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Article *in* The Holocene · December 2022

DOI: 10.1177/09596836221138336

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Research Paper

The Holocene
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Synchronous change in the intensified millet cultivation and ecological environment from the early to middle Holocene on the Inner Mongolia Plateau, northern China

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Abstract
The mechanisms of the origin and dispersal of millet agriculture in northern China are poorly understood. We used plant macroremains, stable isotope compositions of human bone collagen, and pollen records from the Sitai site to reconstruct changes in subsistence strategies and their relationship with the ecological environment from the early to middle Holocene on the Inner Mongolian Plateau in northern China. Charred weed-like seeds, the bones of small mammals, eggshell fragments, together with microliths, indicate the practice of hunter-gatherer subsistence strategies during 10,500–10,200 cal yr BP. Deciduous broadleaved forest-steppe vegetation was present around the Sitai site during the early middle Holocene (8000–7000 cal yr BP). Additionally, isotopic compositions of human bones and plant remains reveal that millet agriculture and hunting-gathering appeared in the early middle Holocene. The spread of millet agriculture on the Inner Mongolian Plateau was likely favored by an increase in precipitation between 8000 and 7000 cal yr BP. The development of millet agriculture on the Inner Mongolia Plateau and the Loess Plateau was the prelude to its subsequent spread to the Tibet Plateau.

Keywords
broomcorn millet, foxtail millet, Mid-Holocene, Neolithic, northern China, stable isotopes, subsistence strategies

Received 25 August 2022; revised manuscript accepted 16 October 2022

Introduction

It is well documented that the cultivation of *Panicum miliaceum* (broomcorn millet) and *Setaria italica* (foxtail millet) originated in northern China (Barton et al., 2009; Lu et al., 2009); however, our understanding of its origin, domestication mechanism, and dispersal process is very limited (Bettinger et al., 2010a; Cohen, 2011; Hunt et al., 2008; Liu et al., 2011; Lu, 2017). Starch grains from Donghulin and Nanzhuangtou, as well as phytoliths from the Cishan site, reveal that the use and domestication of millet began at least 10,000 years ago (Lu et al., 2009; Yang et al., 2012). Bone isotope records and carbonized seeds from the Dadiwan, Xinglongwa, Peiligang, Yuezhuang, Houli, and Xiaojingshan sites indicate that millet agriculture became widespread in northern China from 8000 years ago (Crawford et al., 2016; Hu et al., 2008; Zhao, 2011), and then intensified after 7000 years ago (Bettinger et al., 2010b; Dong et al., 2016).

In recent years, efforts have been made to explore the origin of millet agriculture from the perspective of the Broad Spectrum Revolution and climate change (Bar-Yosef, 2011; Liu et al., 2014; Liu et al., 2018; Zeder, 2012). Triticeae and Paniceae grasses, Vigna beans, *Dioscorea opposita* yam, and *Trichosanthes kirilowii* snakegourd roots were utilized by the Shizitan people between ~23,000 and 19,500 BP, which demonstrates that broad-spectrum subsistence had begun by at least the Last Glacial Maximum in East Asia (Liu et al., 2013). Charred wild millet seeds dated to between 13,800 and 11,600 years ago at Shizitan site 9 provide new evidence for exploring the origin of millet agriculture (Bestel et al., 2014). Millet seeds were found at the Donghulin site (~11,000–9000 cal yr BP), but no

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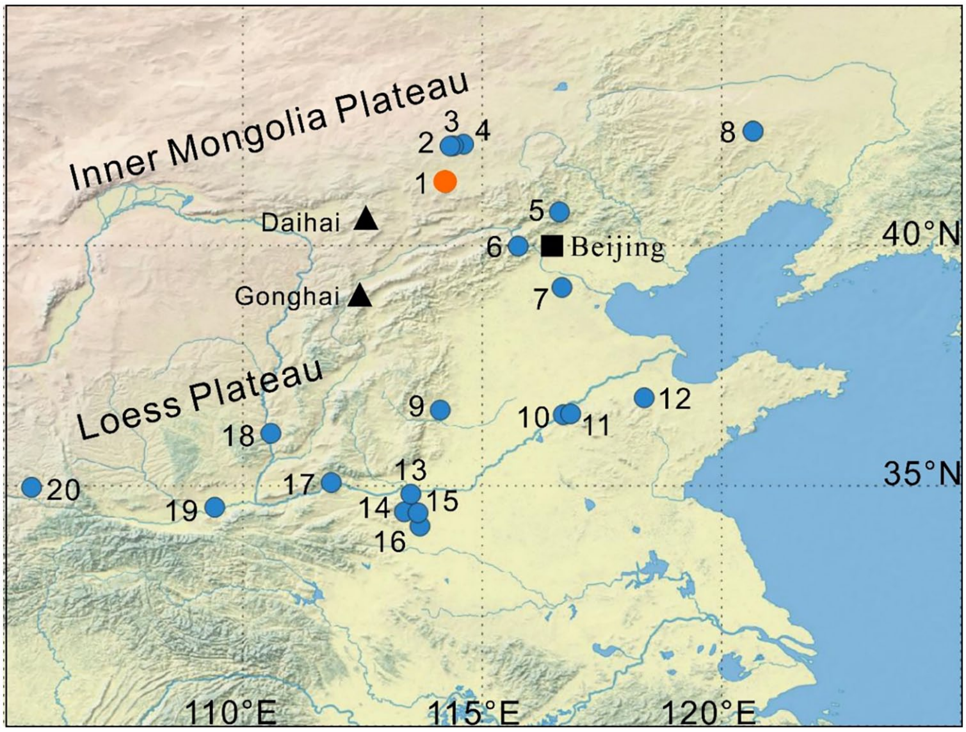

Figure 1. Location of Sitai and other sites referenced in the text. 1.Sitai (orange circle); 2. Yumin; 3.Simagou; 4. Xinglong; 5. Zhuannian; 6. Donghulin; 7. Nanzhuangtou; 8. Xinglonggou; 9. Cishan; 10. Yuezhuang; 11. Xiaojingshan; 12. Houli; 13. Zhuzhai; 14. Egou; 15. Peiligang; 16. Shigu; 17. Bancun; 18. Shizitan; 19. Baijia; 20. Dadiwan.

results of the direct dating of seeds have been reported (Zhao et al., 2020). Overall, despite the available evidence, our understanding of the development of millet agriculture prior to 8000 years ago remains fragmentary.

The southeastern Inner Mongolia Plateau, with an average elevation of 1200 m, is one of the distribution centers of modern millet agriculture (He et al., 2022; Lu et al., 2009). Millet agriculture is thought to have originated in areas of hilly terrain, because most of the early plant micro- or macroremains from millet sites in northern China are found in such areas at elevations below 500 m (Liu et al., 2009; Wang et al., 2019; Zhao et al., 2022). The valleys within hilly terrain can provide adequate temperatures for the cultivation of crop plants (D'Alpoim Guedes et al., 2016). Nevertheless, the Inner Mongolia Plateau was a topographic barrier to the spread of millet agriculture to inner Asia, and it remains unclear how millet agriculture penetrated this barrier and then gradually spread to the whole of the Eurasian continent.

The Sitai site is on the southern Inner Mongolian Plateau in northern China. Archeological remains from two periods have been discovered; the first dated to ~10,300 years ago, and the second to between 8000 and 7000 years ago. A detailed excavation report has been published (Wei et al., 2018). This study presents the results of analyses of plant remains and the isotopic compositions of human bones, which were conducted to understand the differences in the subsistence strategies (i.e. the utilization of plant resources) between these two periods. Palynological analyses were also conducted on a sedimentary profile near the site to determine the relationship between changes in subsistence strategies and the environment, from the early to middle Holocene, on the Inner Mongolia Plateau.

Study site

The Sitai site (N41.31°, E114.23°, H1420) is located on the terrace of a small lake, ~40 km northeast of Shangyi County, Zhangjiakou City, Hebei Province (Figure 1, Supplemental Figure S1, available online). Topographically the area is part of the Inner Mongolia Plateau. One Paleolithic-Neolithic transition site and four Neolithic semi-subterranean houses (F1–F4 in Supplemental Figure S1, available online) have been discovered, together with numerous microliths, stone grinding tools, bone implements, and pottery. These discoveries were reported in Wei et al. (2018). In the present study, we focus on archaeobotanical materials from the site.

The vegetation in the study area is dominated by typical steppe, including *Stipa* steppe and *Leymus chinensis* steppe. The dominant plants in the *Stipa* steppe are *S. krylovii*, *S. breviflora*, *S. grandis*, and *S. Baikal*, with occasional *Cleistogenes squarrosa*, *Leymus chinensis*, and *Festuca.* The *Leymus chinensis* grassland is dominated by *Leymus chinensis*, with *Agropyron cristatum*, *Cleistogenes*, *Artemisia frigida*, *Thymus mongolicus*, *Potentilla chinensis*, *Medicago ruthenica*, *Allium amsopodium*, and *Cymbaria mongolica*. The regional climate is cold and dry, with the annual mean temperature of 2.8°C and annual mean precipitation of 397 mm (Zhang, 2007).

Methods

AMS ^{14}C dating

AMS ^{14}C dating was conducted on three human bones from sites F1 and F3, charred millet seeds from site F2, and charcoal from the Paleolithic-Neolithic transition site (Table 1). The AMS ^{14}C dating of the three human bones was conducted at the Xi'an Accelerator Mass Spectrometry Center, Institute of Earth Environment, Chinese Academy of Sciences, and the other samples were dated by Beta Analytic (Florida, USA).

Extraction of plant macrofossils

The Paleolithic-Neolithic cultural layer is at the depth of 20 cm. Samples for floatation were obtained at 5-cm intervals; a total of

Table 1. AMS ^{14}C dating results for samples from Sitai.

Lab code	Sample ID	Dated Material	^{14}C age (BP)	$\delta^{13}C$ (‰)	Calibrated age (cal yr BP) (95.4%)	Mean
XA53608	ST2015-T1F1	Human bone	6760 ± 20	−12.5	7665–7576	7611
XA53609	ST2015-T1F3C	Human bone	6830 ± 20	−12.9	7696–7607	7658
XA53610	ST2015-T4F1A-L	Human bone	6815 ± 20	−12.8	7685–7604	7644
Beta529462	STF2(4)A	Foxtail millet	6220 ± 30	−12.1	7134–7003 (65.9%)	7098
Beta596388	STF-4	Charcoal	9170 ± 30	−23.7	10,417–10,240	10,329
Beta596389	STF-5	Charcoal	9210 ± 30	−24.3	10,437–10,252	10,345
Beta596390	STF-6(2)	Charcoal	9260 ± 30	−24.8	10,520–10,291	10,406
Beta596391	STF-7	Charcoal	9180 ± 30	−25.2	10,419–10,244	10,332

4 samples were obtained and ~30 kg of sample was used for floatation. Eleven 30 kg samples were obtained from semi-subterranean house F1, and 3 samples from semi-subterranean house F2. Charred nutshells, seeds, and charcoal were selected from the floatation samples in the laboratory.

C, N isotopes

To better understand the subsistence strategies of the Sitai people, analyses of the C and N isotopic compositions of human bone collagen were carried out using an EA-IRMS systems. Isotopic ratios are reported using δ-notation in per mil (‰) relative to the VPDB standard for C and AIR for N. We used two international Standard reference materials USGS40 ($\delta^{13}C_{USGS40/VPDB}$ = −26.39‰, $\delta^{15}N_{USGS40/AIR}$ = −4.5‰) and USGS41a ($\delta^{13}C_{USGS41a/VPDB}$ = 36.55‰, $\delta^{15}N_{USGS41a/AIR}$ = +47.55 ‰) to control the overall precision of the analyses.

Published isotope data from human bones of Holocene age, with both direct and indirect dating, were also collected to characterize temporal changes in dietary composition in northern China. The isotope data from human bones that are directly dated are from Barton et al. (2009), Atahan et al. (2011), Ni et al. (2020), and Hou et al. (2022); while the isotope data that are indirectly dated are from Liu and Reid (2020). The indirect ages were determined by relative dating and from the archeological context (Liu and Reid, 2020) (here, we use the middle values of the indirect ages).

Pollen analysis

To understand the ecological environment of the Sitai people, a 480-cm deep sedimentary section (ST2015 section, Supplemental Figure S1, available online) near the Paleolithic-Neolithic transition site was sampled for pollen analysis to reconstruct the vegetation change. The lithology description, pollen analysis methods and Bacon age model about the section are shown in the Supplemental Text S1, available online. Trees pollen percentages are used to reflect the vegetation changes, while the concentrations of *Sporormiella* fungal spores are used to indicate the presence of large herbivores around the site (van Geel and Aptroot, 2006).

Dates of millet agriculture

Millet data with direct dating are mainly from Leipe et al. (2019), with additional records from Yang et al. (2016); and millet records with indirect dating are from He et al. (2022) (the indirect ages were determined by relative dating and from the archeological context).

Results

AMS ^{14}C dates

The ^{14}C ages of charcoal from the Paleolithic-Neolithic transition site have the range of 10,500–10,200 cal yr BP, which indicates that humans occupied the site from at least the early Holocene. The ages of the human bones from semi sub-terranean houses F1 and F3 are in the range of 7700–7500 cal yr BP (Table 1), and the ages of millet seeds are in the range of ~7150–7000 cal yr BP.

Floatation results

Four plant taxa (*Carex*, *Rumex*, Poaceae, Amaranthaceae) were identified in the Paleolithic-Neolithic sample (Figure 2) (several of the seeds are unidentified because of significant deformation). Some microliths and animal remains (including burnt bones, rodent teeth, and eggshell fragments) were also found in this sample (Supplemental Figures S2 and S3, available online).

No charred seed remains were found in the floatation samples from site F1, but some nutshells and millet seeds were found in the sample from site F2 (Figure 3). Animal remains including rodent bones and numerous fish bones were also found in the samples from site F2 (Supplemental Figures S4 and S5, available online).

Isotopic composition of human bone collagen

Bone collagen was well preserved at the site and all three samples contained sufficient collagen for analysis, some of which was used for AMS ^{14}C dating and the remainder for C and N isotope analysis. The average $\delta^{13}C$ is 13.1‰, and the average $\delta^{15}N$ is 10.7‰. The $\delta^{13}C$ values reveal that the Sitai people consumed a mixture of C_3 and C_4 plants (Table 2).

Pollen analysis results

The pollen assemblages can be divided into four pollen zones (Supplemental Figure S7, available online). The vegetation was dominated by steppe landscape during 15,000–10,500 cal yr BP. Then a forest-steppe landscape appeared after 10,500 cal yr BP. The vegetation may be influenced by human activities after 3800 cal yr BP. A detail description of pollen assemblages was shown in Supplemental Text S1, available online.

Discussion

Ecological environment and subsistence strategies during the early Holocene on the Inner Mongolia Plateau, northern China

The global climatic warming after the Younger Dryas cold event was accompanied by a change in the vegetation ecology in northern China. Although the grassland vegetation landscape around the Sitai site remained dominated by *Artemisia*, Asteraceae, and Polygonaceae, the pollen data indicate an increase in the representation of *Quercus*, *Ulmus* and other woody plants. This pattern of early Holocene vegetation change is similar to that shown by lake sediment records from northern China. For example, the vegetation at Daihai Lake during 10,250–7900 years BP was dominated by xerophytic herbs and shrubs with patches of coniferous and broadleaved mixed forest (Xiao et al., 2004). Grassland vegetation

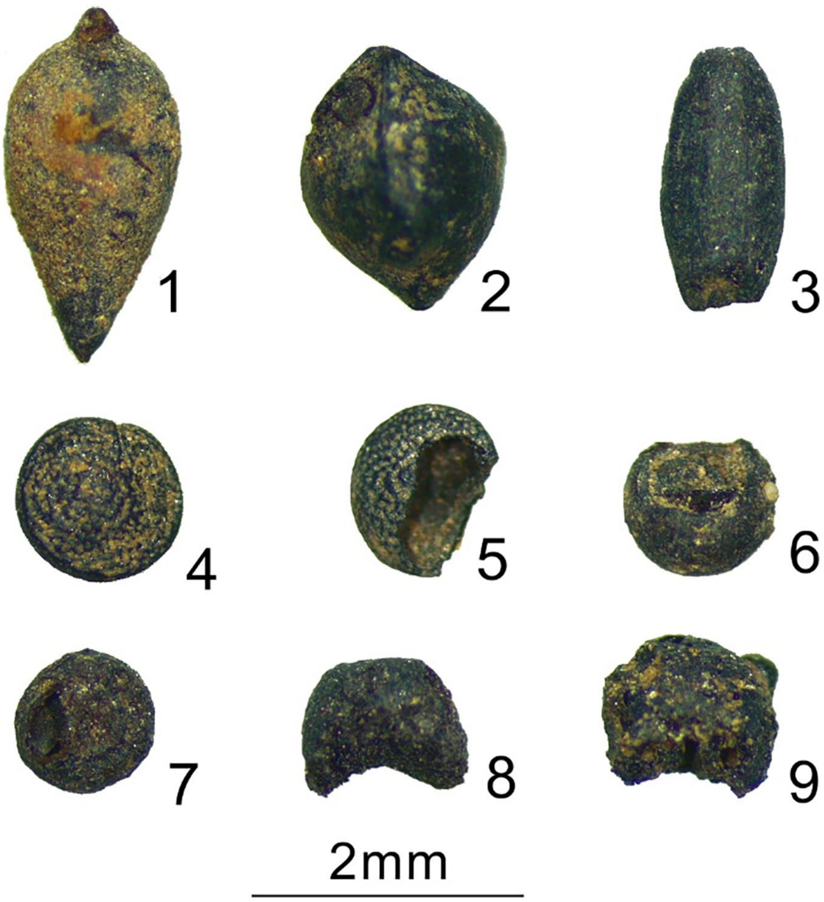

Figure 2. Charred seeds from the Paleolithic-Neolithic transition site. 1. *Carex* sp. 2. *Rumex* sp. 3. Poaceae 4, 5. *Chenopodium* sp. 6,7. Amaranthaceae. 8, 9. Unidentified seeds.

was dominant at Bayanchagan Lake during 11,700–7900 years BP, although there was slight increase in trees (Jiang et al., 2006). At Hulun Lake, steppe vegetation developed during 11,000–8000 years BP and *Betula* was sporadically distributed between and on the surrounding mountains (Wen et al., 2010). Coniferous and broadleaved mixed forest, dominated by *Betula*, *Ulmus*, and *Pinus*, was present at Gonghai Lake during 11,100–9600 cal yr BP (Xu et al., 2017). In some mountainous and hilly areas, deciduous broadleaved forest developed during the early Holocene (Zhao et al., 2022). Overall, the regional climate during the early Holocene was warm and dry (Wen et al., 2010; Xiao et al., 2004).

Due to the lack of plant macroremains, our understanding of subsistence strategies prior to the Holocene is mainly based on plant microremains, such as starch grains and phytoliths. Triticeae, Paniceae, beans, and the roots of several different plants were utilized at Shizitan during the Last Glacial Maximum (Liu et al., 2013). The evidence of starch grains supports the conclusion that millet was utilized by the Donghulin people in the early Holocene (11,000–9500 cal. yr BP) (Yang et al., 2012), but no direct dating of millet grains from the site has been reported (Zhao et al., 2020).

The seeds from Sitai dated to 10,500 to 10,200 cal yr BP include *Carex*, *Rumex*, Poaceae, and Amaranthaceae. These seeds were found together with microlithic tools, small mammal bones, and eggshell fragments. Although there is no direct evidence to indicate that the Sitai people utilized these seeds, they provide information about the available plant resources within the vicinity of human occupation. *Rumex*, Poaceae, and Amaranthaceae seeds are common at Neolithic sites in northern China (Zhao et al., 2020). Wild *Setaria* and *Echinochloa* spp. have been found at Shitizan 9 dated to 13,800–11,600 cal yr BP (Bestel et al., 2014), and waterlogged seeds were found at the Nanzhuangtou site (Yang et al., 2015a). Charred seeds from archeological sites older than ~10,000 cal yr BP are rare in northern China. These weed seeds may have played an important role before or at the beginning of millet agriculture.

The charred seeds together with small animal bones, eggshell fragments, and microliths indicate a hunter-gatherer subsistence economy at Sitai during 10,500–10,200 cal yr BP. Microlithic tools dated to 13,500–10,000 cal yr BP were also found at the Xinglong, Yumin and Simagou sites, ~100 km north of Sitai, but no plant remains predating 10,000 cal yr BP have been reported so far (Bao et al., 2021; Guo et al., 2021; Hu et al., 2021).

Synchronous changes in the ecological environment and subsistence strategies during the early to middle Holocene in northern China

The pollen record of the Sitai profile shows a significant increase in trees during 8000–7000 cal yr BP, indicating the development of a forest-steppe landscape around the site and a more humid climate (Supplemental Text S1 and Figure S5, available online). A transformation of the climate and vegetation during the middle Holocene was also recorded at other sites in northern China. Coniferous and broadleaved mixed forest developed in the Daihai area during 7900–4450 cal yr BP, and the precipitation range of 400–630 mm was higher than during the early Holocene (Xiao et al., 2004; Xu et al., 2010). Pollen records from Gonghai reveal that broadleaved trees attained a maximum during ~7800–5300 cal yr BP, and precipitation was 30% higher than today (Chen et al., 2015; Xu et al., 2017). The pollen records from Hulun Lake reveals a significant increase in monsoon precipitation during

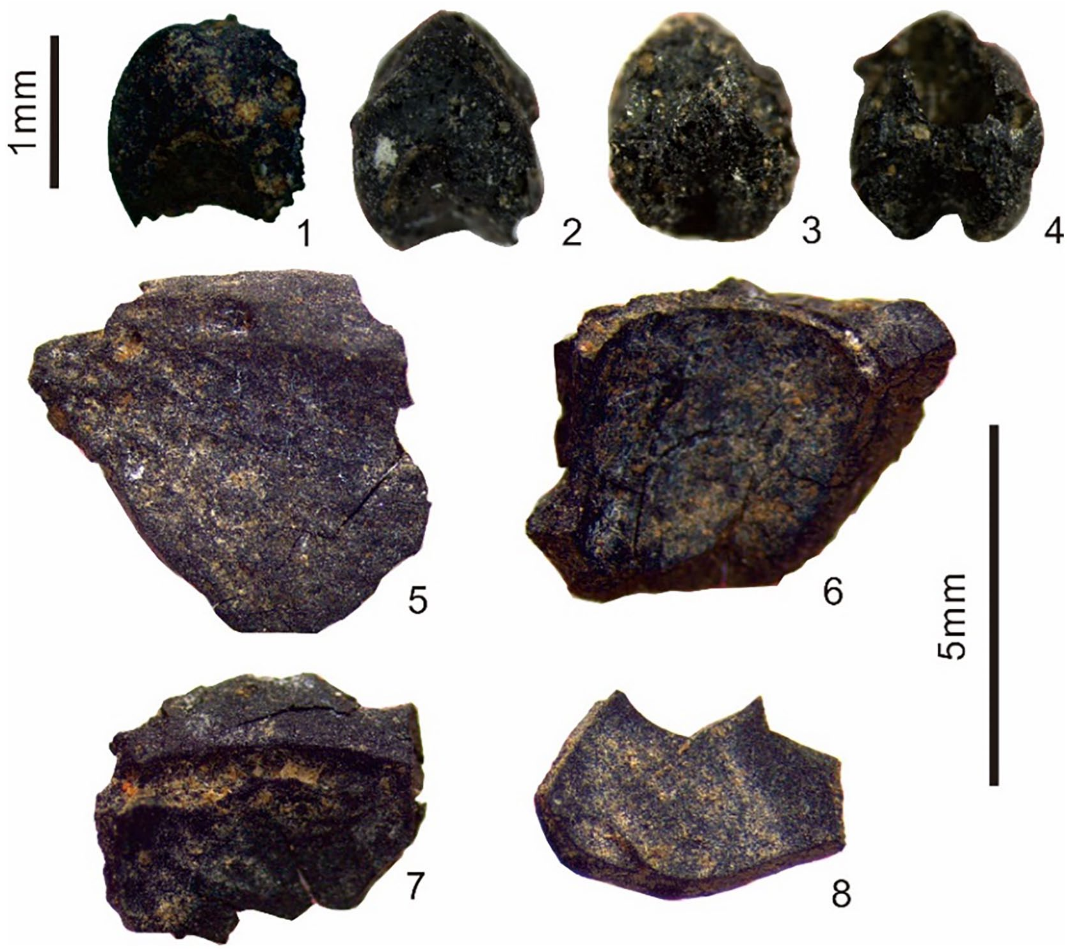

Figure 3. Plant remains from the Neolithic site at Sitai. 1–3. *Panicum miliaceum* (broomcorn millet). 4. *Setaria italica* (foxtail millet), 5–7. Unidentified nutshells.

Table 2. C and N isotopic compositions of human bones from Sitai.

Sample ID	Collagen (%)	%C	%N	C/N	$\delta^{13}C_{VPDB}$ (‰)	$\delta^{15}N_{AIR}$ (‰)
ST2015-T1F1	4.61	44.2	15.9	3.2	−13.3	9.8
ST2015-T1F13C	10.11	44.1	15.9	3.2	−13.6	11.5
ST2015-T4F1A-L	12.52	44.3	16.1	3.2	−12.3	10.9

8000–6400 cal yr BP (Wen et al., 2010). In summary, the deciduous broadleaved forest boundary moved northward after 8000 cal yr BP, and the vegetation of the southeastern Inner Mongolia Plateau was transformed from steppe to forest-steppe (Zhao and Yu, 2012; Zhao et al., 2009).

The $\delta^{13}C$ values of human bones from the Sitai site, dated to ~7700–7600 cal yr BP, range from −12.3‰ to −13.6‰, indicating a significant proportion of C_4 plants in the human diet. C_4 plants such as millet became a food staple for the Xinglonggou people during 8200–7300 cal yr BP (Liu et al., 2012). The isotopic composition of dog bones from the Dadiwan site also provides firm evidence of the contribution of millet to the human diet during 7900–7200 cal yr BP (Barton et al., 2009). According to the $\delta^{13}C$ data from human bones, an important dietary transition from C_3 to C_4 domination occurred in northern China during 8000–7000 cal yr BP (Figure 4a). After ~7000 cal yr BP, C_4 foods became the staple dietary in northern China (Figure 4a, Hu et al., 2008; Liu et al., 2012). This increasing trend of C_4 consumption was consistent with the trend of increasing humidity in northern China. We suggest that the warm and humid climatic conditions during 8000–7000 cal yr BP facilitated the expansion of millet agriculture to the Inner Mongolia Plateau (Figure 4a and d–h).

Charred millet remains also reveal that millet agriculture became important during 8000–7000 cal yr BP, and until now, the direct dating of early millet seeds has focused on this period. The AMS ^{14}C ages of foxtail millet at Sitai are 7134–7003 cal yr BP, and the ages determined by the direct dating of broomcorn millet at Xinglonggou are 7736–7636 cal yr BP, 7876–7718 cal yr BP at Yuezhuang, 7664–7503 cal yr BP at Baijia, and 7736–7640 cal yr BP at Zhuzhai (Bestel et al., 2018; Crawford et al., 2016; Leipe et al., 2019; Yang et al., 2016; Zhao, 2011). The common feature of carbonized plant remains at these sites is the occurrence of only a few millet grains but numerous nutshells. Other early Neolithic sites in northern China where millet remains (including phytoliths and starch grain) and nutshells also coexist include Cishan, Bancun, Peiligang, Egou, and Shigu (Liu et al., 2010). This evidence indicates mixed agriculture and hunting-gathering subsistence strategies at this time, when the warm and wet climate promoted the northward movement of broadleaved forest. The development of a forest-steppe environment not only promoted the development

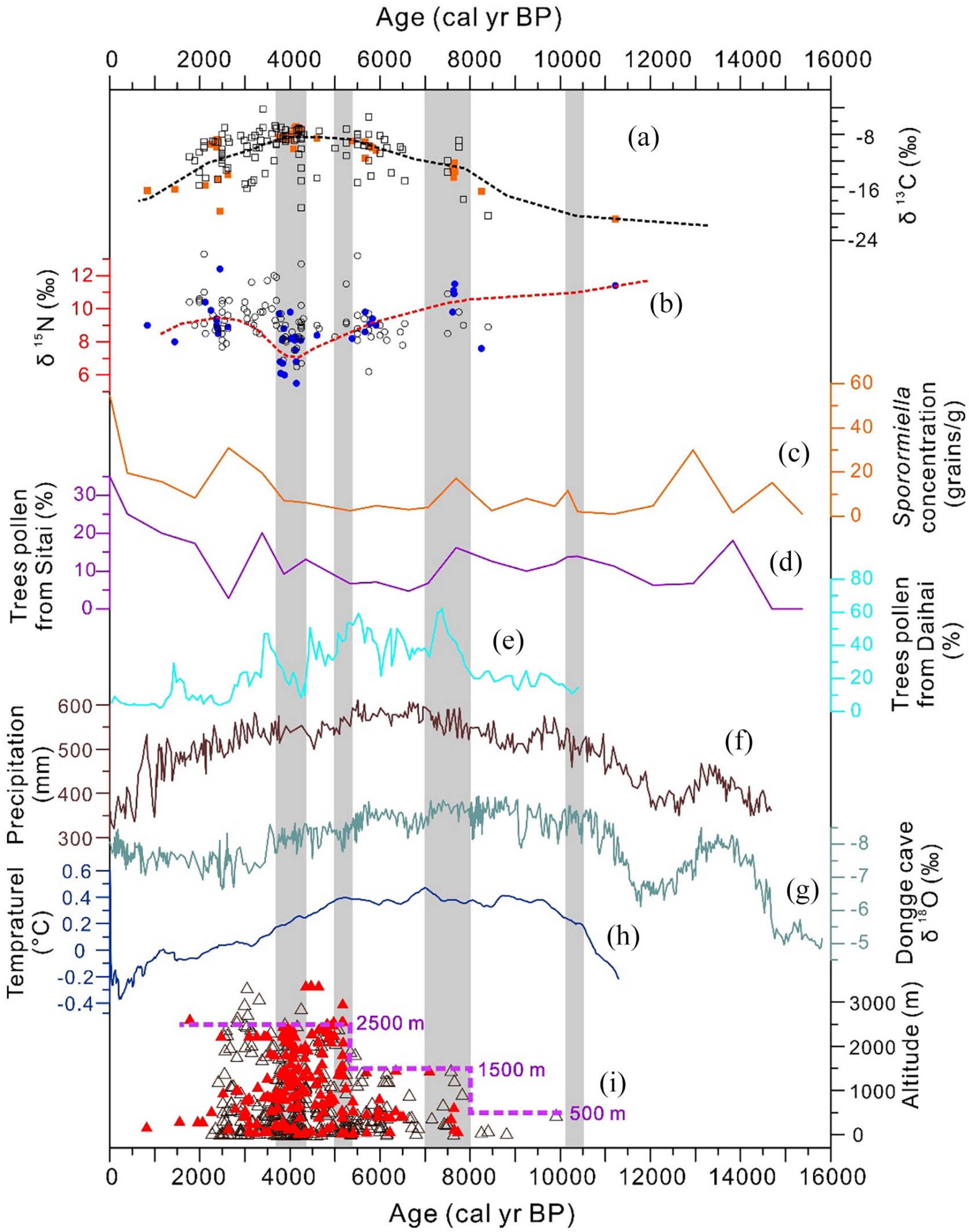

Figure 4. Comparison of archeological and paleoenvironmental records from Sitai compared with selected regional and global paleoenvironmental records. (a) Holocene $\delta^{13}C$ record from human bones from China (orange rectangles are directly dated records, and open rectangles are indirectly dated records). (b) Holocene $\delta^{15}N$ record from human bones from China (blue circles are directly dated records, and open circles are indirectly dated records). (c) *Sporormiella* fungal spore concentrations from the ST2015 section (this study). (d) Trees pollen percentages from the ST2015 section (this study). (e) Trees pollen record from Daihai Lake (Xiao et al., 2004). (f) Pollen-based precipitation reconstruction from Gonghai Lake (Chen et al., 2015). (g) Speleothem $\delta^{18}O$ record from Donge Cave (Dykoski et al. (2005)). (h) Global temperature record for the Holocene (Marcott et al. (2013)). (i) Altitude of millet remains (red triangles are the directly dated millet seed records; open triangles are indirectly dated millet seed records; purple dotted line shows the phase changes of millet cultivation altitude).

of millet agriculture but also provided food resources for humans, including acorns and walnuts (Zhao et al., 2022).

Millet prefers a warm and dry environment. Millet agriculture is thought to have originated in areas of hilly terrain, because most of the early millet agricultural sites in northern China occur in hilly areas with elevations below 500 m a.s.l. (Figure 4i, Liu et al., 2009). However, after 8000 cal yr BP millet agriculture was practiced at elevations of ~1500 m, such as at Sitai (1420 a.s.l) and Dadiwan (1460 a.s.l.). Temperature increases with altitude at the rate of 0.6°C per 100 m. We suggest that the warm and wet climate during 8000–7000 cal yr BP enabled millet plants to break through their previous geographical confines and occupy the Inner Mongolia Plateau and the Loess Plateau. This provided the foundation for millet to adapt to high altitude and high latitude environments and to spread to higher elevation regions such as the Tibet Plateau after 5200 cal yr BP (Figure 4i, Chen et al., 2015; D'Alpoim Guedes et al., 2016).

The $\delta^{15}N$ values of human bones is closely related to ecological changes (Figure 4b–d). A slightly higher *Sporormiella* concentration occurred in the Sitai section during 8000–7000 cal yr BP (Figure 4c), indicating an increase in the population of large herbivores in the surrounding area (Davis and Shafer, 2006). The higher $\delta^{15}N$ values of human bone collagen at this time indicates that these large herbivores were utilized as food resources by humans. During the Holocene, the $\delta^{15}N$ of human bone collagen first decreased and reached a minimum at ~4000 cal yr BP, and then increased. Drought events may have caused a decrease in the population of wild herbivores at ~4000 cal yr BP (Figure 4e, Sun et al., 2019; Xiao et al., 2004; Yang et al., 2015b), but subsequently the increased population of domestic animals such as sheep, goats, and cattle was responsible for the rise in the $\delta^{15}N$ of human bone collagen after that (Zhang et al., 2021).

The trees pollen content has increased significantly since the Late-Holocene (from 3800 cal yr BP to present). The increase was mainly from the contributions of *Quercus* and *Picea* pollen. Vegetation changes during the Late-Holocene were complicated due to possible influences from both human activities and climate change (Zhao et al., 2009). We suggest that the increase of trees pollen may be closely related to human activities during Late-Holocene, because some remains were found from historical periods (e.g. Liao and Song Dynasty) around the Sitai site (Wei et al., 2018). Of course, we can't completely rule out the influence of climate in this study. It needs more work to reveal the mechanisms of Late-Holocene vegetation changes in the site.

Conclusions

The plant remains from the Sitai site provide new reference data for understanding middle Holocene subsistence strategies in the Inner Mongolia Plateau in northern China. Plant macroremains, animal fossils, and eggshell fragments, together with microliths, reveal a hunter-gatherer economy during 10,500–10,200 cal yr BP. Against the ecological background of the vegetation transition from steppe to forest-steppe during 8000–7000 cal yr BP, the subsistence strategies at the study site evolved to a mixture of millet agriculture and hunting-gathering. The warm and humid climatic conditions during this period promoted the northward shift of the deciduous broadleaved forest boundary, and they also resulted in the breakout of millet agriculture through its previous geographical limits and its spread to the Inner Mongolia Plateau and the Loess Plateau. This breakout was the prelude to the further spread of millet agriculture to the Tibet Plateau.

Acknowledgements

We thank Professor Hongen Jiang and Dr. Guilin Zhang for helpful discussion about the identification of plant macrofossils, Dr. Feixiang Wu for discussion about the fish fossils, and Dr. Shixia Yang for discussion about the microlithic.

Funding

The author(s) disclosed receipt of the following financial support for the research, authorship, and/or publication of this article: This study was supported by the National Natural Science Foundation of China (Grant No. T2192952, 41730319, 42072212), the Project of Stable Support for Youth Team in Basic Research Field, CAS (Grant No. YSBR-019), the Strategic Priority Research Program of Chinese Academy of Sciences (Grant No. XDB26000000), and the National Key Research and Development Program of China (Grant No.2022YFF0801102).

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Supplemental material

Supplemental material for this article is available online.

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