynchronous with the maximum ice sheet extent elsewhere in the Northern Hemisphere (Owen et al., 2003). Maritime glaciers were already present on the plateau at 22 ka, and topography was a key factor that influenced the extent of advance (Owen et al., 2005). With an estimated decrease of 6–9°C of average temperature and

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Figure 1. Map of the Tibetan Plateau and evidence of glaciated and non-glaciated regions during the last glacial maximum. (Data from Brantingham et al., 2001b; Owen et al., 2005; Rhode et al., 2007; Wang et al., 2009; Heyman et al., 2011; Zhang et al., 2014; D'Alpoim Guedes and Aldenderfer, 2019; Liu and Zhu, 2022).

heightened aridity, many glaciers froze to their beds and ceased basal sliding (Shi, 2002). The summer monsoon shortened, and the winter monsoon increased in strength but moved farther to the southeast plateau margins (Shi, 2002; Bohner and Lehmkuhl, 2005). Due to the decrease in monsoonal influence, and hence annual precipitation, equilibrium line altitudes at the time only advanced to slightly lower elevations, with original estimates being 1000 m lower, but palaeoenvironmental evidence showing only 300–500 m of descent (Shi, 2002). Much of the dating of the glacial geomorphology on the TP was completed before the development of modern dating techniques, and there have been many retrospective corrections and changes in glacial extent estimates (Owen et al., 2005). Due to the inaccessibility of the terrain, there are also very few research sites for such a large region; predictions must therefore be made from limited in situ data (Owen et al., 2005). Kuhle (2004) most famously suggested a 2.4 million km^2 ice sheet covering the TP during the LGM, while most studies favour a more realistic hypothesis of extended mountain glaciers and ice caps (Lai et al., 2009), with an overall ice coverage of between 300,000 km^2 and 500,000 km^2 (Derbyshire et al., 1991; Shi, 2002). How the LGM mapped on the plateau, however, is less clear (Lehmkuhl et al., 1998). Figure 1 shows how the evidence of glaciation in the literature maps onto the plateau with locations of glacial evidence in blue and regions that were ice-free highlighted in red.

Most of the evidence of glaciation during the LGM is concentrated to the east of the plateau, including prominent peaks like Nianbaoyeze and Gonga Shan; this is partly due to the western precipitation gradient and larger extent of more recent glaciations eroding evidence from the LGM (Owen et al., 2005). With elevations in the northeast reaching above 6000 m, it is theorised here that ice caps and mountain glaciers were extended by ∼10 km but were limited due to reduced precipitation levels (Owen et al., 2003). Glacial moraines are still evident from MIS 3, highlighting the lack of glacial erosion during MIS 2 (Owen et al., 2003). This means that a plateau-wide ice sheet is improbable at the LGM, as glacial features from the penultimate glaciation would not be found if the glacial extent had been more extreme during the LGM (Owen et al., 2003). The plateau is bordered by very high mountains to the west, the Himalayas and the Karakoram range, where there would be extended mountain glaciers (Lehmkuhl et al., 1998; Aldenderfer and Zhang, 2004). From this information, three models of the LGM were estimated for this study. An ice-free plateau in the "LGM" simulation; a "Medium ice" scenario with small amounts of ice in high-elevation areas in the northeast and more ice over the mountains in the west; and a "Large ice" scenario with an almost plateau-wide conglomerate of ice. Further north, in the region of Qinghai Lake and Qilian Shan, a more arid ice-free climate is proposed (Owen et al., 2005; Rhode et al., 2007). Other ice-free zones were said to have persisted through the LGM, and while some were areas of arid desert with saline or dry lakes, others have been suggested as regions of refugia (Chen et al., 2008).

Refugia

In the context of this paper, refugia are areas that maintain a climate during glaciation that enables species of fauna/flora to persist

(Morelli et al., 2016). A good indicator of refugia is endemism, and 33% of all plant species in Tibet are endemic (Miehe et al., 2011). The survival of plant species on the TP through glacial stages shows that the change in temperature was not detrimental to the habitability of the environment, and as most plants remain dormant in winter, seasonal fluxes may not have had a large effect on their survival (Miehe et al., 2011). Wang et al. (2009) suggest approximately three locations on the TP acted as refugia for species such as *Potentilla glabra* (Rosaceae), mostly in the southeast, but potentially in the interior plateau, at elevations above 4000 m asl. Several edible species have been found to have persisted through the LGM on the TP such as species of tuber like *Potentilla*, Gentianceae, wild strawberry (*Fragaria vesca*), and pine nuts (*Pinus pinea*) (Wang et al., 2009; D'Alpoim Guedes and Aldenderfer, 2019).

Tibet also hosts a range of endemic fauna, which there is evidence for during the LGM (Miehe et al., 2011). These include species such as pika (*Ochotona curzoniae*), the Tibetan woolly hare (*Lepus oiostolus*), the Himalayan marmot (*Marmota himalayana*), and steppe lemming (*Lagurus lagurus*), as well as Tibetan dwarf hamster (*Cricetulus alticola*), all of which could have offered sustenance for hunter gatherers (D'Alpoim Guedes and Aldenderfer, 2019). In a study by Liang et al. (2017), it was shown that Siling Co lake offered microrefugia to Schizothoracine fish during the LGM, as a lack of waterways meant their repopulation post-LGM must have come from a small population that remained in situ. This demonstrates not only fresh water at Siling Co but also a food source for Palaeolithic people (Liang et al., 2017).

Archaeological evidence of human settlement

Data alluding to Palaeolithic activity at precisely the time of the LGM on the TP are limited due to many factors (D'Alpoim Guedes and Aldenderfer, 2019). Palaeolithic culture in the region did not appear simultaneously, and thus there is an issue with dating supposed Palaeolithic sites, as the technology overlaps with that dated to the Holocene (Zhang, 2000). Therefore, the term "Epipalaeolithic" is used where tools that are Palaeolithic in nature date to the Neolithic era (Zhang, 2000). This differentiation is important to allow insight into initial colonisation of the plateau and therefore plausibility of survival through the LGM (Zhang, 2000). With no systematic excavations occurring on the TP, most lithic assemblages are found at the surface, so dating must be estimated by the typology of prehistoric technology (D'Alpoim Guedes and Aldenderfer, 2019). In general, the consensus is that larger blade, bladelet, and flake technology were prominent from 40 to 30 ka and smaller microblades appeared at the Palaeolithic/Neolithic border ~25–5 ka (Brantingham et al., 2001a; Li et al., 2019). The lack of precision in the dating of archaeological sites, as well as the lack of specimens found, has given space for two opposing hypotheses for the timing of permanent habitation on the plateau: pre-LGM and post-LGM (D'Alpoim Guedes and Aldenderfer, 2019). Some researchers suggest that Palaeolithic foragers were able to sustain themselves at high elevations, and others reason that colonisation could only occur with the introduction of pastoralism in the Neolithic era and the onset of more favourable climate conditions (Zhang et al., 2018; Li et al., 2019). There is evidence of seasonal use of the plateau by Palaeolithic people, with temporary camps apparent in the archaeological record (Madsen et al., 2006). Ten archaeological sites dating from 165 to 6.4 ka were identified as potential locations of in situ survival through the LGM for this study, with locations on and around the plateau (Fig. 2).

Northeast near the plateau margins: Shuidonggou (<2000 m asl)

Although not actually on the plateau, Shuidonggou being close to the margins and yielding lots of evidence from before and after the LGM (between 46 and 10 ka), advances the understanding of possible migration times (Li et al., 2019). Shuidonggou may not show signs of life from 22 to 18 ka, but it is hypothesised that communities may have sought refuge elsewhere during that time and then returned to the region in the Holocene (Li et al., 2019). The blade types found suggest settlers came from Siberia or Mongolia, which supports theories of Denisovan activity on the plateau (Li et al., 2019). During the LGM, the climate is thought to have been semiarid desert steppe, as the location borders the dry Ordos Desert (Madsen et al., 2001). Remains of woolly rhino (*Coelodonta antiquitatis*), Tibetan antelope (*Pantholops hodgsonii*), and other species have been found in this region, giving evidence of sustenance for hunting communities (Madsen et al., 2001).

Northeast: Baishiya Karst Cave (3280 m asl) and Qinghai Lake (3194 m asl)

Baishiya Karst Cave in Gansu Province is the most prominent location that supports the Siberian migration theory, due to the Denisovan mandible (jawbone) found there, which was dated to 165–155 ka using uranium-thorium (U-Th) methods (D'Alpoim Guedes and Aldenderfer, 2019). This links to the hypothesis of an archaic hominin adapting to and living on the TP and potentially interbreeding with *Homo sapiens* later on (Rhode, 2016). This site, despite being on the periphery of the TP, could have been used as a base to hunt and gather on the plateau itself.

The sites around Qinghai Lake have been dated to 12.5–11 ka in deglacial times, and although hearths have been found, only temporary camps are evident (Madsen et al., 2006). There is still the question of whether these sites could have been home to communities before this. It is thought that the lake itself dried up or held little water during the LGM (Liu et al., 2002). Tools found here were Epipalaeolithic, so there is only evidence of the site being used during the Holocene, when climate was at an optimum and the stronger monsoon encouraged more wooded areas (Rhode et al., 2007).

North: Lenghu (2804 m asl) and Xiao Qaidam, Qaidam Basin (>3100 m asl)

Lenghu, in the Qaidam Basin is one of the only sites that is dated using the geology, as the tools were not found superficially (Brantingham and Xing, 2006). Levallois-like blades between two beach ridges were dated to ~30.5 ka, but evidence of the longevity of the site is lacking (Brantingham and Xing, 2006). Xiao Qaidam was also estimated to be from ~30 ka but has now been dated to 11 ka and yielded an assemblage of stone tools (Sun et al., 2010). In the basin, present-day temperatures are generally between 2°C and 4°C with <50 mm of annual precipitation, but with 3000 mm average evaporation, meaning it is an extremely arid region and therefore most lakes have turned saline or are extinct (Sun et al., 2010).

Northern interior: Chang Tang (>4300 m asl) and Kunlun Pass (4300 m asl)

The same obsidian that was crafted into tools was found at both Chang Tang sites and Xidatan 2 near Kunlun Pass, originating

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Figure 2. Map of 10 archaeological site locations on and near the Tibetan Plateau. (Location data from Brantingham et al., 2001b; Zhang, 2002; Madsen et al., 2006; Brantingham and Xing, 2006; Yuan et al., 2007; Sun et al., 2010; Brantingham et al., 2013; Zhang et al., 2014; Zhang et al., 2018; Chen et al., 2019; Li et al., 2019; D'Alpoim Guedes and Aldenderfer, 2019; Liu and Zhu, 2022).

from a source area ~400 km away (Brantingham and Xing, 2006). Chang Tang constitutes many sites yielding 158 specimens and estimated ages of between 25 and 15 ka, mostly consisting of large blades/bladelets and some microblades (Brantingham et al., 2001b). It is a large region with climate across three biomes: alpine steppe, desert steppe, and alpine meadows (Brantingham et al., 2001b). Indigenous fauna appear predominantly in the last biome and include Tibetan antelope, gazelle (*Procapra picticaudata*), and yak (*Bos mutus*) (Brantingham et al., 2001b).

The tools found at Xidatan 2 by Kunlun Pass were dated to the Pleistocene–Holocene transition (~9.2–6.4 ka) and consisted of typical core and flake assemblages, as well as microliths (Brantingham and Xing, 2006). This high-elevation site (4300 m) was thought to have been home to Palaeolithic communities, but further investigation into climate pre-LGM has shown conditions were perhaps less favourable, so it is thought to be unlikely that humans remained on the site (Madsen et al., 2008; Rhode et al., 2010).

Southern interior: Siling Co (4600 m asl) and Nwya Devu (4600 m asl)

Both Siling Co and Nwya Devu are located at the high altitude of ~4600 m asl, with Nwya Devu being the highest Palaeolithic site on the plateau found to have a lithic assemblage (Yuan et al., 2007; Zhang et al., 2018). The Siling Co site assemblage contained flakes and microcores, whereas the Nwya Devu assemblage was blade tools (Yuan et al., 2007; Zhang et al., 2018). Both of the sites date to between 40 and 30 ka, which is pre-LGM, but leaves room for potential that those communities persisted through the glacial times (Yuan et al., 2007; Zhang et al., 2018). The people of Nwya Devu are assumed to have left during times of less favourable conditions, and D'Alpoim Guedes and Aldenderfer (2019) suggest a potential retreat to Yarlung Tsangpo valley for refuge.

South: Quesang River (4200 m asl)

The site at Quesang River was thought to have been the missing piece of the puzzle, evidence finally dating to the exact time of the LGM (22–21 ka); however, this was later found not to be the case (Zhang, 2002; Meyer et al., 2017). A collection of 19 hand- and footprints identified in the calcareous rock from a nearby hot spring have been found to originate from 12.7–7.4 ka using carbon dating (Meyer et al., 2017). Further U-Th dating by Wang et al. (2023) of the travertine that nearby hand and footprints are imprinted in also dates the human visitations to the site to between ~10.9 and 7 ka. Around this time, the climate became warmer and wetter, which may have encouraged foraging communities to venture to this elevation of 4200 m asl (Meyer et al., 2017). Although it does not give evidence of pre-LGM settlement on the TP, the site does date to before pastoralism and therefore indicates ability to survive at high altitude without subsistence farming (Meyer et al., 2017).

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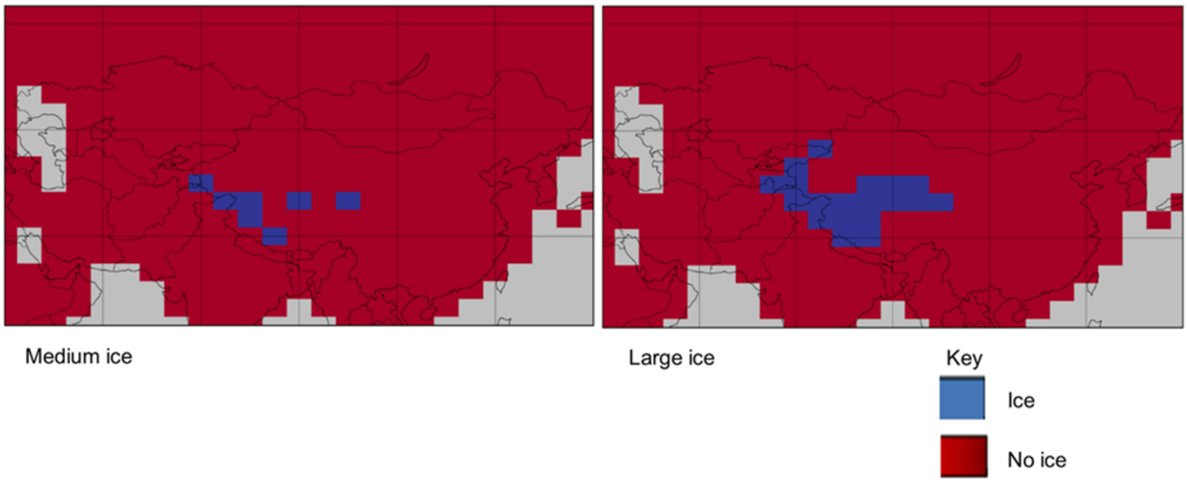

Figure 3. Ice coverage input for the HadCM3 model of Medium ice and Large ice simulations. The area of ice is shown in blue, and the red shows absence of ice.

Methodology

Climate model

The Hadley Centre Coupled Model 3 (HadCM3) version of the UK Met Office Unified Model was used to simulate four different climate simulations, with the MOSES 1 (Cox et al., 1999) land surface scheme (HadCM3B-M1 in Valdes et al. [2017]). HadCM3 consists of a coupled atmosphere, ocean, sea-ice, and land surface model (Gordon et al., 2000; Pope et al., 2000). The resolution of the model is 3.75° × 2.5° with 19 layers for the atmosphere and 1.25° × 1.25° and 20 layers for the ocean. The gravity wave and orographic parameterizations include the impacts of trapped lee waves and high drag states and flow blocking (Gregory et al., 1998; Pope et al., 2000). Precipitation is produced by both a convective and a large-scale precipitation scheme (Smith, 1990). The MOSES1 land classification scheme includes a series of nine physical surface parameters that are specified for each of the Wilson and Henderson-Sellers (1985) land cover classes. Terrestrial ice masses are therefore a specified boundary condition within this model setup, having predefined physical parameters (Cox et al., 1999). HadCM3 has been shown to successfully represent the modern Asian climate (Dabang et al., 2005), with high skill levels in both seasonal and annual climate. For evaluation of the climate model data for the archaeological sites, dry adiabatic lapse rate was used to estimate temperature at specific altitudes; this altitude correction was not completed for precipitation, as it was outside of the scope of this study.

Climate model scenarios

Four different climate model simulations were used as part of this study. Two are standard HadCM3 simulations for the preindustrial (Valdes et al., 2017) and LGM (Hewitt et al., 2003). The other two are sensitivity experiments simulating the impact of larger ice masses on the TP during the LGM or other glacial maxima. Figure 3 shows the varying coverage of ice input into the model. The Medium ice scenario represents extended ice caps and mountain glaciers based on Lehmkuhl et al. (1998), and the Large ice scenario shows an almost plateau-wide ice sheet based on Kuhle (2004). The locations for increased ice coverage are similar to what has been suggested in the literature, with increased snow and ice to the south and west of the plateau, where the elevation is high (Liu et al., 2020).

Vegetation modelling

Although vegetation is fixed in the climate model simulations, the implications of changing climate on vegetation type across the plateau needed to be assessed to estimate the possibility of in situ survival. BIOME4 is a coupled model that uses both carbon and water fluxes to obtain simulations of the distribution and characteristics of vegetation around the world at different points in time (Kaplan et al., 2003). To compute the vegetation model outputs, four climatic variables are input into the BIOME4 model: monthly mean temperature, precipitation, cloud cover, and the lowest monthly mean temperature. These are bilinearly interpolated to a high-resolution 0.5° global grid and input into the vegetation model using an anomaly method. BIOME4 uses 12 plant functional types (PFT) with ecological niches to anticipate the net primary productivity (NPP) and fluxes of both water and carbon (Kaplan et al., 2003). For each PFT, the model decides whether the type could survive in each grid cell under the biological limits that are in place, and from that, each grid cell is placed into one of the 28 biomes (Kaplan et al., 2003). The BIOME4 model has been extensively used for studying LGM vegetation distribution, including some palaeovegetation studies of China, producing a good match to observations when the impacts of both climate and CO_2 change are incorporated into the simulations (Harrison and Prentice, 2003; Ni et al., 2010; Izumi and Bartlein, 2016).

Modelling results

LGM climate

The average surface temperature on the plateau in the Pre-industrial simulation spans from 14.1°C to −10.0°C, with 57% of the plateau being below 0°C on average. In the LGM simulation with no ice over Tibet, there is a drop in temperature of ∼4°C from the Pre-industrial values, with highs of 11.3°C and lows of −15.7°C (Fig. 4). In addition, the proportion of the plateau with temperatures below 0°C increases to 70%. The Medium ice scenario for the LGM shows a very similar average to the standard LGM scenario, the minimum average temperature drops to −30.5°C, more than

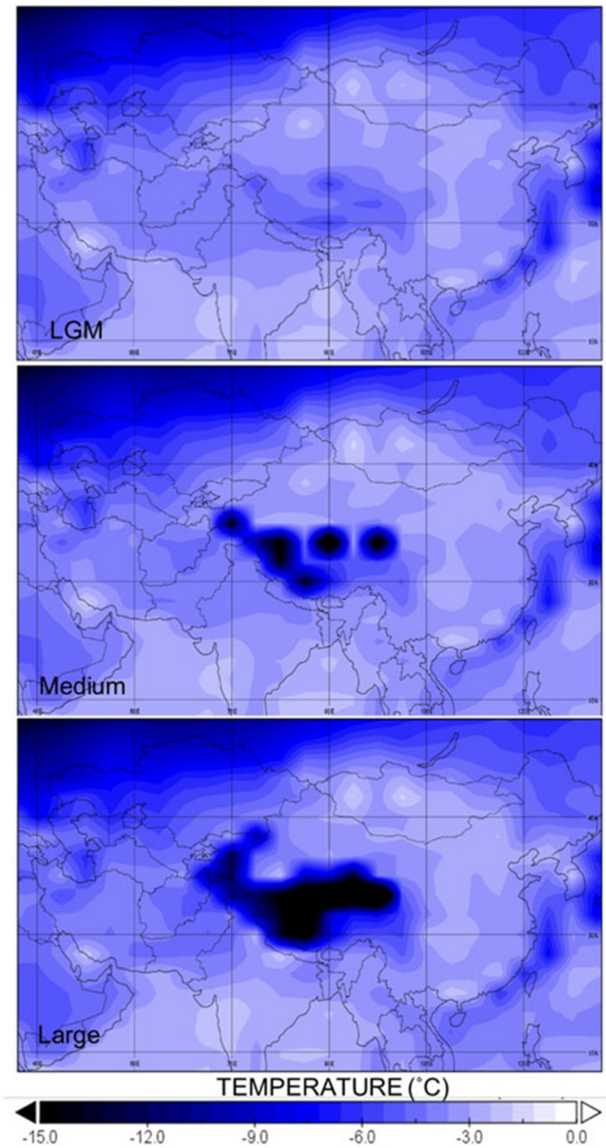

Figure 4. Change in modelled annual mean surface air temperature (°C) from Pre-industrial in scenarios LGM (last glacial maximum), Medium ice, and Large ice. Data minimum −24.4°C and maximum −1.7°C.

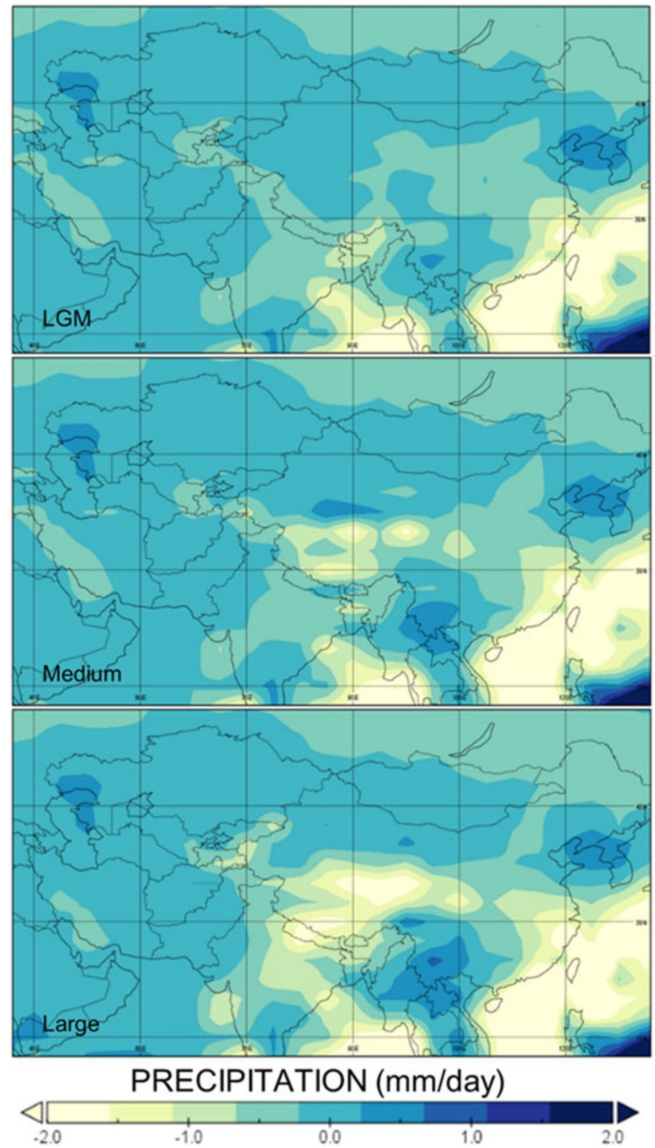

Figure 5. Change in modelled annual mean precipitation (mm/day) from Pre-industrial in scenarios LGM (last glacial maximum), Medium ice, and Large ice. Data minimum −7.8 mm/day and maximum 4.3 mm/day.

20°C less than the Pre-industrial, and the maximum average temperature only drops ∼2°C to 12.0°C (Fig. 4). Although there is a sharp decline in minimum average temperature, the percentage of area below 0°C is similar to that of the standard LGM simulation, at 67%. With a much larger ice coverage, the Large ice scenario shows a steep drop in average surface temperature, the maximum surface temperature is the same as the Medium ice scenario value at 12.0°C, but the minimum surface temperature declines further to −32.7°C (Fig. 4). The percentage of the TP with temperatures below 0°C is the same as the standard LGM value of 70%.

Several of the sites above 4000 m (mostly in the north), including Nwya Devu, Chang Tang, and Kunlun Pass, display the largest declines in temperature from the Pre-industrial, reaching as low as −24°C in the Large ice scenario (Fig. 4). However, Siling Co, despite being close to Nwya Devu, remains relatively stable in the three different LGM scenarios (between −6.2 and −7.6°C). The sites close to the North-East plateau margins (Baishiya Karst Cave and Shuidonggou) appear outside of the areas with large temperature declines and in fact have the warmest annual temperatures (above or close to 0°C) compared with the other sites (Fig. 4).

Glacial climates see a reduction in precipitation over the TP with the standard LGM averaging 697 mm/yr, compared with 778 mm/yr in the Pre-industrial. This reduction is exacerbated when ice is added to the TP with averages of 616 mm/yr and 499 mm/yr in the Medium and Large ice simulations respectively (Fig. 5). Although the northeast and northern interior of the plateau (Xiao Qaidam, Lenghu, Kunlun Pass, and Chang Tang) become drier as the amount of ice in the scenario increases, Baishiya Karst Cave remains the site with the most annual precipitation until the Large ice scenario (Fig. 5).

LGM vegetation on the TP

The results show that compared with the Pre-industrial, there is a general decline in the various types of forest on the TP in all of the

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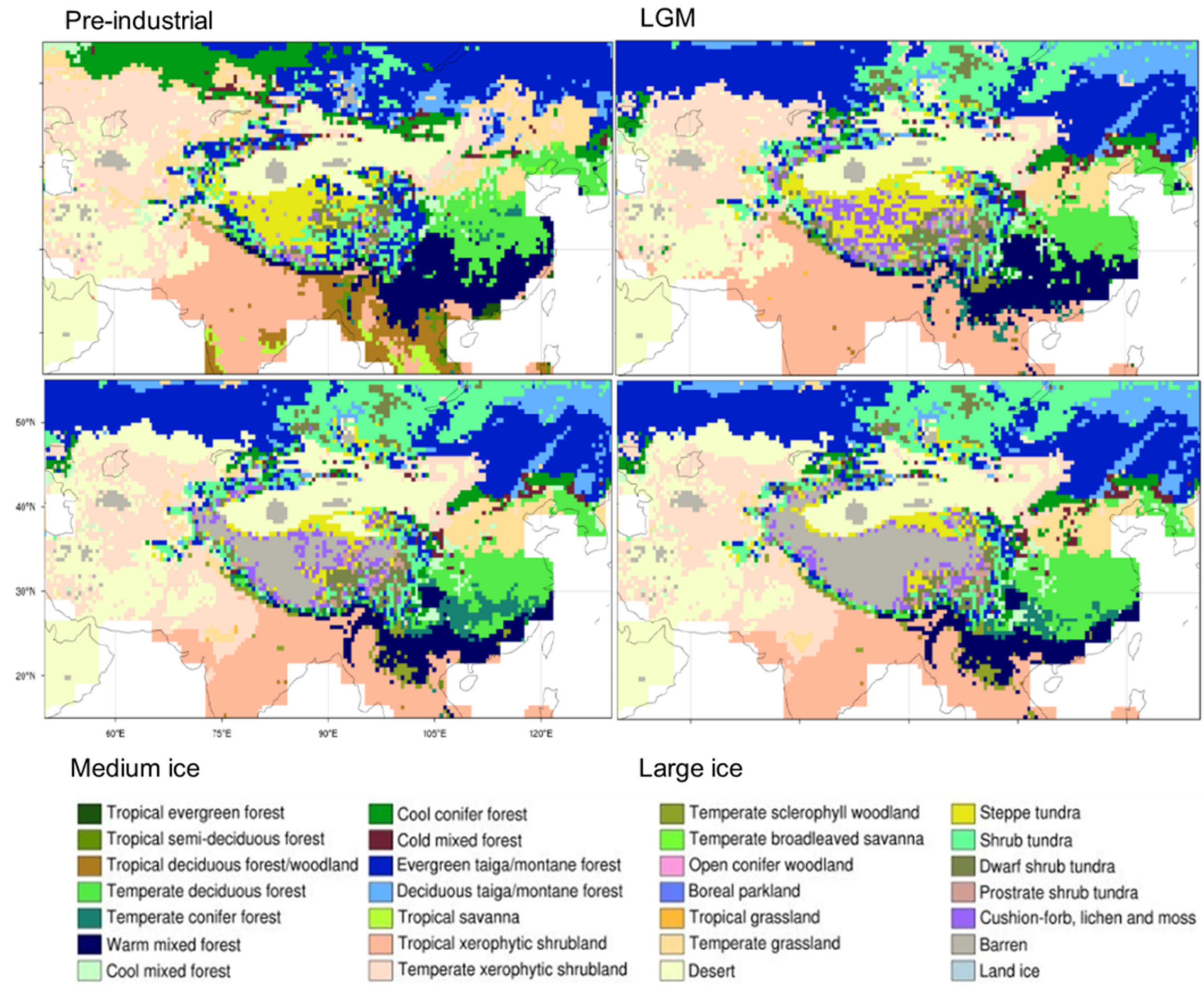

Figure 6. Maps of the central Asian biomes, as simulated in BIOME4, for the Pre-industrial, LGM (last glacial maximum), Medium ice, and Large ice scenarios.

LGM simulations (Fig. 6). However, the percentage of deciduous taiga/montane forest almost doubles for all scenarios. Temperate deciduous, cool conifer, and cold mixed forests stay relatively stable for all simulations (Fig. 6). The Pre-industrial simulation consists of 67.9% of different shrubland and tundra biomes, which is similar to the Medium ice scenario result of 69.5%. However, shrubland and tundra rise to 81.1% in the LGM simulation and decrease to 52.3% in the Large ice scenario. Shrub tundra declines in all of the LGM scenarios and varies from one-half of the Pre-industrial value in the LGM, to one-third in the Large ice simulation (Fig. 6).

In general, steppe tundra, shrub, dwarf shrub tundra, desert, and barren land make up the majority of vegetation distribution for the archaeological sites (Fig. 7). Looking more closely at the evolution of vegetation for each site depending on the amount of ice, it is evident that the lower-latitude biomes are relatively stable until the Large ice scenario, where the highest-altitude localities become barren (Fig. 7). In the Large ice scenario, many of the archaeological sites become covered with the maximum possible extent of ice over Tibet (Fig. 1). BIOME4 is not able to simulate the presence or absence of an ice cap, as it does not contain the necessary physics or input variables to do so. We have chosen to continue to simulate the vegetation in areas covered by ice in the climate model, as this gives the opportunity for a much more realistic simulation of high-resolution biomes in marginal zones. This does, however, mean that a large area of the TP is simulated as barren (Fig. 7), when this just reflects the nature of the climate over ice in the climate model simulation. Where the term "barren" is used, this will mostly refer to an area that is under ice coverage. A majority of the sites fluctuate between types of shrub and tundra, whereas the higher-latitude areas such as Qaidam Basin (Xiao Qaidam, Lenghu) remain desert biomes until the Large ice model simulation, where steppe tundra develops (Fig. 7).

The NPP of the archaeological sites averages 163 g C/m^2 in the Pre-industrial and decreases to 112 g C/m^2 in the LGM, 80 g C/m^2 in the Medium ice scenario, and 65 g C/m^2 in the Large ice scenario (Fig. 7). Qinghai Lake is the most productive locality in both the Pre-industrial and Large ice simulations at between 160 and 268 g C/m^2, whereas in the LGM and Medium ice scenarios, Baishiya Karst Cave has the highest NPP at between 170 and 175 g C/m^2. Lenghu is the least productive site in the Pre-industrial and

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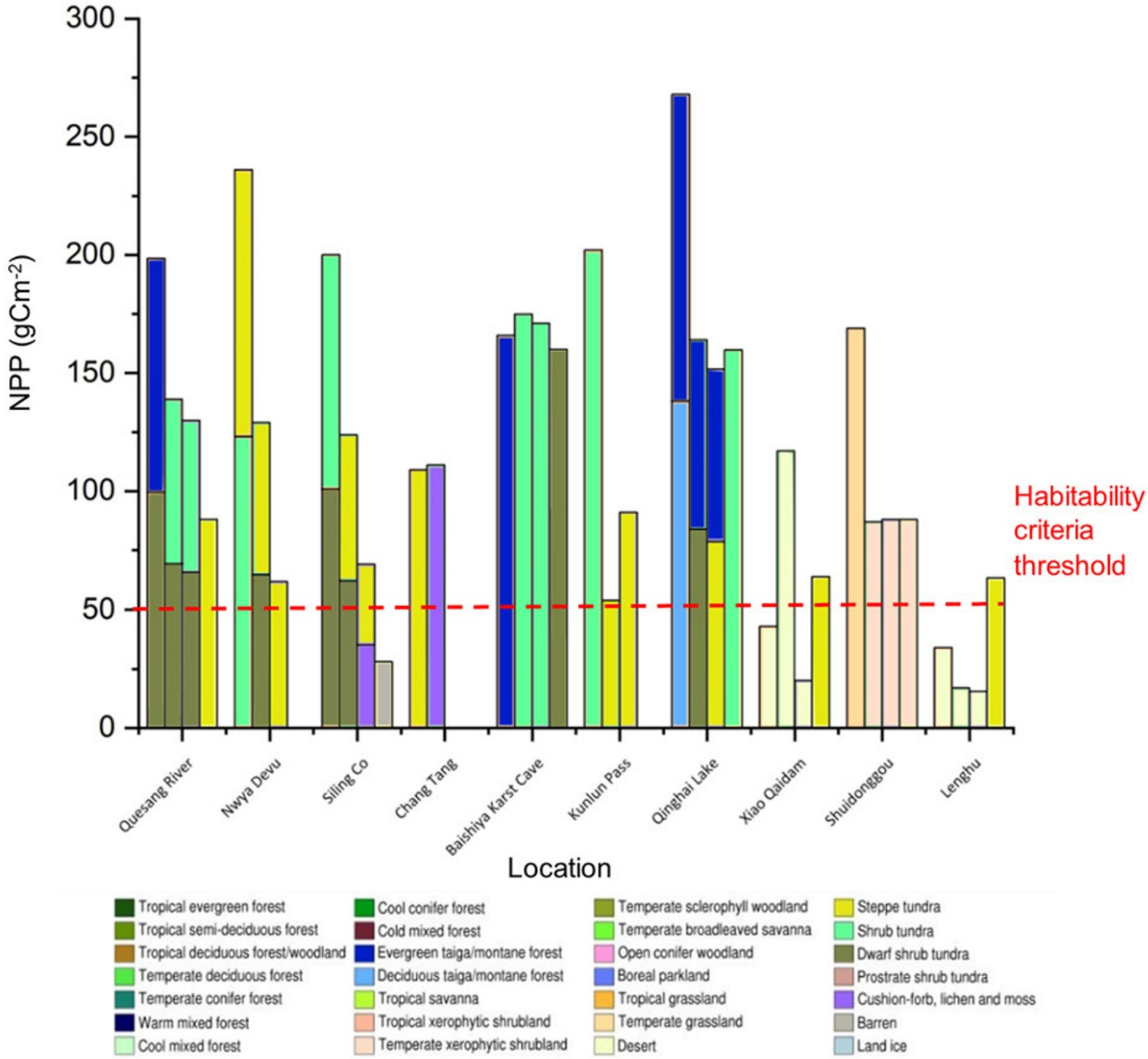

Figure 7. Graph showing net primary productivity (NPP) in g C/m^2 and main biomes at each archaeological location in each climate scenario.

Medium ice simulations at between 15 and 34 g C/m^2, but in the LGM and Large ice simulations, this is Chang Tang at 0 g C/m^2. The other nonproductive areas in the Large ice scenario include Nwya Devu and Kunlun Pass, which also have NPP values of 0 g C/m^2.

Discussion

Habitability criteria

The barrier of extreme temperature was set to a ∼3–4°C drop in average annual temperature from the Pre-industrial control, as this was given by Qiu et al. (2011) as an estimate that would have allowed plant species to remain in situ and persist as a food source. In addition, the lower limit of needed annual precipitation was set as 50 mm/yr, as Miehe et al. (2011) gives this as a threshold for the survival of alpine plants in the region. Through evaluation of the correlation between biomes and NPP, a threshold value of 50 g C/m^2 was chosen as the value at which land became too unproductive to live on. The average annual temperature across the TP in both the LGM and the Medium ice climate scenarios fell by ∼4°C compared with the Pre-industrial, which was in agreement with most of the literature and also within the boundary conditions set for habitability (Qiu et al., 2011; Fig. 4). In contrast, the Large ice simulation average temperature fell by 8°C, which made it evident that many areas in that scenario would likely be uninhabitable. There was only a 5°C difference in the minimum average annual temperature between the LGM and Medium ice scenarios but a 20°C difference with the Large ice simulation, illustrating a potential for much more extreme temperatures. Regions with average annual temperature below 0°C made up ∼70% of the plateau in all simulations set in the LGM. This may indicate that the colder areas of the TP experienced a higher magnitude of temperature decline, whereas areas above freezing could have persisted with more favourable conditions.

The amount of ice in the climate simulations seems to have impacted precipitation significantly, with the LGM no-ice scenario seeing a 10% reduction in annual precipitation compared with the Pre-industrial, and the Medium ice and Large ice scenarios reflecting declines of 21% and 36%, respectively (Fig. 5). Similar to the Pre-industrial, the arid zones in both the LGM and the Medium

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ice simulations were restricted mostly ∼40°N and above, whereas in the Large ice simulation, areas that had <100 mm of annual precipitation extended as far south as 32.5°N. This highlights that in relation to aridity, an LGM with no ice over the TP was most likely to have had habitable biomes, whereas it is probable that if there was a large ice coverage during the LGM, the increased dry conditions would have made in situ survival much less feasible.

As the TP became more glaciated in the climate models, forest biomes decreased in favour of tundra and shrubland (Figs. 6 and 7). In the LGM simulation, only a small area (∼90–95°E) was barren/under ice coverage, whereas when ice coverage was increased, so did the amount of barren land. In the Medium ice scenario, land was mostly unproductive from 30°25′N to 36°25′N, 86°25′E to 92°75′E and from 30°25′N to 36°25′N, 94°75′E to 99°25′E. However, in the Large ice simulation the whole region from 30°25′N to 40°25′N, 86°25′E to 99°25′E was mostly desert or barren. Therefore, these regions could be ruled out as potentially habitable zones. These results illustrated a mostly barren high-elevation plateau interior, whereas previous studies have divided between the arid unproductive regions in the north and the wetter more productive areas in the south (Liu et al., 2020).

Two of the archaeological sites remained within the threshold of habitability even in the most extreme scenario of this study, Baishiya Karst Cave, at 3280 m on the edge of the plateau, and Shuidonggou, well below the plateau at <2000 m. The maximum temperature declines were 2.6°C and 1.9°C, respectively, and precipitation for both remained >300 mm/yr. The minimum winter temperatures were not very extreme at −14.3°C and −5.9°C, and Shuidonggou had the most temperate climate, which reached up to 22.7°C in the summer. Simulated biomes suggest Baishiya Karst Cave was dwarf shrub tundra, whereas Shuidonggou remained as temperate xerophytic shrubland. Baishiya had minimum NPP of ∼160 g C/m^2 and Shuidonggou had 88 g C/m^2, which is relatively productive for this extreme LGM scenario (Fig. 7). Siling Co remained habitable in all scenarios bar the Large ice scenario, with annual temperature averages never reaching −10°C, winter minima of ca. −20°C, annual precipitation above 200 mm/yr, NPP above 68 g C/m^2, and simulated biomes suggesting mostly dwarf shrub tundra (Fig. 7).

Conclusions

The objectives of this study were to investigate how varying ice coverages may have impacted climate on the TP during the LGM and whether refugia were possible under these conditions. In addition, the hypothesis of Palaeolithic occupation of the plateau pre-LGM was expanded upon by exploring the likelihood of in situ living during advanced glaciation in MIS 2. Altering the ice coverage over the TP in the HadCM3 model highlighted the general trend that the region became colder, drier, and less productive with more ice on the TP. The annual average temperature declined in areas already below 0°C, and no matter the volume of ice, forest biomes halved in all LGM simulations and gave rise to increased tundra and shrub landscapes. However, it was only in the Large ice scenario that much of the plateau became extremely arid and barren, driven by the presence of the maximum estimated extent of ice on the TP, which is substantially more than the best estimates of LGM ice volume.

The three LGM simulations were compared against the Pre-industrial control by analysing the climate outputs and generating vegetation data. The results demonstrated the possibility of refugia in the northeast and southern plateau, specifically Baishiya Karst Cave and Siling Co, despite its high elevation (Yuan et al., 2007; Zhang et al., 2018). This was due to the percentage change in annual precipitation being <5% and dwarf shrub tundra persisting with minor changes in temperature. Baishiya Karst Cave being at a lower elevation of 3280 m asl on the edge of the TP may have enhanced its prospect of being habitable during glaciation; however, Siling Co had much more favourable simulated conditions compared with other sites above 4000 m asl, and is still more than 400 m below the current highest settlement in Tibet (Hancco Zirena, 2021). The suspected microrefugia for certain species of fish at Siling Co in Liang et al. (2017) may provide additional evidence of the possibility of human refugia here, alongside the unusual increase of lake level during a shift to more arid climate conditions seen elsewhere on the plateau.

As the Large ice scenario demonstrated that at least two sites remained habitable during this exaggerated extreme, it is most likely that humans were able to persist on the plateau during the LGM, when ice coverage is thought to have been much less. The results of the study suggest some regions retained favourable conditions that could have acted as refugia, both within the monsoon-influenced south, but also potentially in the northeast, as some previous studies have suggested (Shi, 2002; Wang et al., 2009). Two archaeological sites on or at the margin of the plateau particularly stood out as the most probable candidates for Palaeolithic occupation during the LGM, Siling Co and Baishiya Karst Cave.

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