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RESEARCH

A Cold Habitat: Mapping Blade Assemblages Between the Siberian Altai and the Tibetan Plateau During MIS 3

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Abstract

How and why early hunter–gatherers expanded into the challenging environments of the Tibetan Plateau during the Pleistocene remain largely unexplained. The discovery of the archaeological site of Nwya Devu, characterized by lithic blade production, brings new evidence of human expansion to high elevations ca. 40–30 ka. The blade assemblage currently lacks technological antecedents in East Asia. During Marine Isotope Stage 3, the surrounding lowlands to the Plateau were dominated by a distinct type of industry broadly named "core and flake." It is suggested that the Nwya Devu blade assemblage derives from traditions in the eastern Eurasian Steppe, a clustered hub for Upper Paleolithic blade technology. In contrast to the East Asian lowlands, the Tibetan Plateau shares a number of environmental similarities with North and Central Asia such as low temperature and humidity, long winters, strong seasonality, and grassland landscapes. Blade and core-and-flake technologies tend to be associated with different environments in eastern Asia. We hypothesize that this geographic distribution indicates different sets of behavioral adaptations that map onto distinct ecozones and are relevant to human expansion to the Tibetan Plateau during Marine Isotope Stage 3. To evaluate the working model, we characterized the environmental parameters for both blade and core-and-flake technologies in eastern Asia during the period. The results show that environmental conditions on the Plateau and at the Nwya Devu site align with those of blade assemblages documented in the Eurasian Steppe and contrast with those of core-and-flake assemblages. Blade technology is strongly associated with low-temperature environments. These findings suggest that hunter–gatherers from the steppe belt may have benefited from their behaviorally adaptive advantages when moving into the highland environments of the Tibetan Plateau, 40–30 ka.

Keywords Modern human dispersal · Blade technology · Core and flake technology · Cold habitat · Steppe belt · Upper Paleolithic

Background

During the late Pleistocene, anatomically modern humans dispersed into Eurasia and successfully occupied most geographic regions of the continents (Bar-Yosef, 2002; Hublin, 2015; Mellars, 2006; Roberts & Stewart, 2018; Stringer, 2000). Due to geographical and environmental challenges, particularly cold and hypoxia, the Qinghai–Tibetan Plateau was among the last regions in mainland Eurasia where anatomically modern human populations established permanent settlements. When and why early humans entered and adapted to the environment of the world's largest plateau are unanswered questions, yet fundamental for our understanding of human adaptability and evolutionary history (Morgan, 2008). Recent studies suggest that archaic Denisovans and *Homo sapiens* visited the Tibetan Plateau earlier than previously suspected, by around 190 and 40 ka, respectively

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(Chen et al., 2019; Zhang et al., 2018; Zhang et al.,2020a). Archaeological evidence indicating Denisovan presence in the highlands, however, does not offer detailed insights into their physiological and behavioral adaptations. Similar challenges also persist regarding the occupations and adaptations of early modern humans, which is a typical issue in the region lacking systematic research and excavations (Aldenderfer, 2011; d'Alpoim Guedes & Aldenderfer, 2020; Zhang et al., 2022b).

The site of Nwya Devu is located in the interior of the Tibetan Plateau (31.5°N, 88.8°E) and documents human occupation as early as 40 ka (Zhang et al., 2018) (Fig. 1). The site is thus far the only systematically excavated blade assemblage associated with Marine Isotope Stage 3 (MIS 3) on the Plateau. In the absence of plausible local antecedents, the sudden appearance of blade technology is interpreted as evidence for human dispersal from adjacent lowlands (Zhang et al., 2018; Zhang et al., 2022c). Along with the Shuidonggou site complex (localities 1, 2, and 9) in North China (Brantingham et al., 2001; Li et al., 2013, 2020; Peng et al., 2014), these two excavated sites represent rare instances of blade-dominated assemblages in China at latitudes below

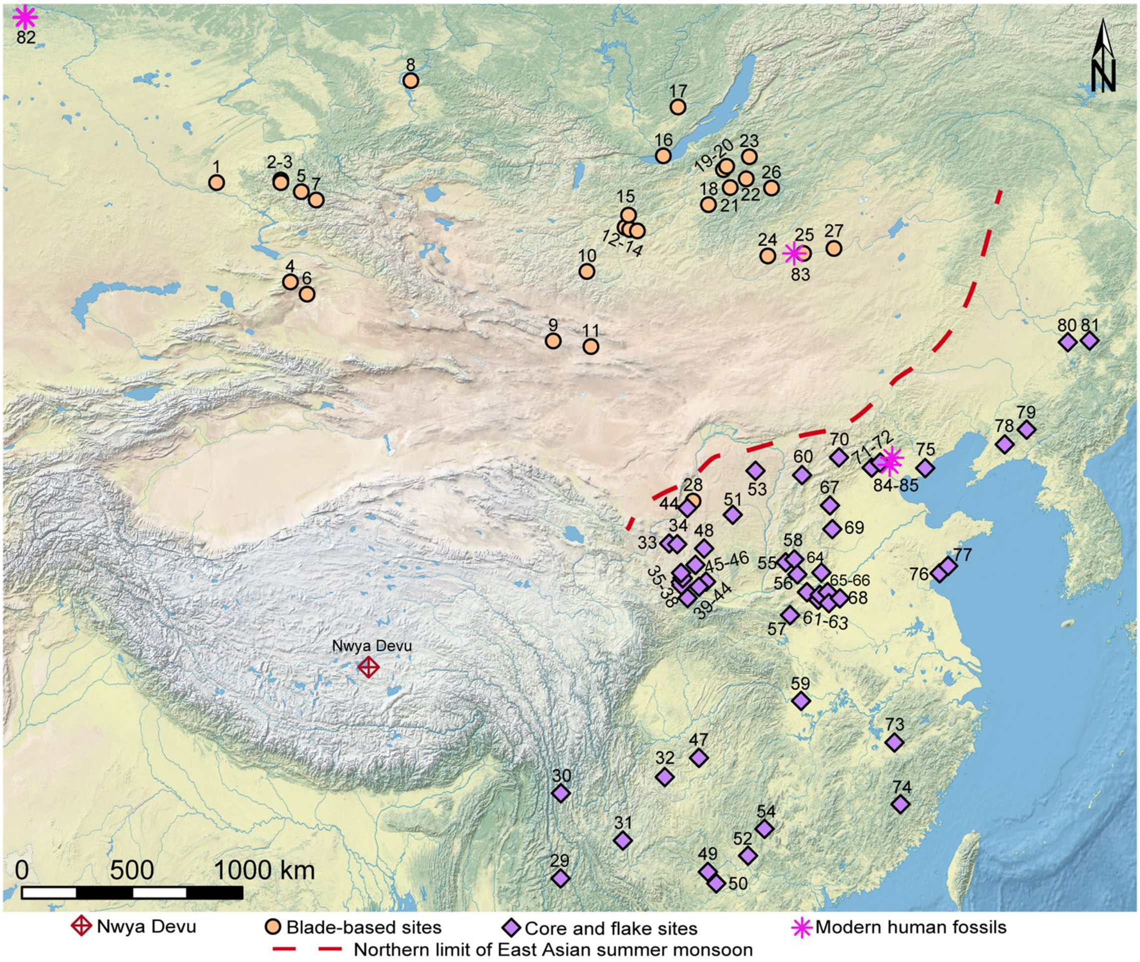

Fig. 1 Map showing the distribution of sites included in the study. Blade-based assemblages: 1, Kara-Tenesh; 2, Denisova Cave; 3, Ust'Karakol; 4, Ushbulak; 5, Kara-Bom; 6, Luotuoshi; 7, Malo Yaloman Cave; 8, Kurtak 4; 9, Chikhen 2; 10, Tsatsyn Ereg; 11, Tsagaan Agui; 12, Tolbor-21; 13, Tolbor-15; 14, Tolbor-16 and Tolbor-4; 15, Egiin-Gol (Dorolj 1–2); 16, Arembovski; 17, Makarovo 4; 18, Podzvonkaya; 19, Vavarina Gora; 20, Kamenka A; 21, Kandabaevo; 22, Tolbaga; 23, Khotyk; 24, Rashaan Khad; 25, Barun-Alan; 26, Khavsgayt and Salkhit; 27, Otson Tsokhio16–18; 28, Shuidonggou locality 1 and 2. MIS 3 core and flake assemblages: 29, Xiaodong Cave; 30, Yushuiping; 31, Longtanshan; 32, Laoya Cave; 33, TX08; 34, TX03; 35, Xujiacheng; 36, Dadiwan; 37, Changweigou; 38, Shuangbuzi; 39, Huagou 5; 40, Yuweigou 1 and 2; 41, ZL05; 42, ZL08; 43, Shuidonggou 2 and 7; 44, Shixiakou; 45, Zhangjiachuan 2; 46, GY03; 47, Ma'anshan; 48, Liujiacha; 49, Gaolingpo; 50, Yahuai Cave; 51, Salawusu; 52, Bailiandong Cave; 53, Wulanmulun; 54, Baojiyan; 55, Dingcun 7701; 56, Licunxigou; 57, Longquandong; 58, Fuyihe (Xiachuan); 59, Jigongshan; 60, Shiyu; 61, Beiyao; 62, Fangjiagou; 63, Zhiji Cave; 64, Tashuihe; 65, Laonainaimiao; 66, Zhaozhuang; 67, Shulian Cave; 68, Huangdikou; 69, Dangcheng; 70, Xibaimaying; 71, Upper Cave; 72, Wangfujing; 73, Xianrendong Cave; 74, Lianhuachishan; 75, Zhuacun; 76, Huangniliang; 77, Dazhushan; 78, Xiaogushan; 79, Miaohoushan; 80, Zhoujiayoufang; 81, Xuetian. Modern human fossil sites: 82, Ust'Ishim; 83, Salkhit; 84, Upper Cave; 85, Tianyuan Cave

42° N where "core-and-flake assemblages" (CAFs) otherwise prevailed during most of the Pleistocene (Gao, 2013; Gao & Norton, 2002; Jia & Huang, 1985; Marwick, 2008; Wang, 2017; Zhang, 1989), albeit with several temporal and regional technological changes (Hou et al., 2000; Li et al., 2018, 2020). In East and Southeast Asia, CAF assemblages lacking predetermination or shaping (e.g., in Fig. 2) persist among successive hominin species, including our own. During MIS 3, they remained the most common technological assemblages in the area (Fig. 1). The ubiquity of CAFs in the Pleistocene possibly reflects selective pressures specific to those regions.

In the neighboring eastern Eurasian Steppe, including Uzbekistan, Kazakhstan, the Siberian Altai, Trans-Baikal, and North Mongolia, the Upper Paleolithic is characterized by the prevalence of blade/bladelet production, which is clearly distinct from the irregular flake production of CAFs in the south (Fig. 2) (Anikovich, 2007; Derevianko & Shunkov, 2009; Derevianko et al., 2013; Gladyshev et al., 2012; Rybin et al., 2016; Zwyns et al., 2014). Such traditions emerged as early as 48–45 ka cal BP, with the Initial Upper Paleolithic (IUP) being recognized by specific technological traits such as the coexistence of burin-core and asymmetrical core reduction methods to produce blades (Derevianko, 2010; Derevianko et al., 2004; Goebel & Aksenov, 1995; Goebel et al., 1993; Kuhn & Zwyns, 2014; Zwyns et al., 2012). Subsequently, from ca. 38–35 to 25 ka cal BP, the Early Upper Paleolithic (EUP) continued to produce blades but with an increased frequency of bladelets (Derevianko et al., 2013; Gladyshev et al., 2010; Rybin et al., 2016; Zwyns, 2012). In eastern Europe, the IUP is directly associated with *Homo sapiens* fossils (Hublin et al., 2020) at

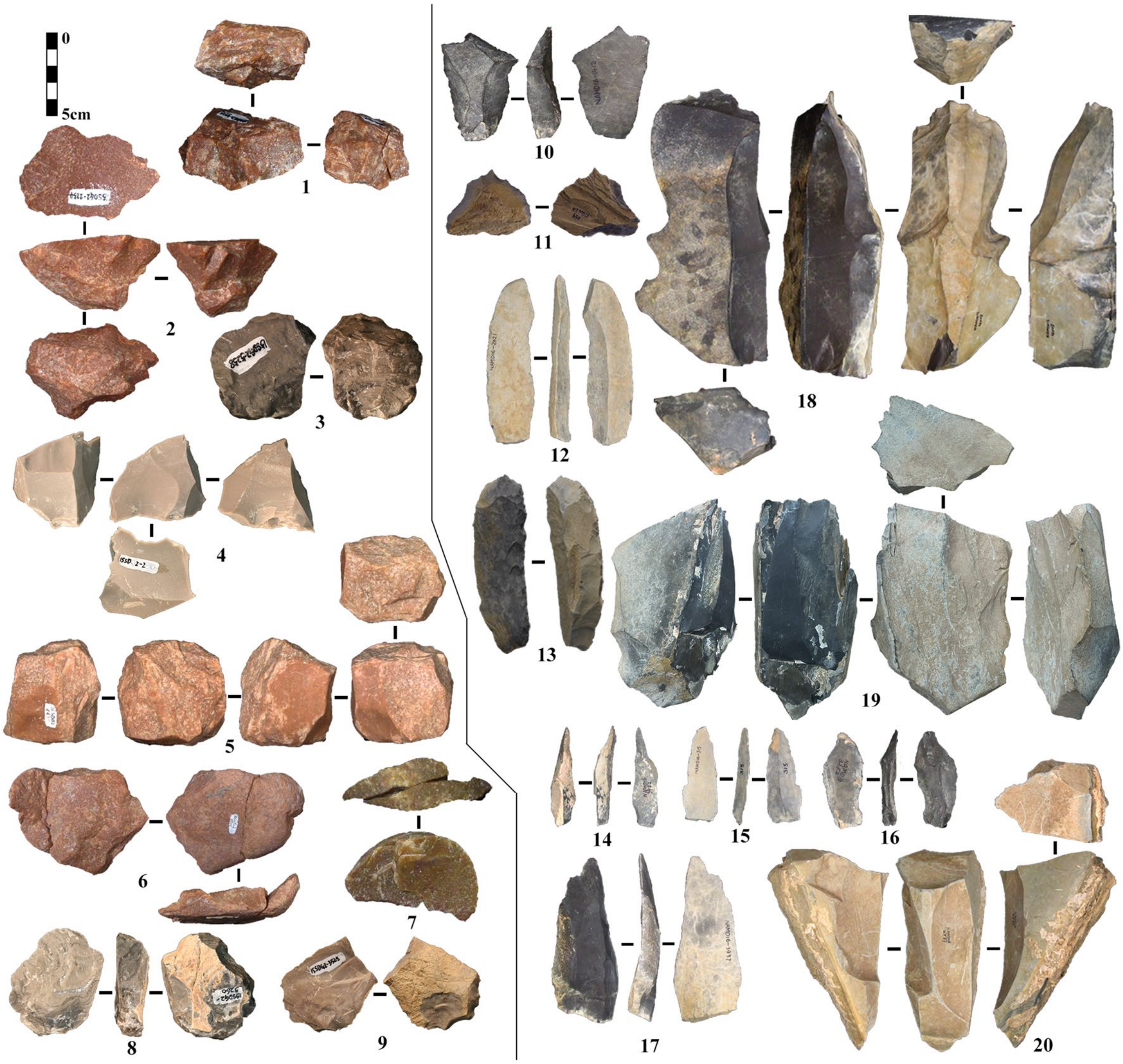

Fig. 2 Flake-based artifacts and blade-based artifacts. 1–9: cores, flakes, and tools from a "core and flake" assemblage of Shuidonggou Locality 2; 11–20: blades, tools, and cores from a blade-based assemblage of Nwya Devu site

approximately 45 ka cal BP (Fewlass et al., 2020). Although the association between IUP and *Homo sapiens* is not as firmly established in eastern Asia, the industry overlaps chronologically and geographically with the earliest modern human fossil remains in Central and North Asia (Fu et al., 2014). Hence, the dispersal of blade-based assemblages (BBAs) is often considered evidence of an inland modern human dispersal into eastern Asia (Fu et al., 2014; Gobble, 2015; Zwyns et al., 2019), followed by the rise of multiple modern human lineages and population turnovers throughout MIS 3 and MIS 2 (Mao et al., 2021; Zhang et al., 2022d). The MIS 3 BBAs in North and Central Asia bear typological similarities with the blade assemblages at the Shuidonggou and Nwya Devu sites (Li et al., 2013; Peng et al., 2014; Zhang et al., 2018), suggesting occasional population movements between the Steppe and the Tibetan Plateau.

During MIS 3, a geographic distribution of CAFs in the southeast and BBAs in the northwest in eastern Asia is evident (Fig. 1). The former lies mostly within the present-day extent of the East Asian summer monsoon, while BBAs are concentrated in a continental westerlies-dominated climate zone. The Tibetan Plateau represents a third climatic zone characterized by alpine environments. The Plateau has similar latitudes to CAF sites, and the southern margin of the Plateau receives limited moisture from the East and South Asian summer monsoons, albeit to a limited extent. However, the Plateau's high elevation creates climatic conditions that are qualitatively more similar to those of more distant northerly latitudes, including low temperatures, long winters, strong seasonality, dry climate, and open grassland landscapes. The observed ecological and technological similarities between the Plateau and the steppe zone in the north raise essential questions: to what extent did basic environmental conditions such as temperature, precipitation, and net primary productivity (NPP) affect hunter–gatherer lithic technology? In turn, to what extent did a specific subsistence strategy, including lithic technology, used by human populations influence human capacity to enter and survive in a given ecosystem?

Given that the Nwya Devu site shares much in common with the Upper Paleolithic from the steppe to the north, both in terms of lithic technology and broad climatic regime, we hypothesize that the distribution of BBAs and CAFs corresponds to different environmental regimes. To investigate this, we compare the environmental conditions of the assemblages distributed in the eastern part of the Eurasian Steppe, the Tibetan Plateau, and lowland China, under the assumption that the relationship between the environment and the distribution of human populations, along with their technologies, provides insight into human adaptations to environments (Banks, 2006; Banks et al., 2013; Leonardi et al., 2022; Timmermann & Friedrich, 2016; Yaworsky et al., 2020). We model the occurrence probabilities of the BBAs and CAFs to understand the impact of ecological conditions on human behaviors. We anticipate that the environmental situation of the Nwya Devu site, and broadly, the Tibetan Plateau, is consistent with the climatic envelope of BBAs in North and Central Asia. It should be distinct, however, from the climatic envelope of lowland MIS 3 sites in the surrounding lowland East Asia.

Fundamentally, hunter–gatherers adapt their subsistence strategies and technologies to obtain natural resources whose distribution and availability are affected by the environment. Environmental conditions thus influence human movement, technological innovation and organization, and settlement patterns (Banks et al., 2013; Barton et al., 2007; Binford, 1980, 1990; Kelly, 1983; Müller et al., 2011). Lithic production and use are instrumental in many subsistence behaviors, and stone artifacts are the most durable material culture in archaeological records. We therefore further explore how hunter-gatherers may have used the two investigated lithic technologies, especially the BBAs, along with other adaptive strategies, in response to their respective environmental conditions. As the blade technology of Nwya Devu was possibly introduced from the north (Zhang et al., 2018; Zhang et al., 2022c), one can expect the behavioral repertoire associated with it to be at least compatible, if not advantageous, for human expansion into similar ecological conditions such as the alpine steppes of the Tibetan Plateau during MIS 3. The corollary implication is that the socioeconomic strategies represented by CAFs commonly used in temperate climates would be less advantageous in a high-elevation environment. In sum, this study examines the role of environmental pressures that might have affected the peopling of these regions and catalyzed technological developments with them.

Materials and Methods

To evaluate the proposed association between the environment and human behaviors, we first compared the environmental values of the two lithic assemblages, testing the null hypothesis of no difference in the environmental conditions for the localities of the BBA and CAF lithic assemblages. Since null hypothesis testing can only reject the absence of a difference, we further applied binomial logistic regression models with paleoclimatic data from MIS 3 to characterize the ecological settings for human populations who employed the two technology types. Additionally, we compared the ecological situations of the two assemblages with the Tibetan Plateau and Nwya Devu to identify areas of climatic overlap, thus allowing us to evaluate our working model.

The Study Area

We considered three geographic areas in our study, encompassing North and Central Asia, lowland China, and the Tibetan Plateau, ranging from 70° E to 125° E and from 23° N to 60° N (Fig. 1). Here, we introduce each sub-region and the associated archaeological assemblages.

The Tibetan Plateau and Nwya Devu Site

The high elevation of the Tibetan Plateau (Supplementary Information Fig. S1), averaging over 4000 m above sea level (masl), gives rise to an extreme environment with long, cold, dry winters and strong seasonality. Hypoxia also constitutes a strong selective pressure here (Beall, 2007; Moore et al., 1998). In the highlands, the average annual temperature is approximately ~ – 5 °C, and during winter, it can be as low as – 25 °C in the west and – 15 °C in the east (Cui & Graf, 2009). The average annual precipitation is approximately 200 mm, more than 60% of which falls in summer (precipitation is generally less than 75 mm in winter) (Liu & Yin, 2002; Wang et al., 2008a). The land cover consists of forest, shrub, meadow, and steppe; the alpine steppe covers approximately 60–70% of the Plateau particularly above 3800 masl (Cui & Graf, 2009; Shen et al., 2011). There is an ongoing debate as to whether MIS 3 was as warm and moist as the southern part of the Plateau. The sedimentary record at Nwya Devu has been interpreted to suggest moister conditions at the time of occupation (Zhang et al., 2018), and lake shoreline records may also support slightly moister conditions (e.g., Zhou et al., 2020), although high MIS 3 lake levels at some localities in the southwestern plateau may be attributable to glacial meltwater influx rather than enhanced precipitation (Zhang et al., 2020b).

The Nwya Devu site is located in the interior of the Plateau, at an elevation of 4600 masl. The primary human occupation was dated to 40–30 ka using optically stimulated luminescence (Zhang et al., 2018), during which time most lowland regions accessible to the Plateau were characterized by CAFs (Li et al., 2013; Peng et al., 2014; Zhang et al., 2022c). There is no earlier example of blade technology in and around the Plateau suggesting that the technology was unlikely to be a local innovation. The closest analogy is the IUP-like assemblages at the Shuidonggou site in North China, which is considered to be an extension of the Steppe zone (Brantingham et al., 2001; Li et al., 2016; Zwyns, 2021).

North and Central Asia and Upper Paleolithic BBAs

The BBAs included in our analysis lie within a relatively diverse region in terms of both climate and biome; they are located in the Siberian Altai, Trans-Baikal, and northern Mongolia, areas currently under taiga, alpine forest, and steppe vegetation in the broad sense (including taiga-steppe and desert steppe). These sites are located in North and Central Asia (Supplementary Information Fig. S1), mostly within the Eurasian Steppe belt that extends from eastern Europe to eastern Asia, currently sitting between around 45° N and 55° N in the west and around 40° N and 50° N in the east, with cold and dry continental climates (Dfb, Dfc, Dwc, and Bsk according to the Köppen–Geiger climate classification). Winters can be extremely cold, with average January temperatures as low as – 28 °C in northern Mongolia (Dulamsuren & Hauck, 2008), while in the most westerly parts of the study area, precipitation falls mainly in the summer. MIS 3 paleoenvironmental records are scarce for the region but are generally indicative of cold and dry conditions; the northern boundary of the steppe seems to have lain above 55° N during mid-MIS 3 (there is limited information for the period before 40 ka). The southern boundary of the steppe currently grades into desert, but the MIS 3 situation for these arid and semi-arid areas is difficult to reconstruct because of apparent variability both spatially and temporally, and because the existing records derive predominantly from lake levels or alpine glaciation, both of which respond to variables other than precipitation.

The majority of these records, however, indicate conditions as dry as or drier than the present during the IUP and EUP occupation. The term “steppe” is therefore used loosely in this paper, considering the lack of detailed environmental data for the period under investigation. Twenty-seven Upper Paleolithic blade sites were reported dated between 48 and 35 ka cal BP from the steppe (Supplementary Information Table S1), which contain IUP or EUP industries. These assemblages include some of the earliest records for volumetric blade production during MIS 3 in the region and are considered a potential source for the blade technology at Nwya Devu and Shuidonggou (Gobble, 2015; Kuhn & Zwyns, 2014; Li et al., 2016; Rybin, 2014; Zhang et al., 2022b; Zwyns, 2021). Thus, modeling the ecological condition of plausible origins for the BBAs provides a better understanding of the environmental pressures that might have been associated with technological development in the study area.

Lowland China and MIS 3 CAFs

The Tibetan Plateau is bounded to the north by rain-shadow deserts (the Taklamakan and Ordos), but the lowlands to the east and southeast of the Plateau are under the influence of the East Asian summer monsoon, which brings significant summer rainfall and warm air. This large region currently experiences very different conditions in the south (humid subtropical climate; CAF and Cwa according to the Köppen–Geiger climate classification) than the north (humid continental climate or cold semi-arid climate, Dwa, Dwb, and Bsw); the annual mean temperature of lowland East Asia ranges from ~ 25 °C in the south to ~ −2 °C in the north, and their annual mean precipitation ranges from ~ 2500 to ~ 300 mm from south to north (Liu et al., 2003). There is a considerable volume of research on the past extent and strength of the East Asian summer monsoon, through which its persistence throughout MIS 3 has been securely established. The northwesternmost extent of the summer monsoon rainfall belt is important to establish for the period under investigation, as several of the CAF sites included in this study, as well as the Shuidonggou site with BBA and CAF, lie in arid or semi-arid regions close to the present-day boundary of monsoon rainfall. The Shuidonggou site itself sits within loess deposits (Boëda et al., 2013), in contrast to the present-day landscape, which is semi-desert, suggesting a different, possibly moister, climate at the time of occupation. Sedimentary and pollen records from the region indicate a northwestward movement of the monsoon rainfall boundary during MIS 3, relative to the present day (e.g., Yang & Ding, 2008; Zhang et al., 2022a; and see a large-scale review in Zhao et al., 2014). This does not negate the dry character of the region but places Shuidonggou and its neighbors outside of a true desert biome at the time of occupation. Chinese speleothem records indicate a generally strong East Asian summer monsoon for MIS 3, which intensified during Greenland interstadials (e.g., Duan et al., 2013; Liang et al., 2022; Wang et al., 2001, 2008b; Zhang et al., 2019), but decreased evaporation means that soil moisture may have independently increased when temperatures were cooler, and the combination of these effects makes it difficult to infer the position of the line of zero effective precipitation with enough spatiotemporal precision to predict the environment at northern and northwestern Chinese sites.

In lowland China (Supplementary Information Fig. S1), archaeological sites dated to MIS 3 consist primarily of CAFs (Fig. 1). Distinct from systematic blade production, CAFs are characterized by a very basic flaking system to produce flakes and tools lacking standardization. As CAFs are represented as small flake industries in North China and as chopper-chopping tools in South China, it is critical to note that the technological diversity of CAFs has been understudied. Here, for modeling purposes, we simply grouped all these assemblages under the label of CAFs. Fifty-three CAF sites (Supplementary Information Table S1) were documented in MIS 3 and used in this study for modeling purposes as a comparative sample to investigate the space-environment correlation with stone tool technologies. The sites included in the study are broadly dated to MIS 3 (Supplementary Information Table S1), which is a crucial period for modern human expansion in eastern Asia.

Paleoclimate Data

Since the archaeological sites examined in the study belong to MIS 3 (Supplementary Information Table S1), we employed MIS 3 paleoclimatic data simulated by Krapp and colleagues (2021) using the R software package 'pastclim' (Leonardi et al., 2023). Considering that the dates of archaeological sites span from early to late MIS 3 and given the frequent millennial-scale fluctuations during this period, it becomes challenging to select a single set of paleoclimate data suitable for modeling all the sites. For this reason, we used the optimal interstadial (46 ka) and stadial (30 ka) periods of MIS 3 as boundary conditions for the cold and warm stages. Here, we considered three basic environmental factors as proxies in our modeling: annual mean temperature (bio01), annual precipitation (bio12), and NPP (npp) (Fig. 3). We note the complexity of the interplay between temperature, precipitation, and NPP in arid landscapes and acknowledge the possibility that conditions may have varied beyond the broad boundary conditions in some parts of the study area. However, the main objective of this research is to study the presence or absence of a pattern indicating that the geographic distribution of the BBAs and CAFs is influenced by the environment. We consider that the use of the two boundary conditions is sufficiently informative for examining the hypothesis outlined.

Analysis

Our analysis began with identifying the environmental distinction between BBA and CAF localities. After examining the difference, we extrapolated the climatic envelopes of the two assemblages to the Tibetan Plateau to evaluate the extent to which the models predict the location of the Nywa Devu site.

Comparing Environmental Values

For each archaeological site, we first extracted the values for each of the three environmental variables. To do this, we used site coordinate pairs to extract values from each environmental raster grid from the paleoclimate data. The Wilcoxon rank-sum test (also known as the Mann–Whitney U test), a non-parametric test that evaluates whether two independent samples come from populations with the same distribution, was used to evaluate whether the environmental values of the BBAs and the CAFs are from the same distribution. A significance threshold of p value < 0.05 was set to determine statistical significance. If the resulting p value is less than 0.05, we reject the null hypothesis that there is no difference in the environmental conditions in which the BBAs and CAFs are distributed; otherwise, we fail to reject the null hypothesis. We also applied the empirical

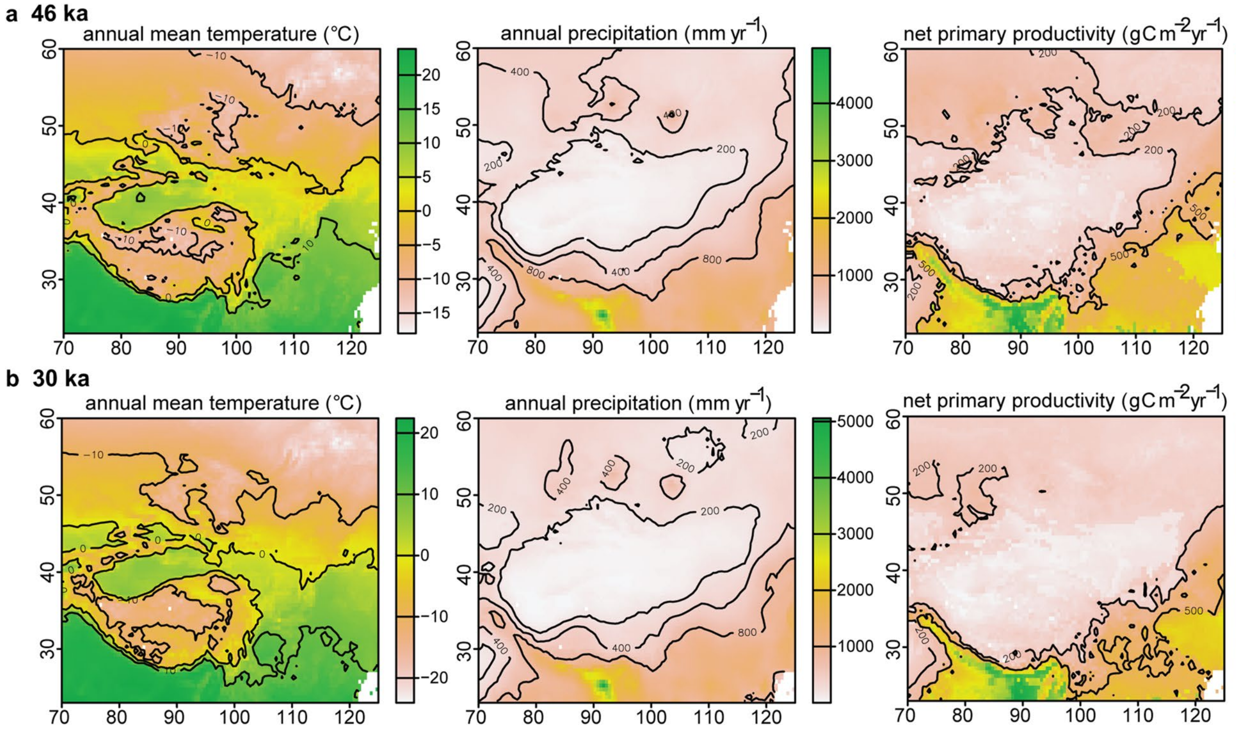

Fig. 3 Temperature, precipitation, and NPP at 46 and 30 ka

cumulative distribution function to assess the probability of a random variable being less than or equal to a specific value, which is to better examine whether the environmental values of the Nwya Devu location fall within the climatic regime of BBAs or CAFs.

Modeling Occurrence Probability

While the statistical comparisons described above offer preliminary insights into the ecological situation of the sites, they do not provide details into the extent to which each of the climatic variables contributed to the Upper Paleolithic occupation patterns. To further examine the environmental conditions of the BBA and CAF traditions, we employed a binomial logistic regression model with a second-order polynomial to compute the occurrence probabilities for BBA and CAF localities. Numerous studies have demonstrated the benefits of investigating occurrence probabilities as an ecological niche for the distribution of human populations in given environments to better understand human dispersals and adaptations in archaeology and paleoanthropology (Banks, 2006; Beeton et al., 2014; d'Errico & Banks, 2013; Franklin et al., 2015; Glantz et al., 2018; Kondo et al., 2018; Yaworsky et al., 2023; Yousefi et al., 2020).

Here, we used a binomial logistic regression model to contextualize the ecological-cultural interaction of human groups using different lithic technologies in their respective environmental settings. Although our research subjects are archaeological sites, they reflect the geographic distribution of the human populations who made stone tools. Our model can effectively work with low-occurrence data and allow for non-linear relationships (Valavi et al., 2022). The presence or absence of BBA and CAF sites was determined for each environmental grid cell in the study area (Supplementary Information Table S1) (Pearce & Boyce, 2006). The three primary explanatory environmental variables were temperature, precipitation, and NPP. Having modeled the relationship between site occurrence and environmental factors, we extrapolated the results throughout the study area, scaling probability densities from 0 to 1. All geographic data management and modeling were conducted in the R statistical computing language (R Core Team, 2023), using the "sp" (Bivand et al., 2013; Pebesma & Bivand, 2005), "raster" (Hijmans, 2023), "rgdal" (Bivand et al., 2023), and "rgeos" (Bivand & Rundel, 2022) packages. All codes are available in the Supplementary Information.

Model Comparison

To determine the most efficacious model for predicting the location of the assemblages, we derived Akaike Information Criterion (AIC) values for each model. Lower AIC scores generally indicate more parsimonious models that simultaneously maximize information content and minimize parameters (Bozdogan, 1987). We examined the statistical plausibility of model coefficients using associated p values. Parameter estimates that generated p values <0.05 are considered statistically plausible. This enabled us to explore which environmental factors are statistically plausible and have the greatest influence on the distribution of technologies. Model fitting and comparison are performed using the R statistical computing language (R Core Team, 2023), and all code is presented in the Supplementary Information.

Results

We began by reporting the results of the environmental comparison to gain a preliminary sense that the environmental situation of Nwya Devu aligns with the environmental variables of technological traditions. We then discuss the model results to identify the relevant roles of environmental factors in the distribution of BBAs and CAFs and the location of Nwya Devu.

Assessment of Environmental Differences Between BBAs and CAFs

Based on the extracted environmental values (Fig. 4; Supplementary Information Table S2), the median values of temperature, precipitation, and NPP for BBAs at 46 ka are –6 °C, 305 mm/year, and 249 gC/m^2, respectively, and at 30 ka are –10 °C, 268 mm/year, and 150 gC/m^2, respectively. The median values of the three factors for CAFs at 46 ka are 6 °C, 476 mm/year, and 426 gC/m^2, and at 30 ka are 4 °C, 407 mm/year, and 235 gC/m^2, respectively. Statistically significant differences between the environment of CAFs and BBAs are observed in terms of temperature, precipitation, and NPP at 46 ka ($W=0$, $p<0.05$; $W=312$, $p<0.05$; $W=201$, $p<0.05$) and at 30 ka ($W=0$, $p<0.05$; $W=298$, $p<0.05$; $W=294$, $p<0.05$). In Fig. 4, clear differences between the two groups can be observed for both time periods. Temperature values show the greatest difference, while precipitation values of a few BBA and CAF sites in the lowlands overlap.

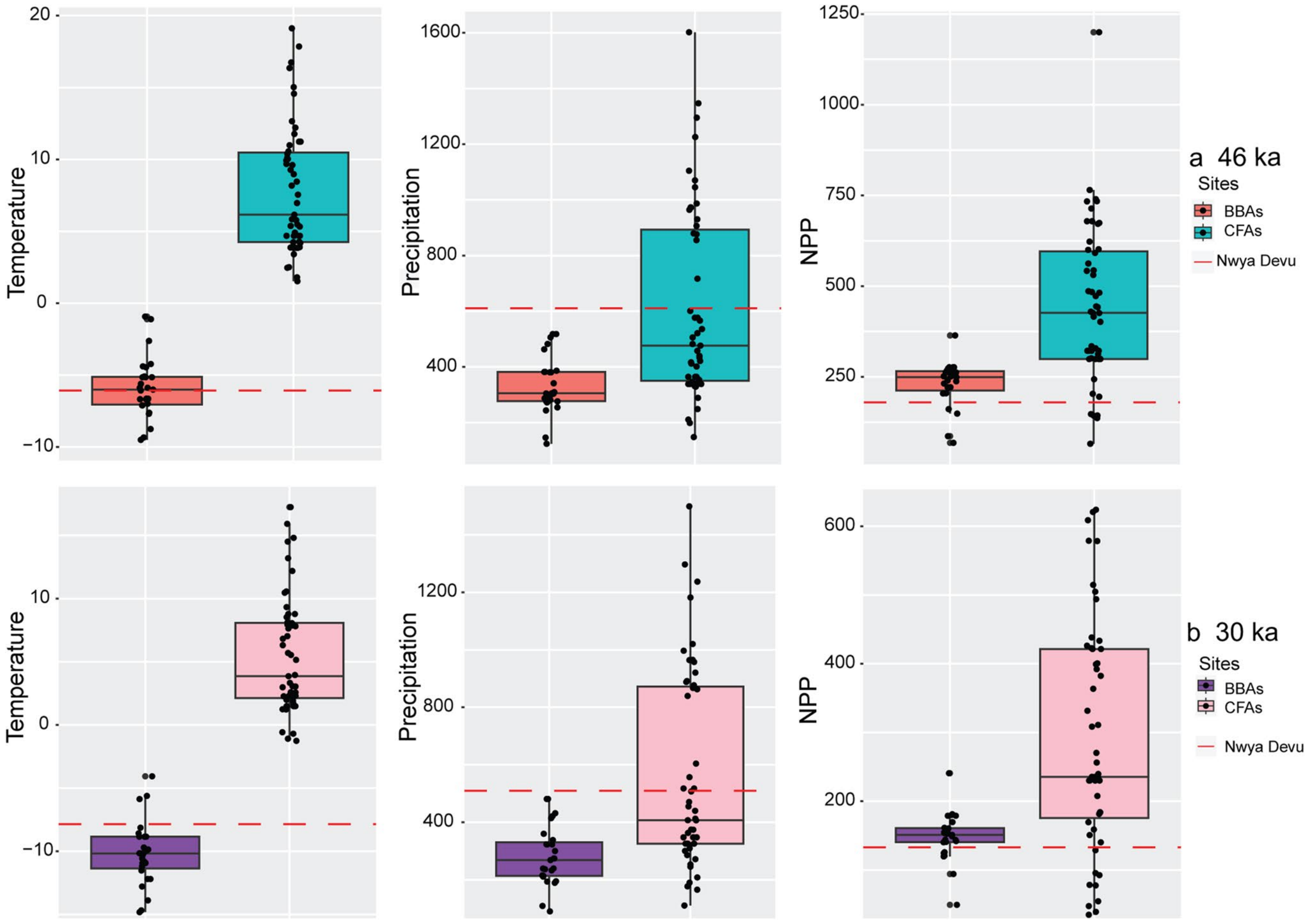

Fig. 4 Environmental values for the archaeological sites at 46 ka (**a**) and 30 ka (**b**). Temperature, precipitation, and NPP values at Nwya Devu and for other BBAs and CAFs. Note that the temperature and NPP Nwya Devu values are consistently closer to those obtained for the BBAs than for the CAFs

At the Nwya Devu site, the values of temperature, precipitation, and NPP at 46 ka are –6 °C, 611 mm/year, and 180 gC/m^2, respectively, and at 30 ka are –8 °C, 509 mm/year, and 133 gC/m^2, respectively. These values align closer with BBAs (Fig. 4). The empirical cumulative distribution function (Supplementary Information Table S3) shows temperature values at Nwya Devu consistently falling within the range of BBAs instead of CAFs, while precipitation values are closer to CAFs than to BBAs. With regard to NPP, the Nwya Devu site has a value that is closer to BBAs.

Therefore, the statistical results clearly show the rejection of the null hypothesis, indicating a significant difference in the environmental conditions in which the BBAs and CAFs are distributed during MIS 3 in the study area. Moreover, the Nway Devu site shares more similarities with BBAs.

Model Results and Evaluation

As environmental factors tend to co-vary across ecosystems, we first modeled the three factors together to assess the effects of the environment. Among the four models for BBAs and CAFs at 46 ka and 30 ka, the AIC values indicate that the two models for BBAs have much lower values than those for CAFs (Supplementary Information Tables S4–S7; Fig. S2). The two former models have very similar values, but the one with paleoclimate data at 30 ka is slightly lower by about 0.64 compared to the one at 46 ka. Based on coefficients, only temperature displays statistically significant values ($p < 0.05$) (Supplementary Information Tables S4–S7), which suggests that temperature played a more substantial role in the implantation of CAFs and BBAs in the landscapes.

As only temperature shows signficant *p* values, we also modeled this factor independently for BBAs and CAFs during the two climate periods. The coefficients of the four single-variant models are all significant (Supplementary Information Tables S8–S11), emphasizing the role of temperature. With lower AIC values of the two models for BBAs (Supplementary Information Tables S8–S11), the results indicate, once again, that the geographic distribution of BBAs appears to be more influenced by environmental factors than CAFs, particularly temperature in this case. Slightly different from the multi-variant models, the model of temperature at 46 ka has a slightly lower AIC value than the one at 30 ka but is still very close. In addition, the AIC values of the two single-variant models for BBAs are almost identical to those of the two multi-variant models for BBAs. The low AIC values of the multi-variant models thereby may be driven by the importance of temperature. Overall, we note that temperature is the most influential variable affecting the geographic distribution of the use of lithic technologies by human populations in the study region, especially the BBAs.

Occurrence Probability of BBAs and CAFs

Regarding multi-variant models (Fig. 5), the two models for BBAs show higher occurrence probabilities in the steppe landscape and the southeast parts of the Plateau (Fig. 5a, b). One major difference between the results of the two periods is that the southern area of the Plateau shows low probabilities of occurrence for BBAs at 46 ka (Fig. 5a). It is possibly related to the enhanced summer monsoon bringing more moister up the high mountains during interstadial (Wang et al., 2008a). Alternatively, CAFs tend to occur in regions below ca. 40° N and, the probability of occurrence on the Plateau is extremely low (Fig. 5c, d). The limits of meridional extension near 20° N likely reflect a sampling bias owing to the restricted study area, as many CAFs are also found further south but are not included in the study. The northern boundary of the occurrence probability for CAFs overlaps the northern limit of the East Asian summer monsoon during MIS 3, which is slightly to the north but very close to the modern one (Chen et al., 2015, 2018; Qian et al., 2009; Yang & Ding, 2008).

According to the AIC and *p* values above, we also independently modeled the most influential facotor, temperature. The model outputs of temperature illustrate high probabilities for BBAs in the Steppe belt and almost the entire Tibetan Plateau (Fig. 6a, b). The CAFs, however, tend to cluster with high probabilities in the south of lowland China (Fig. 6c, d). Overall, the models of temperature display clearly distinct habitats for BBAs and CAFs in lowland eastern, with higher probabilities of finding BBAs on the Tibetan Plateau. While precipitation is also influenced by geography, such as monsoon in this case (e.g., distance to the moisture from oceans), and NPP is strongly affected by precipitation, but these two factors exhibit significantly less predictive power than temperature for the occurrence probabilities of the lithic technologies.

Discussion

Mapping the Spatial Pattern of MIS 3 Lithic Technologies in Eastern Asia

The comparison presented above suggests that in eastern Asia, during MIS 3, the environmental regimes of BBAs and CAFs differ in terms of temperature, precipitation, and NPP, with temperature exerting the greatest influence on the occurrence of BBA and CAF technologies (Fig. 4; Supplementary Information Table S2). Nwya Devu falls within the climatic envelope of BBA sites, and outside the climatic envelope of CAF sites, concerning temperature and NPP. Whereas, precipitation for Nwya Devu is similar to the values of CAFs, which is likely due to the strong summer Asian

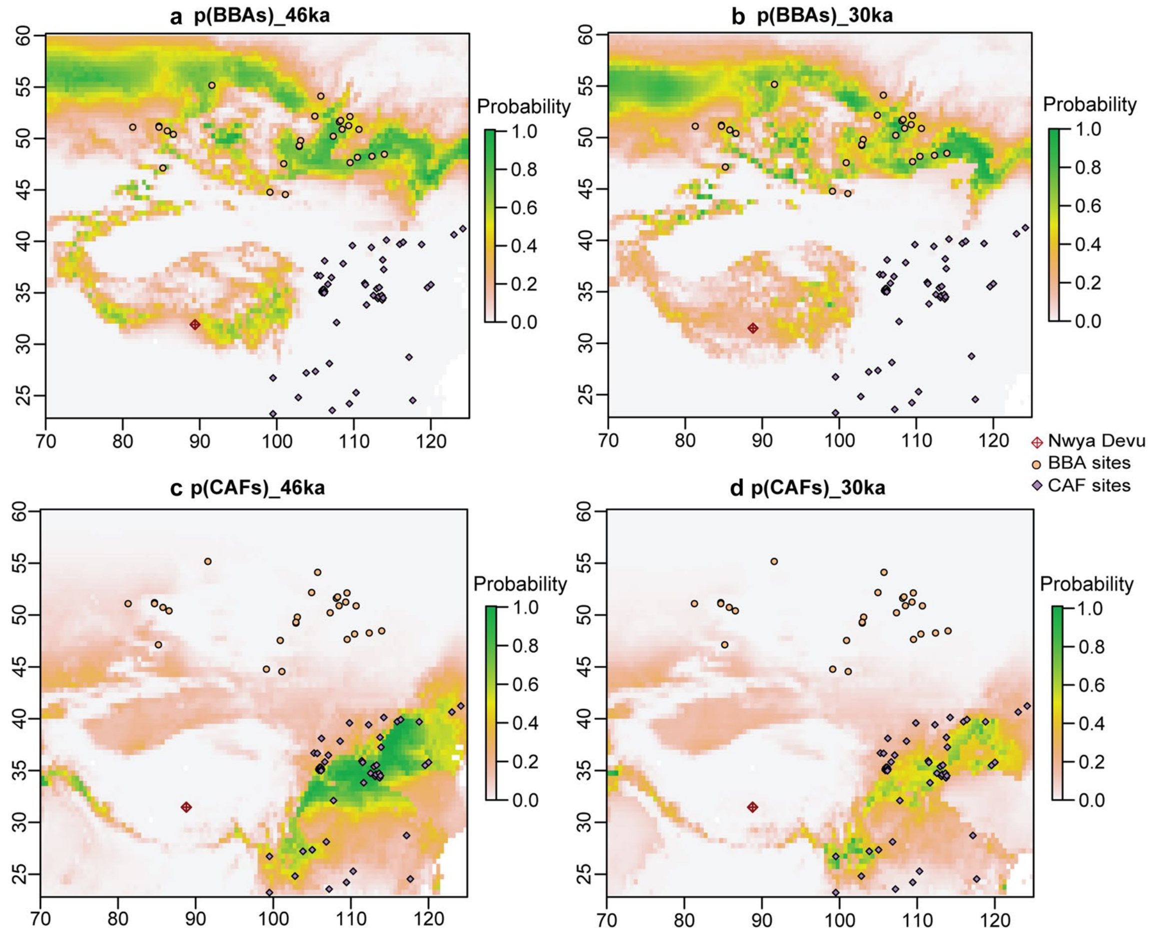

Fig. 5 Occurrence probability of all factors for the BBAs and CAFs

monsoon. The occurrence probabilities indicate that the ecological conditions of BBAs and CAFs differ (Fig. 5; Supplementary Information Tables S4–S11), with a northwest/southeast separation between the two categories of lithic assemblages. The CAFs are predicted to be widely distributed along the eastern and southern lowlands of the study area, where the East Asian summer monsoon brings regular moisture and heat from the Pacific Ocean. The chances that BBA makers exploited this kind of habitat are low. Instead, BBAs are more likely to be found in landscapes under steppe vegetation in the broad sense, both in the Eurasian Steppe and the alpine steppe of the Tibetan Plateau, which holds true for the location of the Nwya Devu site. Although the archaeological record of the highlands is currently very fragmentary, our models suggest that more BBAs could be found in the area. This ecological correlation with BBAs exists despite Nwya Devu being located at a similar latitude to CAFs.

Among the three variables tested, temperature appears to be the most influential factor in the geographic distribution of BBAs and CAFs (Fig. 6; Supplementary Information Tables S4–S11). This is particularly clear for the BBAs within the study area, thereby highlighting a correspondence between the high frequency of blade technology and cold habitats during MIS 3. The relative stability of temperature during warm and cold boundary conditions characterized by a north–south or low-to-high elevation gradient is naturally associated with the pattern of northwest/southeast distribution of the technologies. Other lines of evidence also suggest that in the steppe zone, blades are associated with cold environments. For the Tolbor Valley (North Mongolia), where there is a high density of IUP and EUP sites, cold and arid conditions seem to have recurred throughout MIS 3, and the sections preserve characteristics common in desert and polar desert situations. It is possible that episodes of occupation coincided with humid pulses or other short-lived climatic fluctuations—these could potentially increase NPP and account for the large herbivores represented in the faunal assemblages from these sites (Izuho et al., 2019; Rybin et al., 2020; Zwyns & Lbova, 2019). From Bacho Kiro cave in eastern Europe (Hublin et al., 2020), although it is outside of our study area, oxygen isotope signals of sequentially

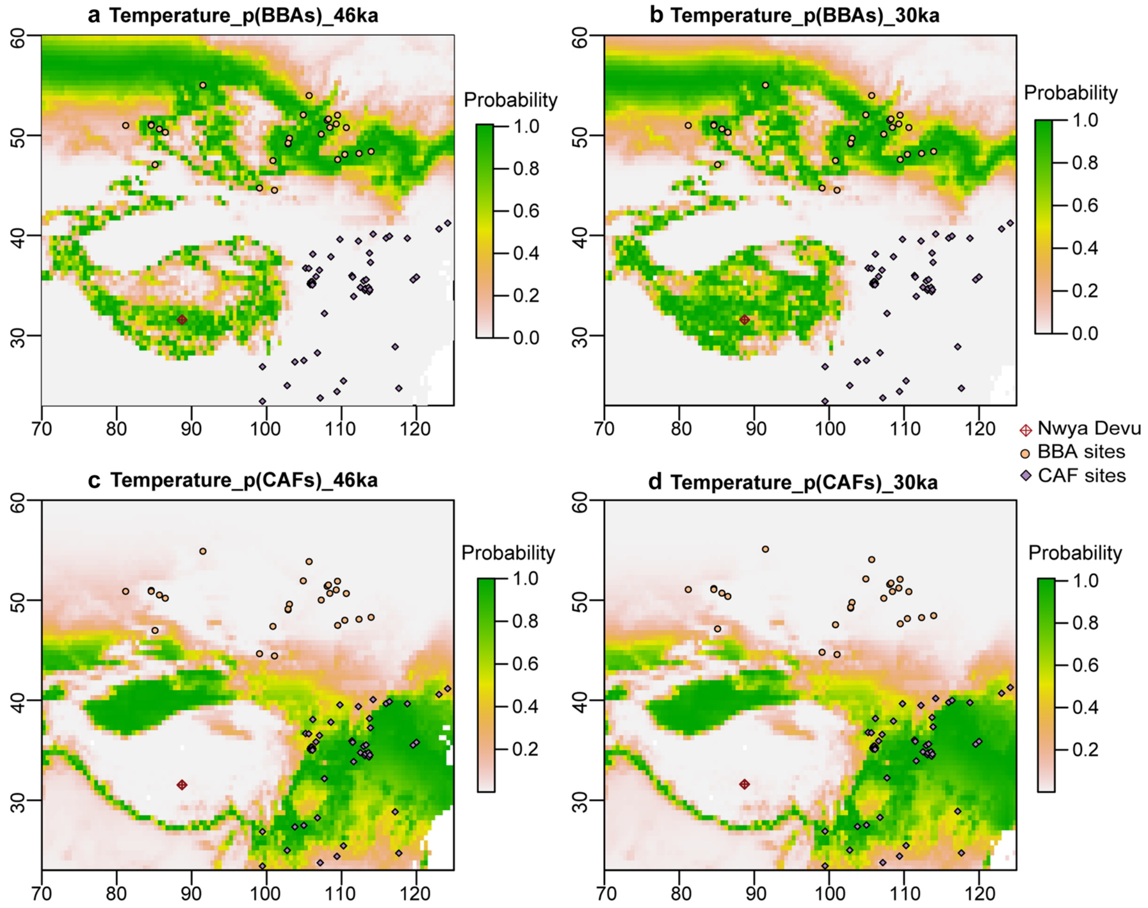

Fig. 6 Occurrence probability of the temperature for the BBAs and CAFs

sampled faunal tooth enamel revealed that the *Homo sapiens* fossils directly associated with IUP artifacts lived under a subarctic climate before and around 45 ka cal BP (Pederzani et al., 2021).

Although we note an overlap between the northern limit of the East Asian summer monsoon and the northern extension of the MIS 3 CAFs (Fig. 1), we have not identified a significant role of precipitation in the models. Within the area of eastern Central Asia where BBAs predominate, moisture (as a function of topography) has previously been seen as a dominant influence on the distribution of Paleolithic sites (Beeton et al., 2014; Glantz et al., 2018). Yet effective precipitation—the balance between precipitation and evaporation—responds to changes in temperature, seasonality, and global atmospheric circulation, as well as vegetation cover, so true MIS 3 moisture conditions for parts of the study area may differ from the statistics of paleoclimate reconstruction. This is significant for our interpretation because, together with variables not directly tested for, including seasonality, season of precipitation, topography, and average wind speed, total precipitation makes a major contribution to the ecology of the regions under investigation. A wide geographic distribution for CAFs as a broad category (noting especially the similar total precipitation in northern lowland China and in the southern part of the BBA-dominated steppe) influences the results of the statistical tests and may obscure the true relationship between precipitation regime, ecology, and the distribution of BBA archaeological sites, even if temperature does emerge as the most limiting factor on northerly or high elevation dispersal of CAFs.

Overall, these findings support that an environmental difference exists between the regions where BBAs and CAFs are distributed and that the Nwya Devu site aligns environmentally with BBA conditions. The Tibetan Plateau shows high occurrence probabilities for BBAs, similar to Central and North Asia. Extrapolating from the observed environmental differences, we propose a correlation between the environment and the lithic technologies used by human populations in eastern Asia during MIS 3. That is, the geographic distribution of the two technologies could be explained, at least partly, by ecological context. The use of blade technologies was possibly associated with cold temperatures within the study area. Temperature is closely tied to elevation and latitude, and it is one of the major factors shaping the distribution of plants and animals on the planet. Therefore, it is likely a crucial factor influencing human movements, settlements, and activities, and one of the most salient variables affecting hunter–gatherer behaviors (Binford, 2001; Gilligan, 2017; Johnson, 2014). Of course, environmental factors do not directly affect the form of stone tools. Nonetheless, it is uncontroversial that hunter-gatherers adjust their behaviors, including their tools, to adapt to diverse environments, particularly during periods of stress or when changing climates lead to a redistribution of natural resources (Binford, 1980, 2001; Kelly, 2013; Nelson, 1991; Shott, 1986; Starkovich, 2014; Starkovich & Ntinou, 2017; Vaquero & Romagnoli, 2018; Yaworsky et al., 2023). Stone tools thus reflect a major component of human adaptive strategies.

Blade Assemblages in Cold Habitats of Eastern Asia

Our analyses suggest that blade technology appears to be a visible aspect of the complex behavioral repertoire relied on by humans during MIS 3 in cold habitats. Countless examples of blade assemblages across various regions and over extended periods (e.g., Delagnes, 1999; Kuhn & Stiner, 1998; Soriano et al., 2007), however, clearly show that this technology is unlikely to be strictly environment-specific or cold-adapted. In the present case, our limited understanding of human activities and stone tool function prevents us from identifying the actual behavioral traits under selection. Here, we discuss two possible mechanisms that may explain the pattern observed.

The first possibility is that blade technology was associated with effective hunting, high mobility, and fitted clothing that would have improved the overall fitness of human groups in the northern steppe and on the Plateau during MIS 3. To survive and settle in such cold environments, Paleolithic hunter–gatherers usually depended on a complex set of behavioral adjustments including high-calorie/fat diet and clothing (Hancock et al., 2011; Hosfield, 2016, 2017). Although these behaviors are also practiced in other environmental contexts, they are more essential in cold situations, and blades potentially represent the preserved part of a complex and direct response to the challenges in cold habitats.

To cope with frequent exposure to cold temperatures, the human body increases its metabolic rate to maintain body temperature in an acceptable range (Gilligan, 2010, 2017; Leonard et al., 2002). This is why populations living in high elevations and latitudes often have elevated metabolic rates and therefore higher nutritional demands (Ge et al., 2012; Leonard et al., 2005, 2014; Levy et al., 2016). A high-fat or high-protein diet, including animal meats, is thereby important to compensate for the energy loss caused by elevated metabolic rates (Beall et al., 1996; Fumagalli et al., 2015; Levy et al., 2016; Speth & Spielmann, 1983). In a cold habitat with patchy resources, hunting efficacy with more complex technologies is more critical to obtaining calorie-rich foods compared with other environments. Blades/bladelets are involved in carcass processing and may have been part of composite weapons that constituted a technological improvement in hunting technologies (Bar-Yosef & Kuhn, 1999; Shea, 2006; Sherratt, 1997). For instance, blades and points of the Upper Paleolithic assemblages could have been related to projectile technology, which enabled effective hunting for varied prey sizes (Fig. 2) (Bar-Yosef & Belfer-Cohen, 2010; Kuhn & Shimelmitz, 2022; Shea, 2006). The most represented taxa in archaeological assemblages from the steppe zone are *Bos*/bisons, horses, antelopes and gazelles, deer, rhinoceros, marmots, and hares (Germonpré & Lbova, 1996; Wrinn, 2010; Turner et al., 2013; Izuho et al., 2019). The composite tools associated with blade artifacts may be effective in hunting these medium- and large-size ungulates or fast-moving small mammals. However, use-wear studies indicate that blades and points are not specifically designated for hunting solely (Berruti et al., 2020; Tomasso & Rots, 2021). It is also possible that blade forms entail advantages for animal processing due to long cutting edges (Bar-Yosef & Kuhn, 1999; Eren et al., 2008; Kitchel et al., 2022; Schick & Toth, 1993). Moreover, a formal and standardized toolkit is suggested to be better suited to the challenging landscapes with low resource availability and requiring high mobility (Bleed, 1986; Kuhn, 1995; Nelson, 1991; Torrence, 1989), in contrast to the low resource exploitation intensity in temperature and stable environments of lowland China.

The human body is sensitive to changes in the ambient environment, and the regular tolerance for the thermoneutral air temperature of a naked human is approximately 27 °C (Rintamäki, 2007). It is crucial to maintain a body temperature of approximately 37 °C to survive (Stolwijk & Hardy, 2011). Even during the Last Interglacial, the average annual temperature in the steppe and Plateau was near or below 0 °C (Otto-Bliesner et al., 2006). Clothing is therefore an essential piece of equipment for humans to maintain their body temperature under these cold conditions (Wales, 2012). Gilligan (2010, 2017) argued that fitted clothing is crucial for human groups to occupy middle- and high-latitude areas. Tailored clothing could be one of the keys to the success of modern humans in nearly all biogeographic zones during the late Pleistocene (and Neanderthal demise) (Collard et al., 2016; Gilligan, 2007; Hoffecker & Hoffecker, 2017; Kuhn & Stiner, 2006; Toups et al., 2011; Wales, 2012). Garvey (2021) argued that the loss of tailored clothing might have a major impact on the slow peopling of high-latitude Patagonia.

Based on ethnographic records, the manufacture of tailored clothing consists of multiple production steps and a variety of tools that are involved in skin acquisition, preparation for removing subcutaneous tissues, tanning, cutting, and sewing (Hatt & Taylor, 1969). Tool types, such as end scrapers, blades, knives, points, and perforators (Gilligan, 2007, 2010), are used in cutting, scraping, and piercing. These lithic types are common in the Upper Paleolithic blade assemblages. A recent study indeed indicates that before the innovation of eyed needles, pointed lithics or bones had been used to make clothing around 39.6 ka cal BP (Doyon et al., 2023). In terms of the bone industry, awls and needles have been documented in Eurasia during the late MIS 3 (d'Errico et al., 2018; Hoffecker, 2005), such as the Upper Paleolithic assemblages from Denisova Cave and Tolbaga (Izuho et al., 2019; Shunkov et al., 2020). Ethnographic data document that the hide of Cervidae, Bovidae, and Leporidae is the main source of clothing in hunter-gatherer societies (Collard et al., 2016; Usenyuk-Kravchuk et al., 2020). These are common fauna in both temperate steppe and alpine grasslands (d'Alpoim Guedes & Aldenderfer, 2020; Mack & Thompson, 1982; Wesche et al., 2016). Overall, we note that blade technology potentially plays a role in various activities and relatively complex behaviors (e.g., effective hunting, clothing, and mobility) crucial for survival in cold habitats. However, the specific adaptive mechanism requires additional research to establish.

Given the wide distribution of blade-based UP assemblages, blade technology was unlikely to be locally innovated in response to cold climates, but successful adaptations to diverse environments still demand behavioral plasticity. This technology could be repurposed to fit the needs imposed by various environments. Here, the semi-arid steppe would have posed a particular set of challenges – lack of cover for hunting (at least in the form of trees, which also would have entailed the use of alternative fuels), intermittent drought, and an ecosystem with possibly sparse plant foods. Moreover, the high mobility entailed by this environment would have created additional constraints in terms of storage and provisioning. As discussed above, blade toolkits could have been integral to the subsistence strategy including cloth making, hunting, and mobility, facilitating adaptation to cold and open habitats, thereby, they were likely under selective pressures.

Alternatively, the other possibility is that blades may have been perpetuated within a package of traits by means of indirectly biased transmission (Boyd & Richerson, 1985; Zwyns, 2021). In this scenario, blade tools per se were not selected for, and other functionally related—currently unidentified—behaviors could have increased the fitness of human populations that happened to produce blades. In other words, behavioral traits in settling in the cold steppes with little involvement of this lithic technology. Instead, for instance, other behaviors such as sheltering and fire could have improved the fitness of humans (Hancock et al., 2011; Hosfield, 2016; 2017).

In fact, most BBAs listed in the study area occur in open-air sites, with only rare examples from caves or rock shelters. Even considering sampling biases, the existing record suggests that past human groups frequently settled in narrow valleys and open landscapes. Artificial shelters must have been advantageous in this context, but the number of Upper Paleolithic structured dwellings in Siberian and Trans-Baikal regions is low (Buvit, 2008; Gladkih et al., 1984; Goebel, 1994; Goebel & Waters, 2000; Izuho et al., 2019; Khlopachev, 2021), which may reflect preservation biases. Although combustion features, hearths, or burnt bones associated with IUP/EUP settlements in Central and North Asia have been relatively frequently reported, only a few of them have been examined using modern analytical standards (Buvit, 2008; Goebel, 1994; Goebel & Waters, 2000; Hoffecker, 2005; Larichev et al., 1990). The frequency of combustion features reflects the complex interplay between human behavior and site formation processes. Even properly identified, evidence for the use of fire may be underrepresented due to preservation issues (Gallo et al., 2021). At least occasionally, humans relied on artificial constructions in addition to natural shelters and fire to protect them from the cold during the Paleolithic period. In such circumstances, BBAs may merely represent one of the traits being preserved in a cultural package that was copied successfully within cold habitats due to cultural linkage (Yeh et al., 2019).

Furthermore, ancient DNA studies indicate the existence of multiple modern human lineages in North China and North Asia during this period (Fu et al., 2013, 2014; Mao et al., 2021), supporting the possibility that different populations used different technologies in their respective regions without effective cultural interactions (Li et al., 2014). Hence, stochastic effects embedded in population dynamics could also have played a role in shaping the observed geographical pattern of the two technologies. Cultural transmission among different populations, even in the absence of any selective pressures for human populations using blades or associated behaviors, could have conceivably resulted in the spread and geographic clustering of tool types in a phenomenon analogous to a neutral model of biological evolution (Kimura, 1979). Overall, blade productions may have been perpetuated by groups of people who adapted to a cold habitat through other unrelated behaviors. Due to the inherent functionality of stone tools during the Paleolithic period, directly testing the extent to which blades themselves were under selection is challenging. The same goes for the persistence of flake-based industries over time, which may be related to stabilizing selection and/or normative behaviors that maintain this pathway of technologies in temperate lowland areas (Marwick et al., 2016).

A Dispersal Scenario for the Blade Technology in Eastern Asia

If BBAs are part of a suite of adaptive traits associated with cold habitats, convergent evolution of blade technology with an independent invention on the Tibetan Plateau is theoretically plausible. However, the lack of evidence for an antecedent lithic technology or any stable human population on the Tibetan Plateau and the surrounding lowland regions, we consider an external origin more likely. The clusters of BBAs distributed in the neighboring Siberian Altai, Trans-Baikal, and northern Mongolia around 48–40 ka cal BP represent some of the earliest and also the densest occurrence of blade technology in eastern Asia (Goebel, 1994; Anikovich, 2007; Derevianko et al., 2013; Derevianko & Shunkov, 2009; Gladyshev et al., 2012; Kuhn & Zwyns, 2014; Rybin, 2014; Zwyns et al., 2014; Zwyns, 2021). The BBAs in the north are slightly older than those from Shuidonggou and Nwya Devu, and they are also geographically proximate to North China and the Tibetan Plateau, indicating some of these BBA cultural connections between the two regions in the broad sense. For example, the dispersal of the earliest BBAs—also known as IUP in the region, is interpreted as evidence for modern human dispersals into Central and North Asia (Fu et al., 2014; Gobble, 2015; Zwyns, 2021; Zwyns et al., 2019). Population movements or contacts with the Steppe zone offer a parsimonious explanation for how blade technology was brought up to the Tibetan Plateau sometime during MIS 3.

The vast expanses of desert environments in inner Asia would have created natural barriers, challenging human expansion onto the Plateau. These barriers may have contributed to the geographic separation of BBAs and CAFs and accounted for the diverse modern human lineages recorded for the region. Despite a relatively low site frequency, the occurrence of BBAs around the margins of the Gobi Desert (e.g., Chikhen 2 and Tsagaan Agui) and in Shuidonggou and Nwya Devu suggests that some arid areas were at least occasionally permeable to the makers of BBAs. Population movements in this case do not necessarily imply that humans crossed many different biogeographic zones in between. MIS 3 climatic variability would have impacted the balance between evaporation and precipitation and would have influenced moisture-bearing systems over central Asia. An occasional southward extension of the steppe biome might have facilitated access to the highlands across relatively homogeneous landscapes. For instance, BBAs and CAFs are both documented at Shuidonggou at the northwest edge of the CAF distribution (Fig. 1). In the semi-arid and arid landscapes of northwest China, the site complex is situated at the northern limit of the East Asian summer monsoon. At a fluctuating boundary between biogeographic zones and between the two technological clusters, MIS 3 climatic oscillations may have triggered the expansion/recession of two contiguous ecozones, potentially impacting human group mobility among other behaviors (e.g., Elston et al., 2011; Li et al., 2014; van der Made, 2011; van der Made & Mateos, 2010). Hence, BBAs at Shuidonggou may represent a southward population movement associated with a meridional expansion of the steppe ecozone (Zhang et al., 2022d). Future paleoecological research in the ostensible transition areas could be used to evaluate this hypothetical scenario.

Considering the extreme biogeographic challenges of the Plateau, the concept of *rugged fitness landscapes* can help in understanding the proposed dispersal scenario. Rugged fitness landscapes are theoretical adaptive landscapes with “peaks” and “valleys” representing the fitness of different adaptive traits (Kuhn, 2006; Lombard, 2012; Palmer, 1991). As a part of the behavioral responses, different lithic technologies denote varying fitness peaks in different environments. In this case, owing to the rigorous environment and strong selective pressures in the Tibetan Plateau, a high fitness peak is required to adapt and settle in the region. Proceeding with the high-fitness peak, climbing from a sub-fitness peak is more reachable than switching to a completely new one concerning faster adaptations (Kuhn, 2006; Marwick, 2013). It would be parsimonious to move from the sub-fitness peak—the behavioral package including BBAs—to adapt to the Tibetan Plateau as BBAs may be related to cold adaptations that had been tested in the Steppe belt. Hunter–gatherers equipped with blade toolkits or other associated functional behaviors may have traversed the adaptive landscape expanding to the Plateau easier when confronted with cold, open grassland environments like the Steppe zone.

Successful high-elevation settlements benefit from both biological adaptations and cultural ones. The biological challenges of hypoxia are well-known to exert strong selective pressures on human biology (Beall, 2007; Moore et al., 1998). Genetic evidence suggests that physiological adjustments related to the *EPAS1* gene in Tibetan populations are inherited from an encounter with Altai-Denisovans or related populations (Huerta-Sánchez et al., 2014), with an introgression into East Asian populations around ca. 48 ka cal BP (Zhang et al., 2021). This is broadly consistent with the dispersal of the IUP-like blade assemblages from the north towards Shuidonggou and Nwya Devu. It remains unclear if an adaptation to year-round settlements happened before the end of the Pleistocene as positive selection on this gene occurred much later (Zhang et al., 2022b). In summary, to adapt to high elevations, human populations would have established a local fitness peak to cope with the region’s distinct set of selective pressures that included extremes of cold, dry, variability, and hypoxia. In comparison to human groups adapted to temperate ecological conditions, which occupy distinct fitness peaks, hunter–gatherers with hunting and mobility strategies that are effective in cold habitats characterized by open landscapes and low resource availability would have had a considerably lower fitness valley to traverse in order to expand onto the similar alpine environments of the Plateau.

Conclusion

During MIS 3, two categories of stone tool technology prevailed in the study area of eastern Asia. The contemporary BBAs and CAFs exhibit distinct geographic distributions, with the former mainly found in the eastern Eurasian Steppe and the latter in the southern and eastern parts of the study area. Our analyses reveal significant environmental differentiation between BBAs and CAFs in MIS 3 temperature, precipitation, and NPP. In particular, temperature appears to have been the most influential factor affecting the geographic distribution of BBA and CAF technologies. Whereas the Steppe Belt and Tibetan Plateau both exhibit high occurrence probabilities for BBAs, the eastern lowlands of China exhibit high occurrence probabilities for CAFs. The environmental conditions of the Nwya Devu site in the interior of the Tibetan Plateau fall within the range of values observed for the Steppe blade sites, contrasting with those of CAFs in lowland China. These findings suggest that blade technology may reflect a visible component of hunter-gatherer adaptations to cold habitats, transmitted from the eastern Eurasian Steppe to the Tibetan Plateau during MIS 3.

Considering the ecological conditions observed for BBAs and CAFs, we envision blade toolkits to have been potentially associated with hunter–gatherer mobility, technological organization, hunting, or clothing that enhanced the adaptation to these cold and open landscapes. In light of documented modern human population dynamics and the dispersal of the blade industry in eastern Eurasia between 48 and 30 ka cal BP, we suggest that, parsimoniously, adaptive strategies, including blade technology acquired in the Steppe zone, may have facilitated a wave of modern human expansion onto the Tibetan Plateau reaching at Nwya Devu site during MIS 3. The extent to which blade technology itself was adaptive remains unclear and requires further investigation. Although such a model seems likely, we cannot yet exclude models of convergent evolution or those that envision indirectly biased or stochastic transmission processes at this point. Overall, our results shed light on an intriguing chapter of the early modern human venture to the interior of the Tibetan Plateau from the Eurasian Steppe while also highlighting a need for additional investigation of the region's archaeology and the function of blade tools. Concerted efforts to locate additional BBAs on the Tibetan Plateau are needed to reproduce the findings at Nywa Devu and validate the working model for the spread of BBA technology onto the highlands due to its adaptability.

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Data Availability The authors confirm that all data generated or analyzed during this study are included in the manuscript and its supplementary information.

Declarations

Ethical Approval This manuscript has not been published and is not being considered for publication elsewhere. All authors have approved the manuscript for submission.

Competing Interests The authors declare no competing interests.

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