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SPECIALTY SECTION

This article was submitted to Quaternary
Science, Geomorphology and
Paleoenvironment,
a section of the journal
Frontiers in Earth Science

RECEIVED 15 January 2023

ACCEPTED 15 March 2023

PUBLISHED 24 March 2023

CITATION

Lu M, Lu Y, Yang Z, Cili N and Ma M (2023),
Diverse subsistence strategies related to
the spatial heterogeneity of local
environments in the Hengduan Mountain
Region during the Bronze Age.
Front. Earth Sci. 11:1144805.
doi: 10.3389/feart.2023.1144805

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Diverse subsistence strategies related to the spatial heterogeneity of local environments in the Hengduan Mountain Region during the Bronze Age

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Human subsistence strategies in East Asia changed significantly during the Bronze Age. The notable spatial variability in these strategies has been mainly attributed to the asynchronous introduction and adoption of new crops and livestock, as well as climate changes. However, the impact of differential local environments on spatial patterns of subsistence strategies in diverse geomorphic areas, such as the Hengduan Mountain Region (HMR), is poorly understood. In this study, we present new carbon and nitrogen isotopic data of human bone collagen from the Adong and Gaozhai tombs in the HMR. Adong is located in a mountain area, and Gaozhai is located on a river terrace. Both sites were dated to the early third Millennium BP (before the present). Our results suggest that human diets at Gaozhai were dominated by C₃ foods. Human diets at Adong, alternatively, displayed more differentiation, with greater consumption of C₄ foods. Further evidence is needed to discuss the significant differences in $\delta^{15}\text{N}$ values of human bone collagen between the Gaozhai and Adong tombs. By comparing published isotopic, archaeobotanical, and zooarchaeological data, as well as the altitude and precipitation at the archaeological sites, we propose that precipitation may have affected the diversity of human dietary strategies in the Bronze Age HMR. We conclude that at higher altitudes, humans adopted diverse subsistence strategies and obtained meat resources by hunting. Some of this preferential behavior is likely explained by the survival pressure in the highlands of the HMR during the Bronze Age.

KEYWORDS

isotopic analysis, subsistence strategies, regional landform, hydrothermal conditions, Bronze Age, Hengduan Mountain Region

1 Introduction

Spatio-temporal patterns of subsistence strategies transformed significantly throughout Eurasia during the late Neolithic and Bronze periods (Jones et al., 2011; Liu et al., 2019; Dong et al., 2022a; Ma et al., 2022a). These patterns' relationship to transcontinental exchange and climate change have been intensively discussed in the past two decades (Chen et al., 2015; Yang et al., 2021; Dong et al., 2022b; He et al., 2022; Li et al., 2022; Yang et al., 2022), with the rapid accumulation of archaeobotanical, zooarchaeological, and stable isotopic data from archaeological sites, as well paleoclimatic studies across the continent (Outram et al., 2012; Brunson et al., 2016; Jia et al., 2016; Dong et al., 2017; Hanks et al., 2018; Du et al., 2020; Zhou et al., 2020; Zhang et al., 2021; Wang et al., 2022). The introduction and utilization of new crops and livestock brought by early trans-Eurasian exchange profoundly influenced the spatial features of human livelihoods on both continental and regional scales (Chen et al., 2015; Dong et al., 2018; Liu et al., 2019; Dong et al., 2021). Some researchers have also suggested that rapid and drastic climatic fluctuations triggered the transformation of human subsistence strategy in local and regional scales during the late Neolithic and Bronze Age (d'Alpoim Guedes and Bocinsky, 2018; Sun et al., 2019; Chen et al., 2020; Li et al., 2022). Despite such studies, not much is known about the influence of diverse local environments (e.g., landform and hydrothermal conditions) on the spatial patterns of human subsistence strategies during the late Neolithic and Bronze periods, especially around high plateau margin areas with significant differences in altitude.

The Hengduan Mountain Region (HMR) lies in the southeast of the Tibetan Plateau and has acted as an essential passageway for human migration and cultural exchange since the late Paleolithic period (Hein, 2014; Gao et al., 2021; Ma et al., 2022b; Huan et al., 2022). Humans engaged in hunting-gathering in the HMR until the arrival of Neolithic farming groups from the Yellow River Valley during the sixth Millennium BP (Chen and Chen, 2006; Zhao and Chen, 2011; Huan et al., 2022). Following this introduction to agriculture, human strategies for food production transformed with notable spatial variability in the subsequent thousands of years (Lu et al., 2021; Ma et al., 2022a). According to the radiocarbon dates of the crop remains, millets, rice, and wheat/barley first spread to the HMR around 5,300 BP, 5,000 BP, and 3,400 BP, respectively (d'Alpoim Guedes et al., 2015; Huan et al., 2022). Archaeobotanical studies suggest that foxtail and broomcorn millet might have served as essential crops in the highlands of the Western Sichuan Plateau during ~5,300 BP–3,700 BP (Chen and Chen, 2006; d'Alpoim Guedes, 2011; Zhao and Chen, 2011; Yan et al., 2016a; Chen et al., 2022). These same crops were utilized in the comparatively low-lying areas of southern HMR until ~4,600 BP (Dal Martello et al., 2018). Cropping patterns in the HMR during the late Neolithic and especially during the Bronze period (~3,400–2,200 BP) demonstrated diverse characteristics across different landforms (e.g., mountain areas, dry-hot valleys) (Lu et al., 2021; Ma et al., 2022a). However, the importance of different crops in plant subsistence and their relation to local environments throughout the HMR remains unclear, mainly due to the absence of human bone collagen stable isotopic data from different geomorphological positions.

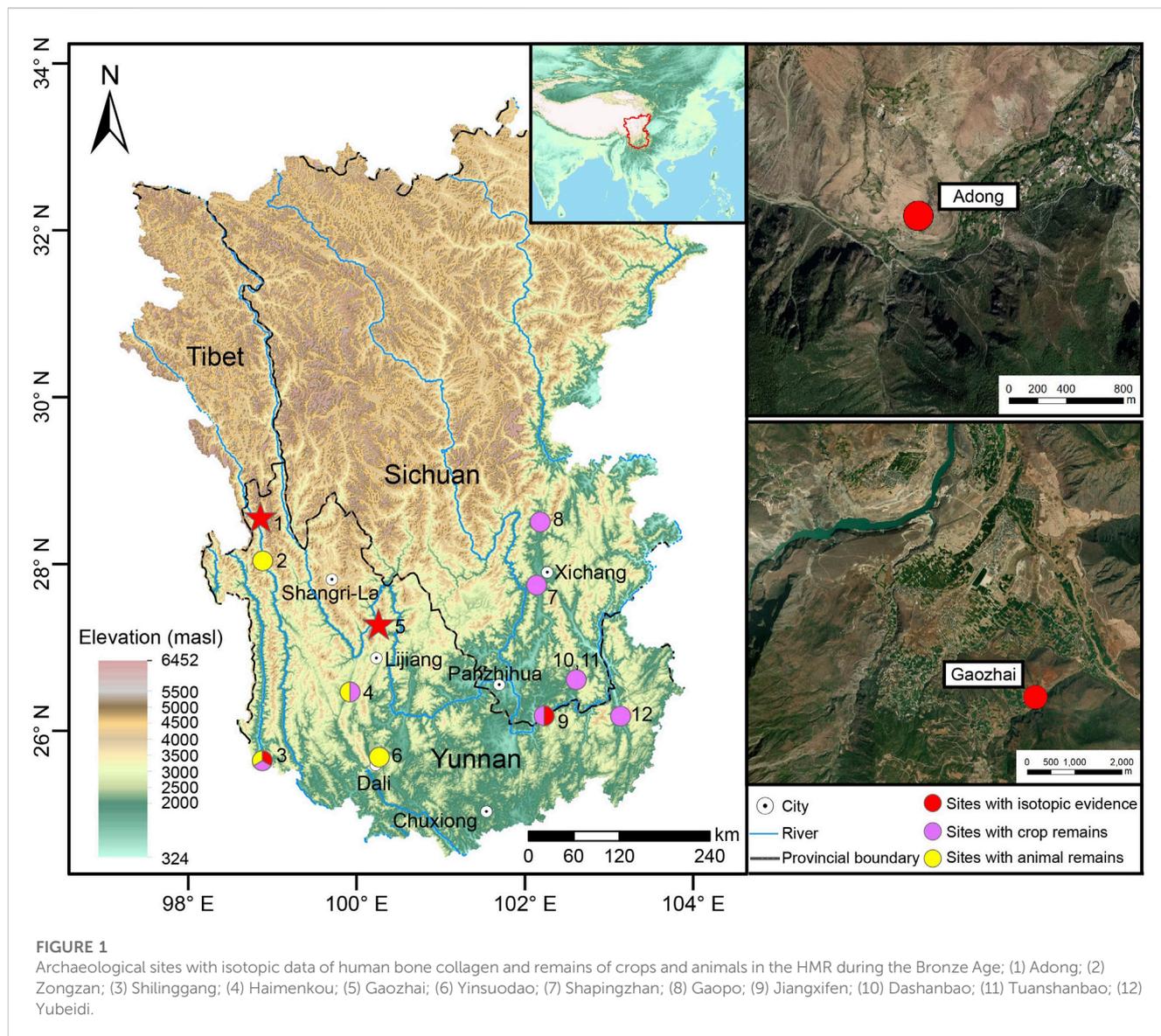
Recent archaeological investigations provided new radiocarbon data from Bronze Age sites in the HMR: Adong tombs (2,517 masl, 2,750 BP–2,450 BP) in mountain areas and Gaozhai tombs (2,080 masl, 2,850 BP–2,450 BP) in river terraces (Figure 1; Ma et al., 2022b). Thirty-one human bones were collected from these two contemporaneous sites, providing an excellent opportunity to examine human diet patterns across different HMR Bronze Age landforms. We analyzed carbon and nitrogen isotopes of human bone collagen from these sites and compared them with published carbon isotopic data of human bone collagen and archaeobotanical and zooarchaeological data from HMR sites during the Bronze Age. Moreover, we explored the relationship between human subsistence strategy and local environments during the third Millennium BP by comparing the altitude and precipitation values of HMR sites, which is valuable to understand human-land relations during the Bronze Age in the HMR with high geomorphic diversity.

2 Study area

The Hengduan Mountain Region (HMR, 24.65°N–33.57°N, 96.97°E–104.45°E) is located in the southeast of the Qinghai–Tibet Plateau (Figure 1), covering a total area of about 5.0 km² × 10⁵ km² (Yang and Zheng, 1989; Bian et al., 2018; Wang et al., 2018). The altitude of HMR is 300–7,000 masl, with higher terrain in the northwest and lower terrain in the southeast. The geography is complex and diverse, with parallel mountains and deep, river-carved gorges (e.g., Jinsha River, Nujiang River, and Lancang River). The climate varies, crossing the subtropical zone, plateau temperate zone, and plateau sub-frigid zone from south to north. HMR southern and northern areas are mainly dominated by monsoon climate and paramos climate, respectively (Bian et al., 2018). The vertical zones of vegetation in HMR vary significantly, with shrubs, coniferous forests, and meadows total accounting for 76% (Wang et al., 2017).

Gaozhai sarcophagus tombs (100.26°E, 27.27°N, 2080 masl)—found in 2020—are located in Daju Town, Yulong County, Yunnan Province. The average annual temperature is 13.3°C, annual precipitation is 968.1 mm, and annual sunshine time is 2,411.7 h. Daju Town is in the dry-hot valley of the Jinshajiang River, with high annual accumulated temperature and significant diurnal temperature variation (Zi, 2011). Shrubs and meadows dominate the vegetation. Modern-day crops include wheat, rice, and corn. A total of four tombs were excavated, and some human bones were unearthed. Human bones allowed researchers to date the tombs to 2,850–2,450 BP (Ma et al., 2022b).

Adong sarcophagus tombs (28.56°E, 98.86°N, 2,517 masl) are located in Adong village, Deqin County, Yunnan Province. The average annual temperature is 5.9°C, annual precipitation is 639.9 mm, and annual sunshine time is 1,964.8 h. The Adong village is a typical Tibetan village located in the high-mountain gorge areas of the HMR. Modern-day residents mainly survive on agriculture and livestock (Haynes et al., 2013; Li, 2020): they plant (e.g., naked barley, wheat, corn) along the river banks and gentle slopes below 2,600 masl, and graze (e.g., yak, cattleyak) above 2,600 masl (Li, 2020). The Adong sarcophagus tombs were found by the Deqin County Cultural Relics Management Institute in 2020 and were dated to 2,750 BP–2,450 BP with human bones (Ma et al., 2022b).



3 Materials and methods

3.1 Collagen preparation and isotopic measurements

Carbon and nitrogen isotopes of bone collagen can reflect an individual's diet before death (Ambrose and Norr, 1993), so it is one of the useful tools to reconstruct human subsistence strategies in prehistory. Various photosynthetic pathways lead to different $\delta^{13}\text{C}$ values of plants (Van der Merwe, 1982; van der Merwe and Medina, 1989), which makes the $\delta^{13}\text{C}$ values of bone collagen can distinguish the plant species that an individual consumes. The $\delta^{15}\text{N}$ values of bone collagen usually reflect the nutritional level of an individual, but it is also affected by metabolism (Chen, 2017). Various factors need to be considered when reconstructing the paleodiet with nitrogen isotope.

We collected a total of 31 human bones from the Gaozhai and Adong tombs: 25 bones from four Gaozhai tombs (25 human individuals) and six bones from three Adong tombs (at least three human individuals, Table 1).

According to the method described by Richards and Hedges (1999), we further removed humic acid with NaOH (Ma et al., 2016) to extract bone collagen samples at the Key Laboratory of Western China's Environmental Systems (MOE), Lanzhou University. We demineralized 0.5 g–1.5 g of bone samples (according to the preserved condition of bones) with 0.5 mol/L hydrochloric acid after cleaning sediment on bone fragments. It took about two weeks of refreshing the hydrochloric acid for bubbles to stop appearing. Next, we placed bones into 0.125 mol/L NaOH for 20 h to remove the humic acid. A 4°C environment housed all of these steps. We gelatinized the bone samples with hydrochloric acid (pH = 3) for 48 h in a 75°C environment. Finally, we obtained the collagen samples by filtering and freeze-drying.

TABLE 1 The collagen isotopic results of human bones at the Gaozhai and Adong tombs.

Site	Sample no.	Skeletal element	Col wt%	C wt%	N wt%	C/N	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)
Gaozhai	2021YDGM1R1⊙	Tibia	3.2	43.2	15.8	3.2	-18.2	7.5
Gaozhai	2021YDGM1R2⊙	Skull	4.9	43.5	15.8	3.2	-18.1	9.7
Gaozhai	2020YDGM1⊙R4	Skull	4.2	43.7	15.9	3.2	-18.7	8.3
Gaozhai	2020YDGM1⊙R5	Skull	4.3	42.8	15.7	3.2	-18.1	6.9
Gaozhai	2020YDGM1⊙R6	Phalanx	4.5	43.3	15.8	3.2	-17.8	8.0
Gaozhai	2020YDWGM2R1	Femur	3.0	42.8	15.5	3.2	-18.8	8.2
Gaozhai	2020YDWGM3R1	Long bone	13.3	43.2	15.7	3.2	-18.4	9.5
Gaozhai	2020YDWGM4R1	Skull	5.1	41.9	15.3	3.2	-18.7	7.4
Gaozhai	2020YDWGM4R2	Skull	1.8	43.5	15.8	3.2	-19.1	8.2
Gaozhai	2020YDWGM4R3	Skull	3.9	43.4	15.9	3.2	-18.7	9.1
Gaozhai	2020YDWGM4R4	Skull	3.9	43.6	15.9	3.2	-18.2	8.3
Gaozhai	2020YDWGM4R5	Skull	3.9	43.6	15.9	3.2	-18.0	8.2
Gaozhai	2020YDWGM4R6	Skull	4.7	42.4	15.5	3.2	-18.4	8.5
Gaozhai	2020YDWGM4R7	Skull	7.1	42.6	15.6	3.2	-18.8	9.3
Gaozhai	2020YDWGM4R8	Skull	4.1	43.4	15.8	3.2	-18.2	7.9
Gaozhai	2020YDWGM4R10	Maxilla	8.3	43.7	16.0	3.2	-17.8	9.4
Gaozhai	2020YDWGM4R11	Skull	4.6	43.6	16.0	3.2	-19.2	8.3
Gaozhai	2020YDWGM4R13	Rib	7.8	43.0	15.7	3.2	-18.6	7.6
Gaozhai	2020YDWGM4R14	Humerus	1.8	44.1	16.2	3.2	-18.2	7.9
Gaozhai	2020YDWGM4R15	Skull	3.3	43.7	15.9	3.2	-17.7	10.1
Gaozhai	2020YDWGM4R17	Mandible	5.3	43.9	16.0	3.2	-18.4	8.9
Gaozhai	2020YDWGM4R20	Skull	5.0	43.9	15.9	3.2	-19.0	8.5
Gaozhai	2020YDWGM4R21	Clavicle	5.9	43.9	16.1	3.2	-18.3	8.4
Gaozhai	2020YDWGM4R22	Tibia	5.1	43.9	15.8	3.2	-17.8	7.9
Adong	AD-M1-B1	Long bone	8.4	44.0	16.1	3.2	-15.2	12.4
Adong	AD-M1-B2	Long bone	13.9	44.5	16.3	3.2	-15.4	12.0
Adong	AD-M2-B1	Metacarpus	16.5	44.5	16.4	3.2	-15.7	12.2
Adong	AD-M3-B1	Mandible	4.0	43.4	15.8	3.2	-17.8	11.4
Adong	AD-M3-B2	Radius	17.4	44.0	16.1	3.2	-18.5	9.7
Adong	AD-M3-B3	Tooth	13.3	43.5	16.0	3.2	-18.4	10.1

We measured C% and N% of bone collagen samples on Elementar Vario EL Cube elemental analyzer at the State Key Laboratory of Applied Organic Chemistry, Lanzhou University, and measured carbon and nitrogen stable isotopic values on Thermo Fisher Flash EA1112-MAT253 mass spectrometer at the Key Laboratory of Western China's Environmental Systems (MOE), Lanzhou University. The carbon and nitrogen isotope ratios were measured relative to VPDB (Vienna Pee Dee Belemnite) and AIR (Ambient Inhalable Reservoir) with 0.2‰ analytical precision, respectively.

3.2 Data collection

We collected the quantity of crop remains, the number of identified specimens (NISP) of animal remains, and carbon isotopic data of human bone collagen to compare the human subsistence strategies in diverse geomorphic areas in HMR during the Bronze Age. Precipitation data were obtained from <http://data.cma.cn>, and we calculated the average precipitation from 1981 to 2010 of weather stations adjacent to the archaeological sites.

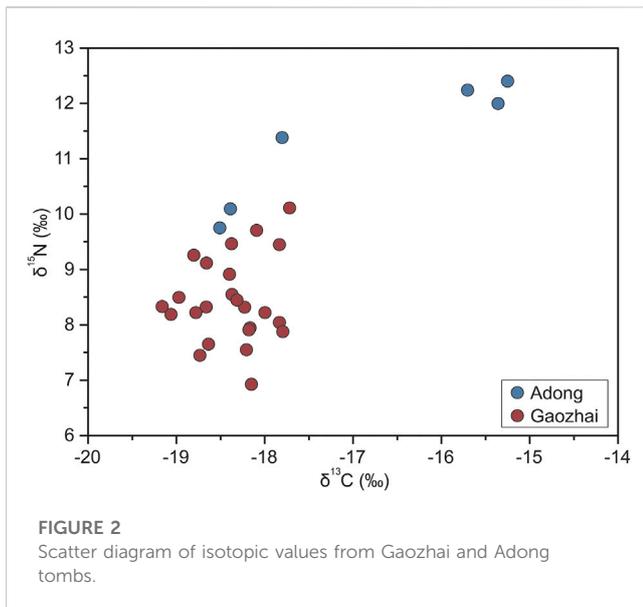


FIGURE 2 Scatter diagram of isotopic values from Gaozhai and Adong tombs.

4 Results

We obtained 30 bone collagen samples; we could not obtain collagen from one human bone from a Gaozhai tomb (Figure 2; Table 1). We believe the bone collagen samples were well-preserved as the ranges of C%, N%, and C: N atomic ratios were 41.9%–44.5%, 15.3%–16.4%, and 3.2, respectively (Table 1). Additionally, collagen yields exceeded 1% (Table 1; DeNiro, 1985; Ambrose, 1990). All bone collagen samples could be further analyzed.

The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of bone collagen samples from the Gaozhai tombs are -19.2‰ – -17.7‰ (mean = $-18.4\text{‰} \pm 0.4\text{‰}$, $n = 24$) and 6.9‰ – 10.1‰ (mean = $8.4\text{‰} \pm 0.8\text{‰}$, $n = 24$), respectively (Figure 2; Table 2). The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from the Adong tombs are -18.5‰ – -15.2‰ (mean = $-16.8\text{‰} \pm 1.6\text{‰}$, $n = 6$) and 9.7‰ – 12.4‰ (mean = $11.3\text{‰} \pm 1.1\text{‰}$, $n = 6$), respectively (Figure 2; Table 2). It should be noted that the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of M1 and M2 are significantly different from those of M3 (Figure 2; Table 1). The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of M1 and M2 are -15.7‰ – -15.2‰ (mean = $-15.4\text{‰} \pm 0.3\text{‰}$, $n = 3$) and 12.0‰ – 12.4‰ (mean = $12.2\text{‰} \pm 0.2\text{‰}$, $n = 3$), respectively, and the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of M3 are -18.5‰ – -17.8‰ (mean = $-18.2\text{‰} \pm 0.4\text{‰}$, $n = 3$) and 9.7‰ – 11.4‰ (mean = $10.4\text{‰} \pm 0.9\text{‰}$, $n = 3$), respectively.

5 Discussion

5.1 Spatial pattern of human dietary strategies in the HMR during the Bronze Age

Stable isotopic data of human bone collagen from the Adong and Gaozhai tombs reveal that humans living in the highlands consumed different foodstuffs during the early third Millennium BP than those living in the dry-hot valley of the Jinsha River. Two groups can be detected from the C-N isotopes of human bone collagen at the Adong tombs. The $\delta^{13}\text{C}$ values (-15.7‰ – -15.2‰) from M1 and M2 (at least two human individuals) indicate that humans consumed a mixed C_3 and C_4 diet and the $\delta^{13}\text{C}$ values (-18.5‰ – -17.8‰) from M3 (at least one human individuals) indicate a C_3 -based diet (Figure 2; Table 1). Three radiocarbon dates of human bones from those tombs ranged between 2,750 and 2,450 BP, indicating that these two groups (C_3 -based and C_3 - C_4 mixed) lived in the Adong area concurrently (Ma et al., 2022b). Previous studies indicated that C_4 plants in the flora gradually decreased or even disappeared when the altitude exceeds 2,000 m–3,000 m (Chazdon, 1978; Boutton et al., 1980; Rundel, 1980; Cavagnaro, 1988; Wang et al., 2004; Li et al., 2009), which suggests that individuals from M1 and M2 might consume a certain amount of C_4 crops. No archaeobotanical evidence was reported from the Adong tombs or other Bronze Age sites above 2,500 masl in the HMR. Archaeobotanical studies from late Neolithic sites in the highlands of the HMR, including Haxiu, Guijiabao, and Karuo, demonstrate that humans utilized foxtail and broomcorn millet in the mountain areas since ~5,300 BP (Chen and Chen, 2006; Yan et al., 2016a; Song et al., 2021). These indigenous crops were also widely cultivated in the HMR during the Bronze Age (Yang, 2016; Xue et al., 2022). Based on this information and our analysis, we conclude that the individuals from Adong M1 and M2 (at least two individuals) likely both consumed millet crops and C_3 food, while those from M3 mainly consumed C_3 foods. Moreover, $\delta^{15}\text{N}$ values of M1 and M2 ($12.2\text{‰} \pm 0.2\text{‰}$) are higher than those of M3 ($10.4\text{‰} \pm 0.9\text{‰}$, Figure 2; Table 1). The possible reason is that individuals from M1 and M2 consumed more animal protein, but the $\delta^{15}\text{N}$ value of millet remains at Jiagezi cemetery suggests that the intake of millet might also be the reason for the high nitrogen isotope of human collagen (Ren et al., 2020). In addition, it is not excluded that individuals from M1 and M2 might migrate from other areas. More samples are needed for further discussion.

The $\delta^{13}\text{C}$ values of human bone collagen from the Gaozhai tombs are relatively clustered compared to those from the Adong tombs (Figure 2). The $\delta^{13}\text{C}$ value ($-18.4\text{‰} \pm 0.4\text{‰}$) indicates that humans at Gaozhai primarily consumed C_3 foods (Figure 2; Table 2).

TABLE 2 Summary of human isotopic values from the Gaozhai and Adong tombs.

Site	Region	Elevation (masl)	Age (BP)	Number	$\delta^{13}\text{C}$ (‰)			$\delta^{15}\text{N}$ (‰)		
					Mean	SD	Range	Mean	SD	Range
Gaozhai	Yulong	2,080	~2,850–2,450	24	-18.4	0.4	-19.2–-17.7	8.4	0.8	6.9–10.1
Adong	Deqin	2,517	~2,750–2,450	6	-16.8	1.6	-18.5–-15.2	11.3	1.1	9.7–12.4

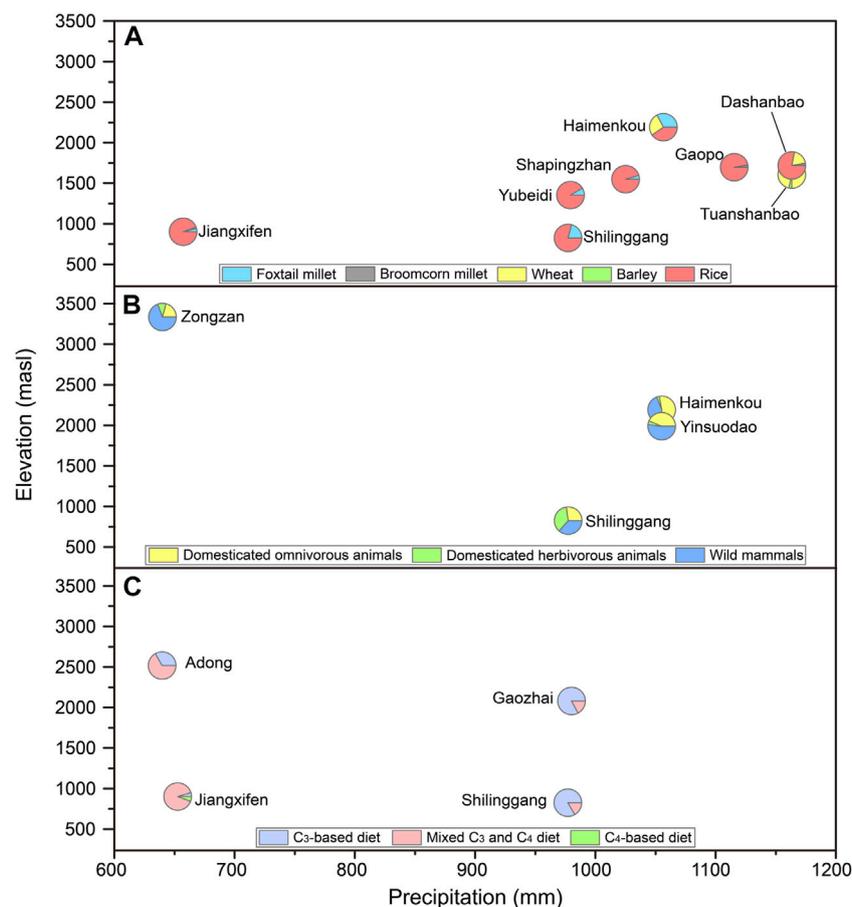


FIGURE 3 Elevation and precipitation variation in the distribution of sites with (A) crop remains; (B) animal remains; and (C) carbon isotopic signals of human bone collagen in HMR during the Bronze Age.

Archaeobotanical studies from contemporaneous sites on the terraces of rivers and lakes in the HRM, such as Yubeidi, Shilinggang, and Jiangxifen, suggest that rice served as the dominant crop (Figure 3A; Yang, 2016; Li et al., 2016; Lu et al., 2021). At the same time, wheat/barley and millets served as auxiliary crops in these areas during the early third Millennium BP. It suggests that rice was the primary crop, though wheat may have served as another staple food at Gaozhai. Further archaeobotanical analysis is needed to ascertain this assumption. $\delta^{15}\text{N}$ values ($8.4\text{‰} \pm 0.8\text{‰}$) of human bone collagen from the Gaozhai tombs are significantly lower than those of the Adong tombs ($11.3\text{‰} \pm 1.1\text{‰}$, $t = 0.000$, Figure 2; Table 2). Due to the lack of vegetation isotopic data and the different opinions on the relationship between vegetation $\delta^{15}\text{N}$ values and altitude (Sah and Brumme, 2003; Yi and Yang, 2006; Liu et al., 2009), it is difficult to determine the reasons for the differences in $\delta^{15}\text{N}$ values between Gaozhai and Adong sites. The differences in animal protein intake and the natural environment are both possible reasons.

Previous studies analyzed human bone collagen's carbon and nitrogen isotopic data from Jiangxifen and Shilinggang Bronze sites in the HMR (Liu, 2016; Lu et al., 2021). The human $\delta^{13}\text{C}$ signals in the Shilinggang site are almost similar to those in the Gaozhai tombs (Liu, 2016); in both sites, the human diet appears to have been dominated by

C_3 foods (likely rice and rice byproducts), and auxiliary with mixed C_3 and C_4 foods (Figure 3C). The Shilinggang and Gaozhai sites are on river terraces in south HMR. The average annual precipitation of these sites is roughly the same, though the elevation of Gaozhai is ~1,200 masl higher than Shilinggang. The Jiangxifen site and the Shilinggang site lie at roughly the same elevation, though the average annual precipitation of Shilinggang is ~300 mm higher. Jiangxifen data suggests that the consumption of C_4 foods exceeded that of Shilinggang and Gaozhai (Figure 3C; Liu, 2016; Lu et al., 2021). Based on such data, we infer that human dietary strategies in the HRM during the Bronze Age were related to precipitation to a certain extent, though more information regarding the specific variation in subsistence strategies is needed.

5.2 Relationship between the spatial pattern of human subsistence strategies during the Bronze Age and local environments in the HMR

Numerous environmental features, including precipitation, temperature, landscape, and vegetation cover, are considered critical influencing factors for cultural evolution, subsistence

strategy transformation, and massive human migration during the Neolithic and Bronze periods (Liu et al., 2009; Preston et al., 2012; Wang et al., 2017; Liao et al., 2019; Dong et al., 2022c; Li et al., 2022). The HMR in particular possesses significant spatial differences in altitude and precipitation. In addition, the average annual temperature in the HMR is closely related to the variation in altitude. To explore the relationship between human subsistence strategies and the spatial heterogeneity of local environments in HMR during the Bronze Age, we compared carbon isotopic data of human bone collagen, archaeobotanical and zooarchaeological data from Bronze Age sites in the HMR, and then assessed those data against the backdrop of altitude and precipitation in those sites (Figure 3).

According to published archaeobotanical data from Bronze Age sites in the HMR, rice dominated the human diet, followed by foxtail millet in most Bronze Age sites below ~1,700 masl in the HMR (Jiang et al., 2013; Yan et al., 2016b; Li et al., 2016; Yang, 2016; Lu et al., 2021). Two exceptions to this trend are the Tuanshanbao and Dashanbao sites, both of which lie at ~1,700 masl (Figure 3A; Yan et al., 2016c). The Tuanshanbao and Dashanbao sites were dated to ~2,700 BP–2,400 BP and 2,400 BP–2,200 BP, respectively (Yan et al., 2016c). Other sites, such as the Gaopo and Shapingzhan sites, were settled during the early third Millennium BP (Jiang et al., 2013; Yan et al., 2016b). This temporal difference might suggest that the cropping pattern of the Tuanshanbao and Dashanbao sites was affected by increasing cultural exchange from the surrounding regions. However, the small number of the crop remains at these sites makes it difficult to understand the crops' cultivated structure well at the Tuanshanbao and Dashanbao sites (Yan et al., 2016c). In the Bronze Age sites above ~1,700 masl, rice was also the primary crop, while foxtail millet and wheat were also important. The cropping pattern of the Haimenkou site was more diverse than the crop remains discovered in sites at lower elevations, typically below ~1,700 masl (Figure 3A; Xue et al., 2022). This suggests that cropping patterns in the HMR during the Bronze Age were primarily affected by the altitude of human settlements. The relationship between cropping patterns and precipitation is difficult to ascertain, likely because the average annual precipitation in each site exceeded 600 mm (Figure 3A), which is sufficient for the growth of different crops.

We obtained zooarchaeological data from only four Bronze sites in the HMR. In the Shilinggang site (~800 masl), omnivorous livestock (e.g., pig and dog), herbivorous livestock (e.g., cattle, sheep/goat), and wild mammals appear to be of similar significance in human diets (Liu, 2016). This suggests that humans in the Nujiang River valley adopted a diverse strategy with various animal utilization to adequately exploit their surrounding natural resources and rice and millet byproducts. In the Yinsuodao and Haimenkou sites (~2,000 masl), the proportion of wild mammals and omnivorous livestock ranged between 44%–52% and 44%–53%, respectively, and the proportion of herbivorous livestock fell below 5% (Figure 3B; Zhao, 2011; Wang, 2012). This suggests that humans mainly hunted game and fed pigs/dogs to obtain animal protein during the Bronze Age. In contrast, the importance of herbivorous livestock herding in livelihoods was limited, possibly due to the absence of contiguous grasslands. In the Zongzan site (~3,300 masl), the proportion of wildlife remains was roughly 70%, while omnivorous and herbivorous livestock

remains accounted for 21% and 10%, respectively (Chen et al., 2019). This suggests that in this site, humans mainly relied on hunting, and only supplemented with livestock to obtain meat resources in mountain areas of the HMR during the Bronze Age.

As shown in Figure 3, the diversity of human dietary strategies and the importance of hunting in the HMR during the Bronze Age increased with altitude: limited agricultural production forced humans to exploit more diverse food resources in high-altitude areas. This relationship is likely due to the decrease in arable land and suitable hydrothermal conditions for the high-yielding rice cultivation at higher elevations, which also limits livestock feeding, while the resources of wild animals are relatively abundant in high-altitude areas. These factors resulted in increased survival pressure in the highlands, which possess lower accumulated temperature and precipitation compared to the river valleys in the lowlands. The relationship between average annual precipitation and cropping patterns or animal utilization strategies in the HMR during the Bronze Age is difficult to evaluate. It seems that humans consumed more diverse diets at the Jiangxifen and Adong sites, both of which experienced relatively low average annual precipitation (~650 mm) than they did at the Shilinggang and Gaozhai sites, which both experienced relatively high average annual precipitation (~1,000 mm) (Figure 3C; Liu, 2016; Lu et al., 2021). Compared to the late Neolithic period, the Bronze Age saw the introduction and utilization of more crops and livestock in the HMR. This facilitated the development of diverse subsistence strategies across different altitudes. Furthermore, the large rivers and mountains resulted in highly fragmented and isolated habitats, which mitigated opportunities for the formation of a dominant subsistence strategy in late Neolithic China (Lu et al., 2021; Ma et al., 2022a), but which supported the emergence of diverse subsistence strategies in the Bronze Age HMR.

6 Conclusion

Carbon and nitrogen isotopes of human bone collagen from the Adong and Gaozhai tombs indicate that human dietary patterns differed across HMR mountain areas and river terraces during the early third Millennium BP. Humans may have consumed diverse mixed C₃/C₄ foods at Adong during ~2,750 BP–2,450 BP. Humans at Gaozhai mainly relied on C₃ foods, supplemented only by a few C₄ foods. The difference in animal protein intake between the two sites needs more evidence for discussion. By comparing published isotopic, archaeobotanical, and zooarchaeological studies, as well as analyzing the altitude and precipitation of investigated sites, we deduce that, in general, humans engaged in more diverse subsistence strategies and hunted more wildlife with the increase of altitude. This is likely due to the severe survival pressure in the HMR highlands during the Bronze Age. In addition, cropping patterns throughout the Bronze Age HMR were likely affected by various factors, such as the introduction and utilization of wheat/barley, localized landform, and hydrothermal conditions. The diverse subsistence strategies in the HMR during the Bronze period were rooted in the convergence of numerous crops and livestock in the critical passageways for culture exchange, the relatively abundant wild resources, and the highly fragmented habitats cut by large mountains and rivers in the southeast margin of the Tibetan Plateau.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material, further inquiries can be directed to the corresponding author.

Author contributions

MM designed the study. ZY and NC provided archaeological samples. YL experimented. ML, MM, and YL participated in the discussion. ML and YL wrote the manuscript.

Funding

This work was supported by the Second Tibetan Plateau Scientific Expedition and Research Program (STEP) (Grant No. 2019QZKK0601), National Natural Science Foundation of China

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- (Grant No. 42271160), and International Partnership Program of Chinese Academy of Sciences (Grant No. 131C11KYSB20190035).

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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