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Population history and subsistence of farming communities in an agro-pastoral transition zone of northern China: ancient DNA and isotopic evidence from the Erdaojingzi site

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ABSTRACT

This study investigates the population history and subsistence of farming communities at the Erdaojingzi site (ca. 3700–3330 cal. BP), a well-preserved Bronze Age settlement located in the agro-pastoral transition zone of the West Liao River Basin in northern China. We apply a multidisciplinary approach, combining ancient DNA, carbon and nitrogen stable isotope analysis, zooarchaeological data and archaeobotanical evidence, to evaluate population affinities at the site and to characterise subsistence practices in relation to environmental and cultural conditions. Ancient DNA from two individuals shows ancestry profiles closely related to farming populations of the Yellow River Basin, rather than to previously published Neolithic groups from the western Liao region, indicating strong genetic connections with Central Plains related farming communities. Stable isotope results from 43 animal and two human bone samples demonstrate that millet and its by-products formed dietary staples for both humans and domestic animals. Humans, pigs and dogs primarily relied on C_4 plants, whereas cattle and sheep consumed mixed diets of C_3 and C_4 plants. Nitrogen isotope values point to a diet rich in animal protein for humans. Combined age at death and isotopic data from pig remains further indicate that young pigs constituted an important component of meat consumption. Variation in nitrogen isotope values among sheep suggests differences in grazing and foddering regimes, and may also reflect localised soil enrichment by dung and other management practices. Taken together, these results provide new insight into how farming communities organised their subsistence and how population history and economic strategies were intertwined in an agro-pastoral transition zone of prehistoric East Asia.

Keywords: farming communities; subsistence; agro-pastoral transition zone; Erdaojingzi site; ancient DNA; stable isotopes

1 INTRODUCTION

Human migration and environmental adaptation have long been recognized as key drivers in the formation and evolution of ancient societies[1][2][3][4]. When people enter new regions, especially ecologically marginal areas, they often need to adjust their subsistence, resource use and social practices in relation to local landscapes and established traditions[5][6][7]. This was especially true when agricultural populations moved into agro-pastoral transition zones, where they faced important choices about whether to maintain their original subsistence systems or to adapt them to local environmental and cultural contexts[8][9][10]. These issues have been extensively discussed in ethnography, archaeology, ecology and genetics[11][12][13][14][15][16].

Gao has recently proposed a simple set of models to describe interaction between incoming and local populations in prehistoric Eurasia (Fig. 1)[17]. In reality, many prehistoric cases fall between these simple patterns, and cultural change does not have a direct one to one correspondence with genetic replacement or admixture. Gao's framework is therefore best regarded as a heuristic tool, which in this study serves as a conceptual starting point for exploring how mobility and interaction may have shaped subsistence practices in a specific region.

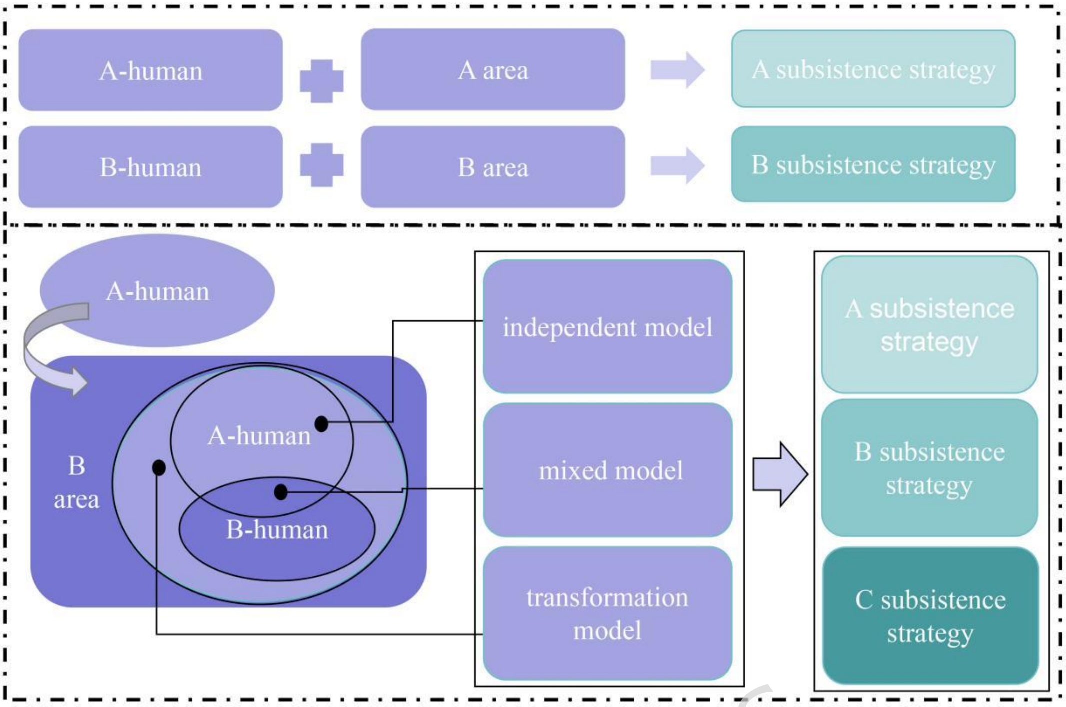

Fig. 1 This flowchart illustrates the interaction between populations with different genetic profiles and their corresponding subsistence strategies. Population A, with genetic profile A, practices a type A subsistence strategy in its native region, while population B, with genetic profile B, practices a type B strategy in its own region. When population A moves into region B, three potential interaction models may occur. If population A maintains genetic independence without exchanging genes with population B, it follows an independent model. If gene exchange occurs between the two groups, it constitutes a mixed model. If population A largely replaces the original population in region B, this can be described as a transformation model. These interaction patterns may result in subsistence strategies that continue the original practices of population A, maintain the established practices of population B, or give rise to a novel type C subsistence strategy that emerges from their interaction.

For the first model, where migration is closely linked to new economic strategies, two well studied cases can be cited. In northern China, genomic studies indicate that the transition from early mixed hunting and millet cultivation to more intensive agriculture and later to pastoral or agro-pastoral lifeways broadly follows changes in ancestry, with increasing contributions from northern farming populations and then from Inner Asian steppe related groups[18]. In Europe, the spread of early farming from Anatolia involved large scale movement of early farmers into areas previously occupied by hunter gatherers, and stable isotope data show a clear shift away from diets dominated by aquatic and wild resources toward C_3 plants and domestic animals[19][20]. These examples illustrate cases in which substantial genetic influx is closely tied to major changes in subsistence.

For the second model, in which ancestry changes but subsistence remains broadly similar, the Bell Beaker phenomenon in Britain is a well known case. Ancient genomes show that individuals associated with Beaker material culture in Britain experienced almost complete replacement of local Late Neolithic farmer ancestry by ancestry related to continental groups, pointing to major demographic change[21]. However, isotopic and archaeological evidence suggests that communities continued to practise mixed farming based on C_3 crops and domestic herbivores, without adopting a pastoral economy similar to that of steppe herders despite strong genetic links with populations from the European grasslands[22]. In such cases, large scale migration does not immediately produce a fundamentally new subsistence system.

The third model is represented by situations in which local genetic continuity is accompanied by substantial innovation in subsistence practices. On the eastern Eurasian steppe, Late Bronze Age communities in northern Mongolia retained predominantly local hunter gatherer related ancestry with only limited input from western steppe groups, yet proteomic evidence from dental calculus demonstrates intensive consumption of milk from cattle, sheep and goats[23]. This combination of local ancestry and newly adopted dairy pastoralism indicates that key elements of a pastoral economy could spread mainly through cultural transmission and small scale contacts rather than through large scale population replacement. These contrasting examples underline that migration, admixture and cultural transmission can be separated from subsistence change, and that each regional case needs to be evaluated with combined archaeological, isotopic and genomic data.

During the transition from the Late Neolithic to the Bronze Age, population mobility across Eurasia increased significantly due to expanding interregional contacts and climate deterioration, especially the 4.2 ka BP aridification event[24]. This period witnessed the emergence and expansion of mixed economies in grassland and forest steppe zones, where agriculture and pastoralism became increasingly integrated[25]. Archaeological research indicates that, in response to climatic and social pressures, farming communities in the Central Plains established and intensified connections with regions to the north and north east. Archaeological and genetic evidence from northern China suggests that groups carrying ancestry associated with Central Plains related farming populations may have moved into agro-pastoral zones, bringing drought tolerant crops and elements of farming based subsistence that were incorporated into local mixed economies[26][27][28][29]. Rather than representing a simple replacement of local lifeways, these processes contributed to the formation of agro-pastoral zones and increasingly complex regional economic systems.

The Erdaojingzi site, located in the steppe region of the West Liao River Basin, presents a compelling case study for exploring these transformations. Archaeological findings reveal significant cultural shifts at the site, including the appearance of bronze tools, strong defensive architecture and the replacement of traditional cylindrical pottery jars, tongxing guan *筒形罐*, with new forms such as pottery li *鬲*, which show close stylistic links to ceramics from the Yellow River Basin[30]. The site also yields ritual vessels closely resembling those from Erlitou related contexts in the Yellow River Basin, such as jue *爵* and hu *壶*, as well as turquoise inlaid artifacts and lacquered wooden items that suggest shared or closely connected ritual practices and ideology across regions[31][32][33][34][35][36]. In addition, divination bone production techniques that combine drilling and burning in the Lower Xi

ajiadian culture are consistent with divination bone traditions of pre Shang cultures in the Central Plains, and may even be slightly earlier in date[37], further suggesting close connections between these regions in ritual practice and knowledge.

Zooarchaeological and archaeobotanical data further reflect substantial changes from the Neolithic to the Bronze Age, marked by a notable increase in domesticated pigs, dogs, cattle and sheep, alongside a decline in wild game such as deer, and by the widespread cultivation of millets and other crops[38][39][40][41][42]. These shifts point to more intensive and diversified animal exploitation and to well developed crop farming, and they raise key questions about the driving mechanisms behind these transformations, including the relative roles of technological diffusion, cultural exchange and population movement.

In summary, archaeological and zooarchaeological evidence points to significant economic and cultural transformation during the Lower Xiajiadian period in the West Liao River Basin[43]. However, the precise demographic background of these changes and the organisation of local subsistence systems remain unresolved. In this study, we address three specific questions. First, how are the Erdaojingzi individuals related, in genetic terms, to previously published populations from the West Liao region, the Yellow River Basin and neighbouring areas. Second, what do stable carbon and nitrogen isotope values from human and animal remains reveal about the relative importance of C_3 and C_4 resources, the balance between plant and animal protein and the management of different domestic species. Third, how can these genetic and isotopic lines of evidence, together with existing zooarchaeological and archaeobotanical data, be combined to assess how farming communities organised their subsistence and how population history and economic strategies were intertwined in an agro-pastoral transition zone of northern China. By integrating these approaches, this study aims to contribute to understanding of resilience, innovation and human environment interaction in Bronze Age Northeast Asia.

2 MATERIALS

2.1 Archaeological background of the Erdaojingzi site

The Erdaojingzi site is located on a northern slope near the Erdaojingzi Administrative Village in Hongshan District, Chifeng City (Fig. 2a). It is considered one of the best preserved Bronze Age sites in China and is often referred to as the "Pompeii of the East" because of its large size, excellent preservation and substantial architectural remains[44] (Fig. 2b). The settlement lies among low hills and occupies a gentle east to west slope. In 2009, the Inner Mongolia Institute of Cultural Relics and Archaeology carried out large scale excavations as part of an infrastructure development project.

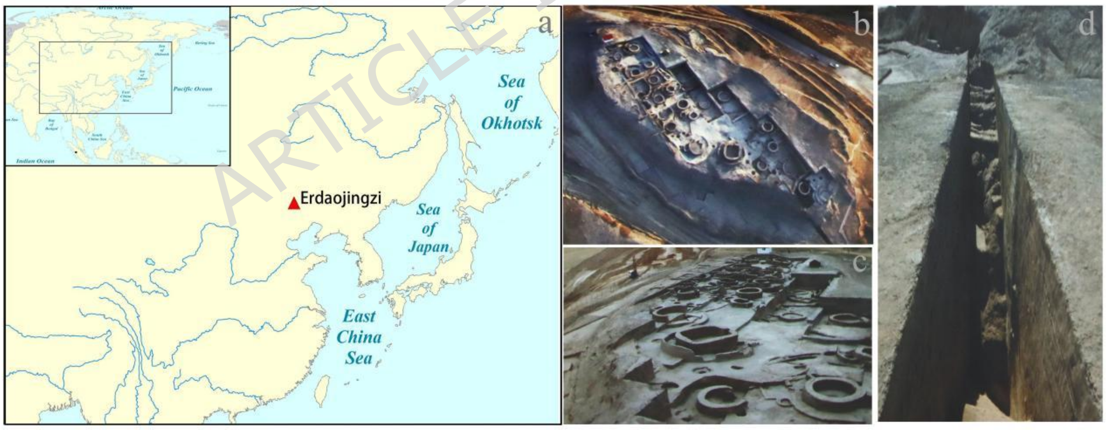

Fig. 2 Geographic Location and Excavation of the Erdaojingzi Site. **a**: Geographic location of Erdaojingzi site. Base map derived from the Standard Map of the Ministry of Natural Resources of the People's Republic of China (Map Approval No. GS(2016)1667). Generated using ArcGIS 10.8 (ESRI, https://www.esri.com/). Archaeological site locations were added by the authors. **b:** Aerial photograph of the whole site of Erdaojingzi site. **c**: Panoramic view of the excavation area. **d**: Section of city wall and trench.

The excavation covered an area of 5,200 square metres, while the entire site measures approximately 190 by 140 metres, with an estimated area of 27,000 square metres (Fig. 2c). Archaeologists identified 305 features, including city walls, moats, courtyards, houses, roads, storage pits and graves (Fig. 2d). Charred remains of broomcorn millet, foxtail millet and other cereal crops were recovered from storage pits together with woven grass objects, pointing to a predominantly agricultural economy[45]. More than one thousand artefacts made from pottery, stone, bone and bronze were also excavated. On the basis of pottery forms and agricultural tools, previous research has argued that Erdaojingzi shows close cultural links with the Dashanqian site, which has been interpreted as representing farming communities with strong connections to the Yellow River Basin[46][47]. Erdaojingzi is generally regarded as a representative settlement of the Lower Xiajiadian Culture and is recognised as one of the largest and best preserved Bronze Age sites so far identified in China. It has played an important role in discussions of the development of complex societies in northern China and their interactions with Central Plains traditions[48].

In the West Liao River region, many previously known large slope type settlements of the Lower Xiajiadian Culture have been disturbed or truncated by later remains of the Upper Xiajiadian Culture, whereas Erdaojingzi shows no such overlying occupation. Archaeological findings further indicate that painted pottery deposited in graves served similar functions to ritual vessels in the Central Plains. The decorative motifs on this painted pottery closely resemble those on bronze vessels of the Xia and Shang periods in the Central Plains. These observations suggest significant cultural connections between the Lower Xiajiadian Culture and contemporary Central Plains cultures, distinguishing Erdaojingzi from other major archaeological cultures of northeastern China. Two human bone samples from the site were selected for collagen analysis, radiocarbon dating and stable isotope analysis (Table 1). Calibrated using the Beta Cal4.20: HPD method and the INTCAL20 curve, the radiocarbon dates indicate that Erdaojingzi was occupied between approximately 3700 and 3330 calibrated years before present.

Table 1 Radiocarbon date and C, N stable isotope results of two human bone samples from the Erdaojingzi site.

Lab number	Collagen species	Calibrated date	C (%)	N (%)	C/N	δ^{13}C (‰)	δ^{15}N (‰)
Beta-691987	human	3360±30	40.4	15.2	3.1	－5.9	10.0
Beta-691988	human	3400±30	42.0	15.6	3.1	－6.7	9.5

2.2. Zooarchaeological analysis

A total of 1,189 mammal bone fragments were recovered from the Erdaojingzi site. Of these, 11 intrusive human bones were excluded from the faunal analysis, leaving 1,178 mammal specimens (NISP) for zooarchaeological study (Table 2). All remains were cleaned, sorted and examined following standard zooarchaeological procedures. Taxonomic identification, skeletal element, side, fusion state and surface preservation were recorded for each specimen. Identifications were made using published osteological manuals and modern comparative collections housed at Jilin University and collaborating institutions. In this study we focus on mammalian remains, as bird and fish bones are rare in the assemblage and are not suitable for quantitative analysis.

Table 2 Quantitative statistics of mammal bones from the Erdaojingzi site.

Species	NISP	NISP%	MNI	MNI%
Pig (*Sus domesticus*)	588	49.9	65	61.3
Dog (*Canis lupus familiaris*)	78	6.6	11	10.4
Sheep (*Ovis* sp.)	169	14.4	10	9.4
Cattle (*Bos taurus*)	275	23.3	8	7.6

Horse (*Equus* sp.)	1	0.1	1	0.9
Red deer (*Cervus canadensis*)	11	0.9	1	0.9
Roe deer (*Capreolus pygargus*)	18	1.5	2	1.9
Raccoon dog (*Nyctereutes procyonoides*)	3	0.3	1	0.9
Fox (*Vulpes vulpes*)	1	0.1	1	0.9
Rodents (*Myomorpha*)	3	0.3	1	0.9
Hare (*Lepus* sp.)	8	0.7	3	2.8
Human (*Homo*)	23	2.0	2	1.9
Total	1178	100.0	106	100.0

We created a stacked bar chart (Fig. 3) based on the quantitative data in Table 2 in order to visualise the relative proportions of the major taxa. Pigs are by far the most abundant species, accounting for about half of the identified mammal specimens by NISP. Dogs and sheep are also well represented, with MNI percentages of 10.4% and 9.4%, respectively. Cattle are present in smaller numbers but still make a clear contribution to the domestic assemblage. Wild mammals, including red deer, roe deer and hares, occur at much lower frequencies. Overall, pigs are the most prominent species and domestic animals dominate the faunal assemblage, while hunting of wild game appears to have played a secondary role (Table 2; Fig. 3).

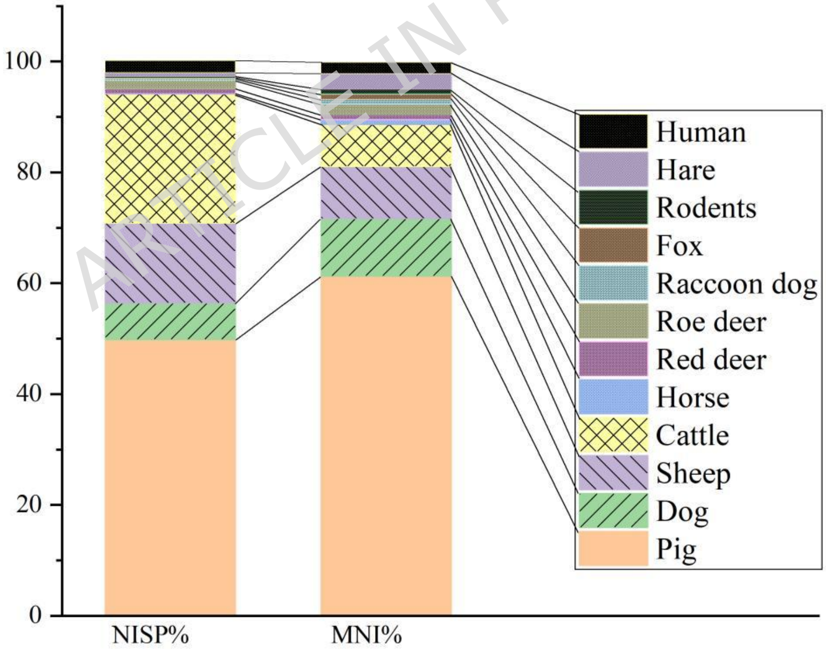

Fig. 3 Stacked bar chart showing the relative proportions of major mammal taxa at the Erdaojingzi site, based on NISP values in Table 2.

In addition to food remains, a significant quantity of bone artefacts was discovered at Erdaojingzi. These include awls, needles, spatulas and other tools, as well as a large spade made from the scapula of a cow (Fig. 4). The frequent use of cattle bones to manufacture agricultural implements, together with the dominance of domestic mammals in the faunal assemblage and the abundant remains of millet crops, provides further evidence for a well developed farming economy at the site.

Fig. 4 Five views of a bone spade made from a cow scapula (09CWE F2:5).

2.3 Archaeobotanical analysis

Archaeobotanical evidence shows that crop seeds dominate the plant remains from Erdaojingzi. Systematic flotation of soil samples from houses, storage pits and other features recovered abundant carbonised grains of foxtail millet (Setaria italica) and broomcorn millet (Panicum miliaceum), which together account for the great majority of identified plant remains. Smaller quantities of other cultivated plants and weed seeds are also present. The absolute counts and ubiquity of the main crops are summarised in Table 3[49].

Table 3 Absolute counts and ubiquity of crop remains from the Erdaojingzi site.

Species	Absolute Quantity	Absolute Quantity Ratio (%)	Ubiquity
Foxtail millet (*Setaria italica*)	181685	81.4	100
Broomcorn millet (*Panicum miliaceum*)	41266	18.5	92.2
Soybean (*Glycine max*)	179	0.1	24.7
Total	223133	100	100

Wild plant remains occur in much lower numbers and were probably used as supplementary resources rather than forming a major part of the diet. Taken together with the faunal data, the archaeobotanical results indicate that Erdaojingzi was a permanently occupied settlement with a millet based farming economy and diversified animal exploitation. These lines of evidence provide essential context for the ancient DNA and stable isotope analyses presented below and for assessing the relative importance of C_3 and C_4 plant resources in human and animal diets at the site.

2.4 Ancient DNA and Isotopic background

Ancient DNA refers to genetic material preserved in archaeological or palaeontological remains, usually at low quantity and with extensive fragmentation and chemical damage. Since the late twentieth century, the development of clean laboratory protocols, high throughput sequencing and in solution enrichment techniques has made it possible to obtain genome scale data from human and animal bones and teeth in many different environments[50][51][52]. Such studies can reveal biological affinities between individuals and groups, reconstruct population history and admixture, and identify kinship relationships within sites or cemeteries[53]. When combined with archaeological context, ancient DNA provides a direct way to investigate whether cultural and economic changes are associated with the arrival of people carrying different ancestry, or whether they took place mainly among long established local communities.

Stable carbon and nitrogen isotope analysis of bone collagen has become a standard method for reconstructing human and animal diets in archaeological contexts[54][55][56][57]. In temperate regions, carbon isotope values primarily distinguish between C_3 plants and C_4 plants such as millets, and between marine and terrestrial food sources. Nitrogen isotope values mainly reflect trophic level, with consumers generally enriched in nitrogen fifteen relative to their diet. However, a growing body of work has emphasised that isotopic signatures are influenced not only by simple trophic position but also by ecological and physiological factors, including aridity, soil and manure management, plant functional type, nursing and weaning, nutritional stress and disease[58][59][60]. Careful interpretation therefore requires integration of isotopic results with environmental data and independent archaeological evidence for plant use, animal management and mobility.

At the Erdaojingzi site, previous zooarchaeological and archaeobotanical studies have already indicated a mixed economic system in which pigs, dogs, cattle and sheep were exploited alongside wild animals, and drought tolerant crops such as millets and other domesticated plants formed an important component of the subsistence base. Within this context, ancient DNA and stable isotope analyses provide complementary perspectives. Ancient DNA from human remains can clarify whether individuals at Erdaojingzi mainly represent local population continuity or whether they include substantial ancestry associated with Central Plains related farming populations. Stable carbon and nitrogen isotope data from humans and animals can document the relative importance of C_3 and C_4 resources, the balance between plant and animal protein, and differences in feeding and management strategies among domestic species. By outlining these wider methodological and ecological considerations, this section provides the background for interpreting the genetic and isotopic results from Erdaojingzi, and for linking patterns of population history to variation in subsistence practices in an agro-pastoral transition zone.

3 METHODS

3.1 Ancient DNA analysis

3.1.1 Sample collection

The Erdaojingzi site was excavated as a rescue project ahead of construction. Because of time and space constraints, most human skeletons received only basic osteological recording in the field and were then reburied in situ. Only a small number of bones were collected and transferred to the repository of the Bioarchaeology Laboratory at Jilin University. When the present study was undertaken, well-preserved human remains from the site were therefore very scarce. We limited ancient DNA sampling to two individuals with clear archaeological context and relatively good preservation. Sampling permissions were obtained from the relevant cultural heritage authorities and from Jilin University and Fudan University.

3.1.2 Ancient DNA extraction and library preparation

We extracted DNA from two samples in a dedicated aDNA facility at Fudan University, following established precautions for working with ancient human DNA[61][62]. Human remains were surface-cleaned and ground to a fine powder. We used 50 mg of bone powder to extract DNA[63]. The lysis step included the addition of 1 ml extraction buffer to each 50 mg sample, containing 0.45 M EDTA (PH 8.0), 0.25 mg/ml Proteinase K (Merck, Germany), 0.05% (vol/vol) Tween-20 (Sigma Aldrich, Germany). After suspending the sample powder by vortexing, the sample was incubated overnight (15–24 h) at 37 °C. After centrifugation, we transferred the lysate supernatant to a fresh tube. We mixed 17.5 µl magnetic beads (G-Biosciences, USA) with 2.5 ml binding buffer containing 5 M GuHCl, 40% (vol/vol) Isopropanol, 0.12 M sodium acetate, 0.05% (vol/vol) Tween-20 (Sigma Aldrich, Germany). Then, we transferred the supernatant (500µl) to a binding buffer/bead mixture, followed by an extraction using a robot (Enlighten Biotech, China) procedure. Finally, the DNA was eluted with 50 µl TET buffer (QIAGEN, Germany). We prepared initial double-stranded and double-indexing libraries following Meyer's protocols[64] but with minor modifications[65][66] outlined below. The end-repair step was performed in 25 µl reactions using 20 µl DNA extract. This was incubated for 20 mins at 12°C and 15 mins at 37°C, purified using a standard MinElute (Qiagen, Germany) purification step, and eluted in 15 µl TET (Qiagen, Germany). Next, Illumina-specific adapters were ligated to the end-repaired DNA in 25 µl reactions. The reaction was incubated for 15 mins at 20°C and purified with another MinElute purification step before being eluted in 20 µl EB Buffer (Qiagen, Germany). The adapter fill-in reaction was performed in a final volume of 25 µl and incubated for 20 mins at 37°C followed by 20 mins at 80°C to inactivate the Bst enzyme (NEB, USA). Libraries were amplified with indexing primers using Q5 High-Fidelity DNA Polymerase (NEB, USA). We purified indexed products using the MinElute PCR Purification Kit (Qiagen, Germany). We qualified the clean-up libraries using Qubit 2.0 (Thermo Fisher, USA). Finally, the shotgun libraries were converted into circular single-strand libraries adapted to the DNBSEQ-T7 instrument using 2×100-bp chemistry at the Geneplus Company, China[67][68].

3.1.3 Nuclear SNPs capture and sequencing

The double-stranded shotgun libraries with lower endogenous DNA content were enriched using the Twist Ancient DNA panel, following the protocol developed by David Reich's lab (short for twist 1240K)[69]. The sequencing of the double-stranded library was performed using the Illumina Nova6000 platform at the Mingma Technologies Company, China, in the 150-bp paired-end sequencing design.

3.1.4 Sequence data processing

Adapter Removal v2.3.1[70] was utilized to trim sequencing adapters and merge paired-end reads into a single sequence, retaining only those reads with at least 11 bp of overlap. BWA v0.7.17[71] with parameters -l 1024 and -n 0.01 was employed to align the merged reads to the human reference genome (hs37d5; GRCh37 inclusive of decoy sequences). Deduplication of PCR sequences was accomplished using Dedup v0.12.3[72].

Based on mapDamage evaluation, trimBam from BamUtil v1.0.14 (https://github.com/statgen/bamUtil) was used to clip a corresponding number of bases from both ends of the sequences, in order to avoid excessive C>T and G>A transitions at the sequence termini. Subsequently, the parameters of samtools mpileup were configured to -q30 and -Q30 for quality filtering and comparison. Ultimately, the 1240k dataset served as a reference, and pseudohaploid calls for two samples were generated using RandomHaploid in the pileupCaller software (https://github.com/stschiff/sequenceTools).

3.1.5 Authentication of ancient DNA

We analyzed the deamination patterns, specifically 5′C>T and 3′G>A misincorporations, of ancient DNA employing two methods: mapDamage and pmdtools software, respectively. Subsequently, we estimated contamination rates for all male samples utilizing ANGSD, and mtDNA contamination rates were assessed using schmutzi v1.5.5.5[73].

3.1.6 Genetic sexing and uniparental haplogroup assignment

We determined genetic sex from the relative coverage of reads mapping to the X and Y chromosomes compared with the autosomes, following published methods for ancient DNA[74]. Mitochondrial haplogroups were assigned from the consensus mtDNA sequences using HaploGrep2 with PhyloTree build 17 as reference[75]. Y-chromosome haplogroups were inferred with Yleaf v2, and assignments were checked by visual inspection of informative SNPs in IGV.

3.1.7 Data merging

We utilized the mergeit tool within the EIGENSOFT software package[76] to compare our data of two samples with two previously published datasets[77][78][79]. Specifically, the “Human Origins” dataset comprises 597,573 SNPs spanning a diverse array of modern populations and is employed for smartpca and ADMIXTURE analyses. Additionally, the “1240k” dataset, containing 1,233,013 SNPs across numerous representative modern and ancient populations, is suitable for analyses based on f-statistics.

3.1.8 Principal components analysis (PCA)

We conducted Principal Component Analysis (PCA) on the Human Origins dataset utilizing the smartpca program, version 16000, within the EIGENSOFT software package. The default parameters were employed, with the 'lsqproject' option set to 'yes', as recommended by Patterson et al. Principal components (PCs) were calculated based on modern populations, and ancient samples were subsequently projected onto the resultant first two principal components. A total of 470,607 Single Nucleotide Polymorphisms (SNPs) were utilized in the computation of the principal components.

3.1.9 ADMIXTURE analysis

Chain imbalances were initially pruned using the indep-pairwise parameter, as recommended by Peter[80] and Lawson et al[81], in PLINK v1.90[82]. Subsequently, an unsupervised confounding analysis was conducted using ADMIXTURE v1.3.0[83] on a dataset of 220,388 SNPs. The analysis employed a five-fold cross-validation approach with 100 bootstrap replicates, and the ancestral population (K) was varied from 2 to 7 in order to perform unsupervised confounding analyses.

3.1.10 f-statistics

To ascertain which populations shared greater genetic drift with the target samples, we utilized qp3Pop v651 to compute the outgroup-f3 statistic, with the inbreeding parameter set to YES. Additionally, we employed qpDstat v980 to calculate the f4 statistic using the f4-mode parameter, enabling a further investigation into the ancestral flow of the target samples[84]. Both analyses were conducted within the ADMIXTOOLS software package.

3.1.11 Admixture modeling

To estimate the ancestral proportions of individuals from various source populations, we employed the qpAdm v810 tool within the ADMIXTOOLS framework. During the analysis, we configured the parameters with allsnps: YES and inbreeding: YES to ensure comprehensive utilization of genetic data and consideration of potential inbreeding effects.

3.2 Stable isotope analysis

3.2.1 Sample selection

Stable carbon and nitrogen isotope analysis of bone collagen was used to reconstruct the diets of humans and animals at Erdaojingzi. In order to reduce intra skeletal variation, we preferentially selected the same long bone element within each taxon, mainly humeri with good cortical preservation that had already been recorded in the zooarchaeological study.

In total, 43 animal bone samples were analysed, including pigs (n = 15), sheep (n = 17), dogs (n = 5), hares (n = 3), roe deer (n = 2) and cattle (n = 1). Two human bone samples were analysed separately and are reported together with radiocarbon dates in Table 1. It should be noted that the δ^{13}C and δ^{15}N values of the human remains were obtained from Beta Analytic as part of the radiocarbon dating procedure, whereas the faunal isotope data were generated at the stable isotope laboratory of the Chinese Academy of Agricultural Sciences (CAAS). As a result, direct comparison between the two datasets may involve minor inter-laboratory offsets. Details of the animal specimens, collagen quality indicators and isotope results are listed in Table 4, and the distributions of δ^{13}C and δ^{15}N values are illustrated in Fig. 8 and Fig. 9.

Table 4 Results of stable isotope tests on animal skeletons at the Erdaojingzi site.

Lab ID.	Context	Species	Element	C (%)	N (%)	C/N	δ^{13}C (‰)	δ^{15}N (‰)
ED1	09CWEF2s：25	Pig	humerus	47.3	16.6	3.3	-6.5	9.2
ED2	09CWEF9：3	Pig	humerus	47.1	16.9	3.3	-6.8	10.0
ED3	09CWEF14：11	Pig	humerus	46.1	16.5	3.3	-7.3	8.1
ED4	09CWEF8s：40	Pig	humerus	44.2	15.5	3.3	-7.2	10.6
ED5	09CWEF8s：88	Pig	humerus	42.0	15.0	3.3	-6.8	7.7
ED6	09CWEF22：6	Pig	humerus	47.0	16.5	3.3	-5.9	8.0
ED7	09CWEF21s：4	Sheep	humerus	47.6	17.0	3.3	-15.3	5.6
ED8	09CWEF22：7	Pig	humerus	47.7	17.2	3.2	-9.3	9.6
ED9	09CWEF2f：2	Pig	humerus	46.7	16.8	3.2	-7.1	7.6
ED10	09CWEF102：25	Pig	humerus	48.0	16.9	3.3	-7.2	8.5
ED11	09CWEF81s：3	Pig	humerus	49.5	17.8	3.2	-6.6	8.4
ED12	09CWEF15s：1	Pig	humerus	47.8	17.2	3.2	-7.1	9.0
ED13	09CWEF14：20	Pig	humerus	49.0	17.5	3.3	-7.4	8.5

Lab ID.	Context	Species	Element	C (%)	N (%)	C/N	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)
ED14	09CWEF54：1	Pig	humerus	49.1	17.7	3.2	-7.1	8.1
ED15	09CWEF69：9	Pig	humerus	45.6	16.6	3.2	-6.7	7.6
ED16	09CWEF8s：18	Pig	humerus	47.8	16.9	3.3	-7.5	7.3
ED17	09CWEF54s：15	Sheep	metacarpal	43.0	15.5	3.2	-14.6	6.6
ED18	09CWEF14：3	Sheep	metacarpal	47.2	17.1	3.2	-16.3	6.0
ED19	09CWEF11：1	Sheep	metacarpal	46.0	16.6	3.2	-16.5	6.0
ED20	09CWEF54D：7	Sheep	metacarpal	47.0	16.8	3.3	-16.3	6.6
ED21	09CWEF69：5	Sheep	metacarpal	47.5	17.4	3.2	-15.7	7.4
ED22	09CWEF60:3	Sheep	metacarpal	46.5	17.0	3.2	-14.7	7.4
ED23	09CWEF20Q：12	Sheep	metacarpal	44.0	15.8	3.3	-17.3	6.8
ED24	09CWEF20Q：10	Sheep	metacarpal	46.7	16.4	3.3	-13.3	7.3
ED25	09CWEF15s：5	Sheep	metacarpal	47.9	17.4	3.2	-14.6	5.3
ED26	09CWEF2B：1	Sheep	metacarpal	45.2	15.9	3.3	-15.5	7.5
ED27	09CWEF15①: 1	Sheep	metacarpal	49.2	17.6	3.3	-16.9	6.5
ED28	09CWEF20s：9	Sheep	metacarpal	47.5	17.1	3.2	-16.6	8.9
ED29	09CWEF63s：10	Sheep	metacarpal	47.1	17.0	3.2	-17.8	7.1
ED30	09CWEF8s：97	Sheep	metacarpal	45.7	15.9	3.3	-16.2	8.6
ED31	09CWEF75s：2	Sheep	metacarpal	47.5	17.0	3.3	-13.4	10.5
ED32	09CWEF3：4	Sheep	metacarpal	48.4	17.1	3.3	-14.1	7.6
ED33	09CWEF53：10	Dog	humerus	47.6	16.8	3.3	-7.6	8.4

Lab ID.	Context	Species	Element	C (%)	N (%)	C/N	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)
ED34	09CWEF9s：6	Dog	humerus	49.2	17.2	3.3	-8.4	8.6
ED35	09CWET1310:1	Dog	humerus	48.2	17.5	3.2	-7.4	7.2
ED36	09CWEH71：5	Dog	humerus	41.4	14.5	3.3	-6.6	8.9
ED37	09CWEF54D：8	Dog	humerus	47.8	16.9	3.3	-6.9	9.0
ED38	09CWEF2：1	Roe deer	tibia	47.9	16.9	3.3	-17.9	6.1
ED39	09CWEF111SF：1	Roe deer	tibia	44.1	15.6	3.3	-17.4	6.3
ED40	09CWEF54s：44	Hare	femur	48.0	17.2	3.3	-18.0	5.0
ED41	09CWEF1s：7	Hare	femur	44.1	16.2	3.2	-20.0	7.4
ED42	09CWEF54s：32	Hare	femur	46.4	16.3	3.3	-19.7	5.1
ED43	09CWEF26s：5	Cattle	tibia	44.5	15.7	3.3	-16.7	6.9

3.2.2 Preparation and testing of collagen

The preparation of animal bone collagen from Erdaojingzi followed the protocol of Jay and Richards[85]. Bone surfaces were mechanically cleaned and abraded to remove adhering soil and potential contaminants. Approximately 2–3 g of compact cortical bone from each specimen were removed with a drill and placed in 50 ml beakers. Samples were decalcified in 30 ml of 0.5 M HCl at 4°C, with the acid solution replaced every two days until the bone became soft and no visible effervescence was observed. Decalcified samples were then rinsed repeatedly with deionised water until neutrality, soaked in 0.125 M NaOH at 4°C for 20 hours to remove humic acids, and again washed with deionised water to neutrality. The residue was subsequently gelatinised in 0.001 M HCl at 70°C for 48 hours. The hot solution was filtered to remove insoluble particles, and the filtrate containing soluble collagen was frozen and lyophilised for 48 hours to obtain purified collagen.

Carbon and nitrogen stable isotope analyses were carried out at the Testing Center of the Institute of Environment and Sustainable Development in Agriculture, Chinese Academy of Agricultural Sciences (CAAS), Beijing. Aliquots of freeze-dried collagen were weighed into tin capsules and analysed for C and N elemental composition and isotopic ratios using an Elementar Vario–Isoprime 100 continuous-flow isotope ratio mass spectrometer (Isoprime 100 IRMS coupled to an Elementar Vario elemental analyser). Sulfanilamide was used as the reference material for C and N elemental calibration. Carbon isotope ratios ($\delta^{13}C$) were calibrated against USGS24 CO_2 reference gas on the VPDB scale, and nitrogen isotope ratios ($\delta^{15}N$) were calibrated against IAEA-N-1 N_2 reference gas on the AIR scale. A laboratory collagen standard ($\delta^{13}C = -14.7 \pm 0.2‰$; $\delta^{15}N = 6.9 \pm 0.2‰$) was run after every ten unknowns to monitor analytical precision. The analytical reproducibility was better than ±0.2‰ for both $\delta^{13}C$ and $\delta^{15}N$. Isotopic values and collagen quality indicators are summarised in Table 4.

4 RESULTS

4.1 Ancient DNA analysis results

In this study, we generated genome-wide data from two ancient individuals from the Erdaojingzi site using a hybridisation capture approach to enrich endogenous DNA, followed by sequencing on an Illumina NovaSeq platform. Both individuals show characteristic patterns of post-mortem damage, confirming the authenticity of the ancient DNA. Estimates of contamination indicate no detectable autosomal contamination and mitochondrial DNA (mtDNA) contamination levels below 2%. Genetic sex determination shows that both individuals are male.

Haplogroup assignments based on Yleaf and inspection in IGV indicate that individual J30603 belongs to Y-chromosome haplogroup O2a1b1a1a1a1e1-Y15980/etc*, which is today frequent in eastern and northern China, whereas J12213 belongs to N1a3~-F1228, a lineage commonly observed among Han Chinese and other northern East Asian populations. Haplogrep2 assigns mtDNA haplogroups D4a1e to J30603 and D4a3 to J12213, both falling within northern East Asian clades.

Trimmed sequencing reads were mapped to the human reference genome (hs37d5; GRCh37), and pseudohaploid genotypes were called on two commonly used single nucleotide polymorphism (SNP) panels: the Affymetrix "Human Origins" (HO) array and the Illumina "1240k" panel[86][87]. Coverage on the 1240k panel is relatively high, with 562,025 sites covered in J30603 and 104,558 in J12213. These data were merged with previously published ancient and present-day genome-wide datasets for comparative analyses.

4.1.1 Overall genomic structure and affinities to Yellow River–related populations

Principal component analysis (PCA) using a reference panel of present-day East Asians provides an overview of the genetic affinities of the Erdaojingzi individuals. When projected onto the first two principal components, J30603 and J12213 fall among populations from the Yellow River Basin, especially those dating to the middle and late Neolithic periods (YR_MN, YR_LN and YR_LBIA). Along PC1, J30603 is slightly shifted towards present-day Northeast Asian populations relative to J12213. Both individuals plot close to previously published WLR_LN individuals from Erdaojingzi but show a small displacement towards Yellow River Basin groups (Fig. 5).

Consistent with these observations, outgroup-f_3 statistics indicate that both J30603 and J12213 share substantial genetic drift with WLR_LN, followed by populations from the Yellow River Basin (Fig. 5; Fig. S2).

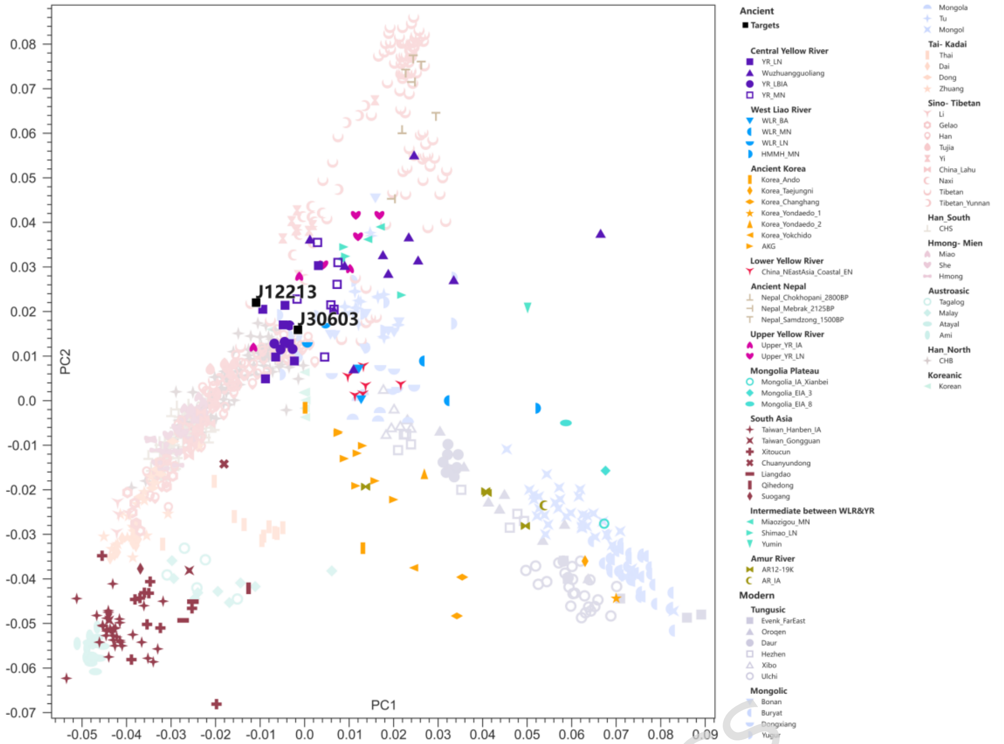

Fig. 5 Principal component analysis (PCA) of East Asian populations. Present-day individuals are shown as semi-transparent points; ancient individuals, including the two Erdaojingzi males, are projected onto the first two principal components.

In unsupervised ADMIXTURE analyses, the ancestry components of J30603 and J12213 closely resemble those of YR_LN and WLR_LN (Fig. S3). Their profiles are dominated by a component (shown in red) that reaches its highest frequency in Tibetan populations, together with a smaller component (violet) typical of southern East Asian groups. Individual J12213 also carries a trace amount of a component (yellow) most frequent in Yakutians. This subtle signal motivates further formal tests to evaluate whether additional gene flow from northern Northeast Asia is required by the data.

4.1.2 Genome-wide analyses and the extent of expansion of Yellow River–related populations during the Yangshao–Longshan period

To further investigate the ancestral composition of the Erdaojingzi individuals, we combined insights from PCA and ADMIXTURE with a series of f_4-statistics. We first examined tests of the form f_4(ANA, Mbuti; J30603, YR) and f_4(DevilsCave_N, Mbuti; J12213, YR_MN/YR_LBIA) (Fig. 6). For J30603, f_4(ANA, Mbuti; J30603, YR) yields Z-scores that are not significantly different from zero, indicating no strong evidence that J30603 shares more alleles with ANA-related groups than with Yellow River farmers under the tested models. In contrast, f_4(DevilsCave_N, Mbuti; J12213, YR_MN/YR_LBIA) produces significantly positive Z-values (> 3), suggesting that J12213 may share some additional affinity with DevilsCave_N-like ancestry relative to YR_MN/YR_LBIA.

To situate Erdaojingzi in a broader regional context, we next calculated f_4(Mbuti, reference; Erdaojingzi, X), where “reference” represents 45 ancient Eurasian populations and “X” includes WLR- and YR-related groups of similar age. The WLR-related populations comprise WLR_LN (from Erdaojingzi), WLR_BA (from Longtoushan) and WLR_BA_o2 (from Majiazishan), whereas the YR-related populations include Jinchankou, Lajia, Shengedaliang, Yangshaocun, Wadian, Haojiatai, Pingliangtai and Sanlihe. These tests show that the Erdaojingzi individuals share the highest affinity with

WLR_LN. A significantly positive f_4(Mbuti, AR_EN; Erdaojingzi, WLR_BA) with Z = 2.78 indicates that WLR_BA has additional ANA-related ancestry compared to Erdaojingzi. Similarly, significantly positive f_4(Mbuti, Taiwan_Hanben; Erdaojingzi, Haojiatai/Sanlihe) values ($Z > 2.41$) suggest that Haojiatai and Sanlihe harbour more southern East Asian–related ancestry than Erdaojingzi.

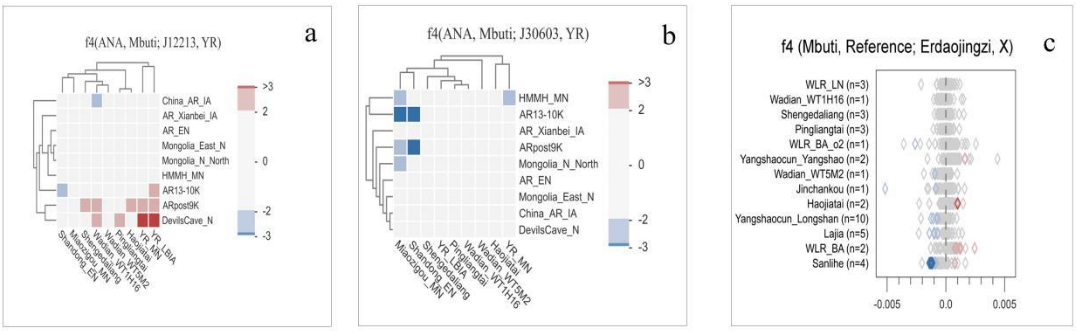

Fig. 6 f_4-statistics used to test for additional ancestry components in the Erdaojingzi individuals. Values of $|Z| \geq 3$ are shown in dark red or dark blue, and $2 \leq |Z| < 3$ in light red or light blue. (a) Results of f_4(ANA, Mbuti; J12213, Yellow River Basin groups). (b) Results of f_4(ANA, Mbuti; J30603, Yellow River Basin groups). (c) Results of f_4(Mbuti, reference; Erdaojingzi, X) illustrating the close genetic similarity between the Erdaojingzi individuals and Late Neolithic West Liao River populations.

We then used qpAdm to model the ancestry of East Asian populations dating to 4.0–3.5 ka BP (Fig. 7). Based on their admixture profiles, the tested groups can be divided into three broad categories. Group 1 comprises J30603, J12213, WLR_LN, WLR_BA_o2, Yangshaocun_Yangshao and Wadian_WT5M2. Under the tested set of sources and outgroups, these groups can be modelled as deriving their ancestry entirely from YR_MN, a middle Neolithic farming population from the central Yellow River Basin. Because previous analyses hinted at a possible ANA signal in J12213, we explicitly included ANA-related sources in the qpAdm outgroup set. In this framework, the single-source model with YR_MN provides an acceptable fit for J12213 ($p > 0.05$), whereas a two-source model with YR_MN and DevilsCave_N does not yield a valid solution (the coefficient for DevilsCave_N is smaller than its standard error). These results indicate that additional ANA-related ancestry is not required by our current data for J12213, although small contributions cannot be excluded given the limited coverage.

Group 2 includes WLR_BA, Jinchankou, Lajia, Shengedaliang and Yangshaocun_Longshan. These populations can be modelled as having 66.1–85.2% ancestry from YR_MN, with the remaining proportion attributed to ANA-related ancestry represented by DevilsCave_N. Group 3 consists of Wadian_WT1H16, Haojiatai, Pingliangtai and Sanlihe, which can be modelled as having 78–89.9% Yellow River–related ancestry and the remainder from southern East Asia, represented by Amis.

Overall, these results highlight substantial variation in the balance between Yellow River–related, ANA-related and southern East Asian–related ancestry components among Neolithic and early Bronze Age populations in the Yellow River and West Liao River basins during the Yangshao–Longshan period.

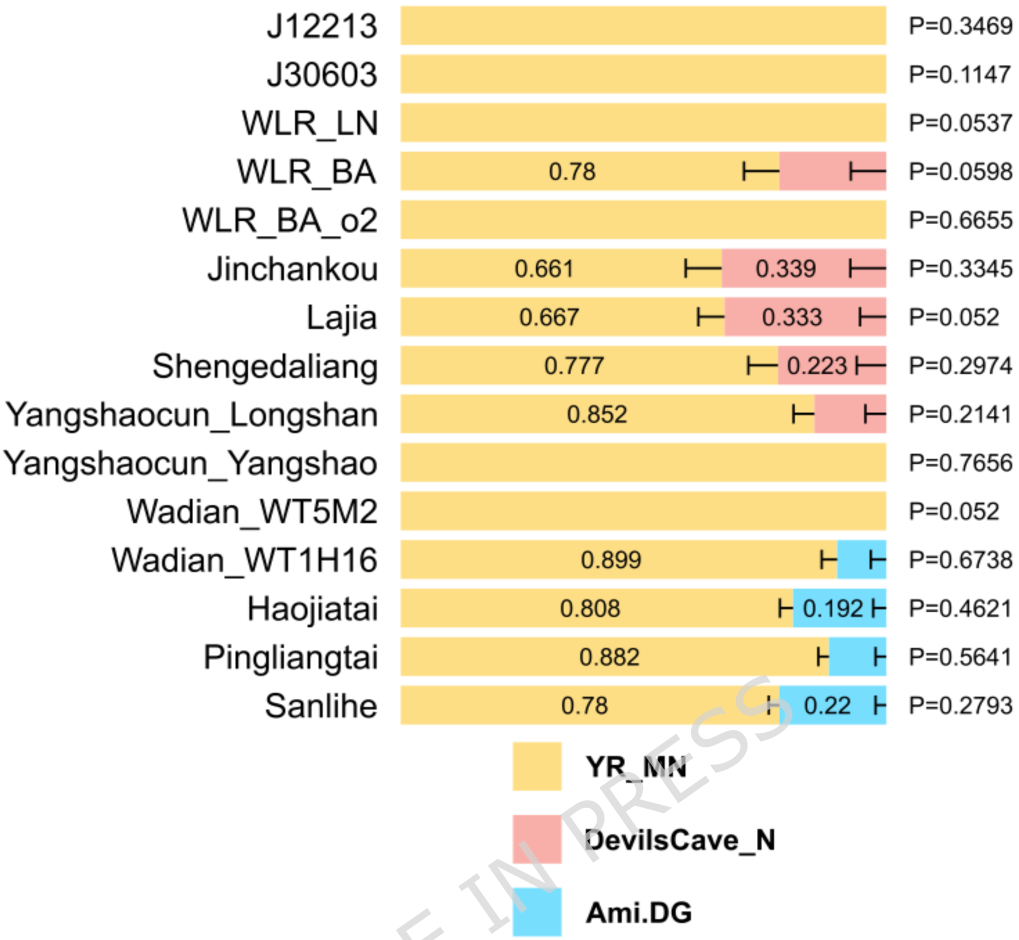

Fig. 7 Admixture compositions of Erdaojingzi populations and other reference groups via qpAdm. Error bars represent one standard deviation. A P-value larger than 0.05 indicating that there is not enough evidence to reject the null hypothesis.

4.2 Stable isotope results

4.2.1 Collagen preservation and quality control

Because of molecular alteration during burial, bone collagen can undergo varying degrees of degradation. At Erdaojingzi, the C content of animal bone collagen ranges from 41.4 to 49.5% (mean 46.7 ± 1.9%, n = 43) and N content from 14.5 to 17.8% (mean 16.7 ± 0.7%, n = 43). These values are comparable to those of modern bone and indicate good preservation. The C/N molar ratios fall between 3.2 and 3.3, with a mean of 3.3 ± 0.04 (n = 43), within the accepted range for well-preserved collagen[88][89][90]. Together, these indicators suggest that the samples are not significantly affected by exogenous contamination and are suitable for reconstructing pre-mortem dietary signals.

4.2.2 Animal dietary structure

The stable isotope compositions of animals provide direct evidence for livestock feeding practices and also reflect broader environmental conditions[91][92][93][94][95][96][97][98]. In this study, we measured $\delta^{13}C$ and $\delta^{15}N$ values for at least six taxa, grouped into wild animals (roe deer and hares) and domestic animals (pigs, dogs, sheep and cattle). The results are shown as scatter plots and error-bar diagrams in Figs. 8 and 9[99].

In general, the stable isotope values of wild herbivores such as hares and roe deer can be used to approximate the baseline for local wild vegetation, especially when these animals mainly consume natural plant communities dominated by C_3 species. C_3 plants typically exhibit low δ^{13}C values (−28.5‰ to −24.4‰, mean −27.5‰)[100]. At Erdaojingzi, hares have the most negative δ^{13}C values and the lowest δ^{15}N values (δ^{13}C = −19.3 ± 0.9‰, δ^{15}N = 5.8 ± 1.1‰, n = 3), indicating a varied diet largely based on C_3 plants, such as grasses and leaves. Roe deer (δ^{13}C = −17.9‰ to −17.4‰, mean −17.7 ± 0.2‰, n = 2) and cattle (δ^{13}C = −16.7‰, n = 1) show slightly higher δ^{13}C values than hares, but still fall within the C_3-dominated range. A δ^{13}C value higher than about −18‰ may indicate some consumption of C_4 plants [101][102]. The δ^{15}N values of roe deer (6.1–6.3‰, mean 6.2 ± 0.6‰, n = 2) and cattle (6.9‰) are slightly higher than those of hares but remain within the typical herbivore range.

Taken together, the mean δ^{13}C and δ^{15}N values of wild animals and herbivores suggest that the vegetation surrounding the Erdaojingzi site during the period of occupation was predominantly composed of C_3 plants.

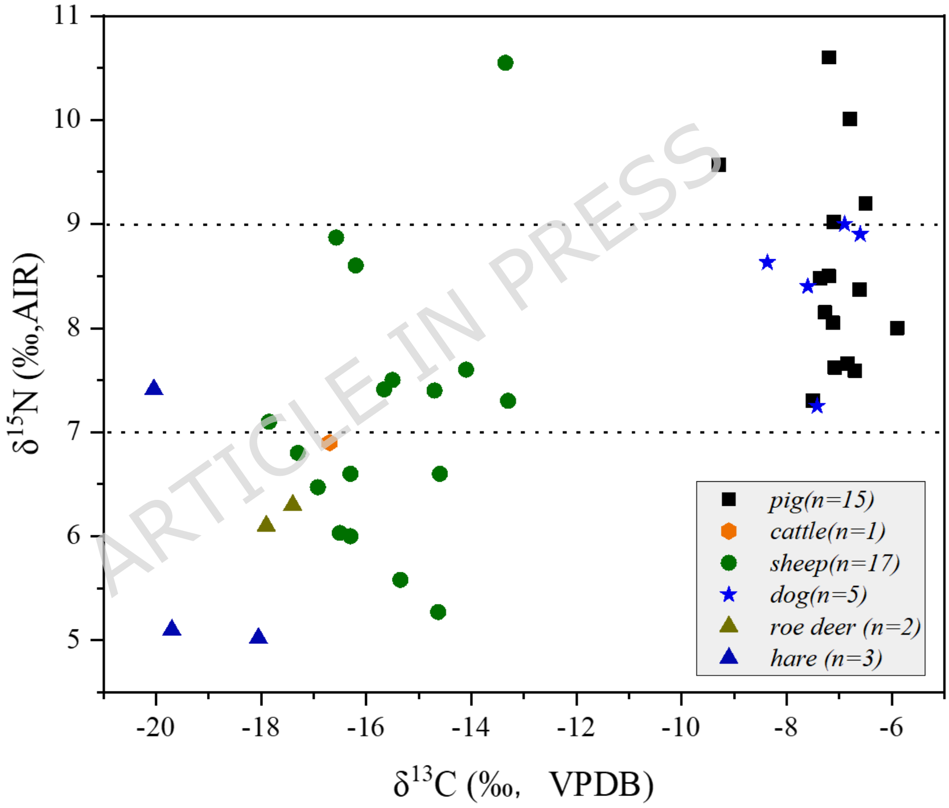

Fig. 8 Scatter plot of bone collagen δ^{13}C and δ^{15}N values for animals from the Erdaojingzi site.

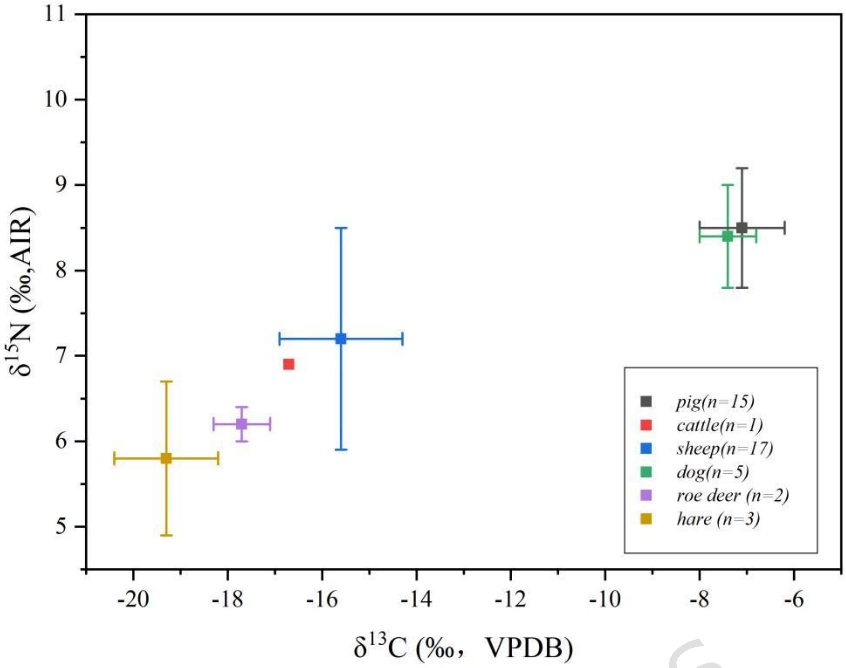

Fig. 9 Error-bar plot of animal bone collagen $\delta^{13}C$ and $\delta^{15}N$ values from Erdaojingzi.

Sheep exhibit $\delta^{13}C$ values ranging from −17.9‰ to −13.3‰ (mean −15.6 ± 1.3‰, n = 17), indicating the consumption of both C_3 and C_4 plants. The C_3 component likely derived from natural vegetation, surplus human food and agricultural by-products, reflecting their management as domestic animals. Their $\delta^{15}N$ values range from 5.3‰ to 10.6‰ (mean 7.2 ± 1.3‰, n = 17), which are generally higher than the typical herbivore range of 3–7‰[103][104]. Notably, one adult sheep (ED31) has a $\delta^{15}N$ value of 10.55‰, suggesting a particularly complex or protein-rich diet.

Domestic pigs have $\delta^{13}C$ values between −9.2‰ and −5.9‰ (mean −7.1 ± 0.7‰, n = 15), and domestic dogs between −8.4‰ and −6.6‰ (mean −7.4 ± 0.6‰, n = 5). Both taxa show substantially higher $\delta^{13}C$ values than the wild animals, indicating a strong reliance on C_4 plants under human management (Hou, 2019). The $\delta^{15}N$ values of pigs range from 7.3‰ to 10.6‰ (mean 8.5 ± 0.9‰, n = 15) and are slightly higher on average than those of dogs (7.3–9.0‰, mean 8.4 ± 0.6‰, n = 5), implying that pigs may have consumed somewhat more animal-derived or otherwise protein-rich resources.

Two human bone samples yielded reliable isotopic measurements (Table 1). Human $\delta^{13}C$ values range from −6.7‰ to −5.9‰ (mean −6.3 ± 0.4‰, n = 2), consistent with diets primarily based on C_4 plants. Human $\delta^{15}N$ values range from 9.5‰ to 10.0‰ (mean 9.8 ± 0.3‰, n = 2), indicating that the main protein sources came from terrestrial food webs[105].It should be acknowledged that although the human and faunal stable isotope data were generated by different laboratories, the pronounced C_4 isotopic signal observed in the human samples is sufficiently robust that minor inter-laboratory variation would not affect the overall interpretation. Nevertheless, this factor is taken into consideration when evaluating fine-scale dietary differences.

In summary, the stable isotope signatures of terrestrial wild animals indicate that the local ecosystem around Erdaojingzi was dominated by C_3 vegetation. In contrast, domestic pigs and dogs, whose diets were strongly shaped by human management, show markedly different isotope values, reflecting substantial consumption of C_4 plants closely linked to the development of millet agriculture.

5 DISCUSSION

5.1 Adaptation of agricultural populations' livelihood strategies to the steppe environment at the Erdaojingzi site

Ancient DNA and stable isotope analyses suggest that the two individuals analysed from the Erdaojingzi site are genetically closest to farming populations in the Yellow River Basin and that, on the basis of the currently available data, the community practised a millet-based mixed farming and herding economy (Fig. 2). Rather than representing a purely agricultural system, the evidence indicates that the inhabitants of Erdaojingzi maintained key elements of an agricultural subsistence strategy while at the same time expanding livestock husbandry and increasing the contribution of animal protein to their diet. In this sense, Erdaojingzi provides a case study of how farming communities with Yellow River related ancestry organised their livelihoods in a steppe setting. The main aspects of this adaptive strategy are outlined below.

5.1.1 Increasing sheep and cattle while pigs remained the primary domestic animal

Archaeobotanical and faunal evidence show that the inhabitants of the Erdaojingzi site made use of both cultivated fields and surrounding grasslands, combining elements of farming and herding. Plant remains indicate a dietary pattern comparable to that of the Central Plains, in which C_4 crops, especially broomcorn and foxtail millet, played an important role in human food and in livestock fodder. In terms of animal husbandry, the inhabitants of the Erdaojingzi area primarily raised domestic pigs and dogs (pigs: 49.9% of NISP; dogs: 6.6% of NISP), while also keeping substantial numbers of cattle (23.3% of NISP) and sheep (14.4% of NISP). This pattern suggests that pigs and dogs remained central to household economies, as in many Yellow River farming communities, but that cattle and sheep were more heavily emphasised at Erdaojingzi than at many contemporaneous sites in the Central Plains. This greater reliance on herd animals is consistent with higher investment in grazing livestock in a steppe environment.

5.1.2 Isotopic variation among sheep and possible soil fertilisation practices

Sheep at the Erdaojingzi site show a broad range of δ^{13}C and δ^{15}N values (Figs. 8 and 9). In particular, the relatively high and variable δ^{15}N values in the flock may be related, at least in part, to soil fertilisation practices.

China has a long history of using manure and other organic materials to improve soil fertility[106]. Early agricultural texts from the pre-Qin period describe methods for enhancing soil through fertilisation, and archaeological evidence suggests that pig manure composting can be traced back at least to the Yangshao Culture (ca. 5500 BP)[107]. Experimental studies show that the mean δ^{15}N values of plants grown on unmanured and organically manured plots are 3.6 ± 0.6‰ and 4.4 ± 0.8‰, respectively, indicating significantly elevated δ^{15}N in millet fertilised with pig manure[108]. Herbivores that consume such millet and its by-products are therefore expected to show higher δ^{15}N values in their bone collagen[109].

In this context, the elevated δ^{15}N values observed in sheep at Erdaojingzi are consistent with, but do not on their own demonstrate, the use of pig manure and other organic fertilisers in some fields. Comparisons of average δ^{13}C and δ^{15}N values for rabbits (−19.3 ± 0.9‰, 5.8 ± 1.1‰, n = 3) and roe deer (−17.7 ± 0.2‰, 6.2 ± 0.6‰, n = 2) at Erdaojingzi with those of rabbits (−17.7‰, 4.4‰, n = 1) from Haminmangha (3600–3100 BC)[110] and deer (−20.8‰, 2.1‰, n = 1) from Xinglonggou[111] also suggest an upward trend in δ^{15}N values through time.

However, δ^{15}N values in herbivores can also be influenced by other factors, including differences in grazing locations, corralling in dung-enriched areas, access to stored fodder, local microenvironments and animal physiology. To test the manuring hypothesis more directly, future work should include isotopic analysis of charred millet grains and other plant remains from Erdaojingzi, together with larger comparative data sets for wild herbivores and domestic sheep from neighbouring sites.

5.1.3 Isotopic differences among pigs and implications for human diet

Published isotopic data for agricultural populations from the Central Plains region indicate traditional dietary patterns characterised by relatively enriched carbon values and lower δ^{15}N values. Typically, δ^{15}N values for these populations fall within the omnivore range of 7 to 9‰ and rarely exceed 9‰. In contrast, the two individuals analysed from Erdaojingzi show higher δ^{15}N values (9.75 ± 0.3‰, n = 2), which may indicate a greater contribution of animal protein to their diet. This interpretation is broadly consistent with the abundance of animal bones found at the site (NISP = 1178, MNI = 106) and with evidence for the consumption of young pigs. Stable isotope analysis reveals that the primary diet of the pigs consisted of C_4 plants, particularly millet and its by-products. The elevated δ^{15}N values observed in the pig group indicate that millet-based foods were directly incorporated into their diet, with human leftovers likely contributing significantly as well[112].

Figures 10 and 11 show that the δ^{13}C values within the pig group are relatively homogeneous, whereas δ^{15}N values exhibit considerable variation. Examination of the pig bone samples indicates that Group A (Fig. 10a) and Group B (Fig. 10b) comprise piglets, whereas Group C (Fig. 10c) consists of adult pigs. The isotopic results for Groups A (−7.1 ± 1.5‰, 8.9 ± 0.7‰, n = 3), B (−7.0 ± 0.2‰, 10.3 ± 0.3‰, n = 2) and C (−7.1 ± 0.3‰, 8.1 ± 0.5‰, n = 10) indicate that Groups A and B have higher δ^{15}N values, which are typically associated with suckling and lactation[113][114]. Notably, Group B exhibits the highest δ^{15}N values among all groups. Analysis of the ages at death suggests that Group B (over six months old) was still strongly influenced by suckling and the associated bone-turnover effects, despite the older average age at death compared to Group A (under six months). In contrast, Group C, approaching 18 months old, was likely fed a typical omnivorous diet similar to that of domestic pigs in North China.

Fig. 10 Carbon and nitrogen isotope values of pig bone samples from Erdaojingzi. The pigs can be divided into three age-at-death groups based on epiphyseal fusion: (a) Group A, unhealed epiphyses,

thin metaphyses, more slender bones; (b) Group B, unhealed epiphyses, thinnest diaphyses, slenderest bones; (c) Group C, healed epiphyses.

Additionally, we analysed the mortality patterns of domestic pigs from the Erdaojingzi site, focusing on 97 specimens for which the age at death was identifiable. The ages at death were distributed as follows: 1–8 months (7.2%), 8–14 months (15.5%), 18–24 months (51.6%), 25–36 months (24.7%) and over 42 months (1.0%). Nearly a quarter of the pigs died before 14 months of age (Fig. 11).

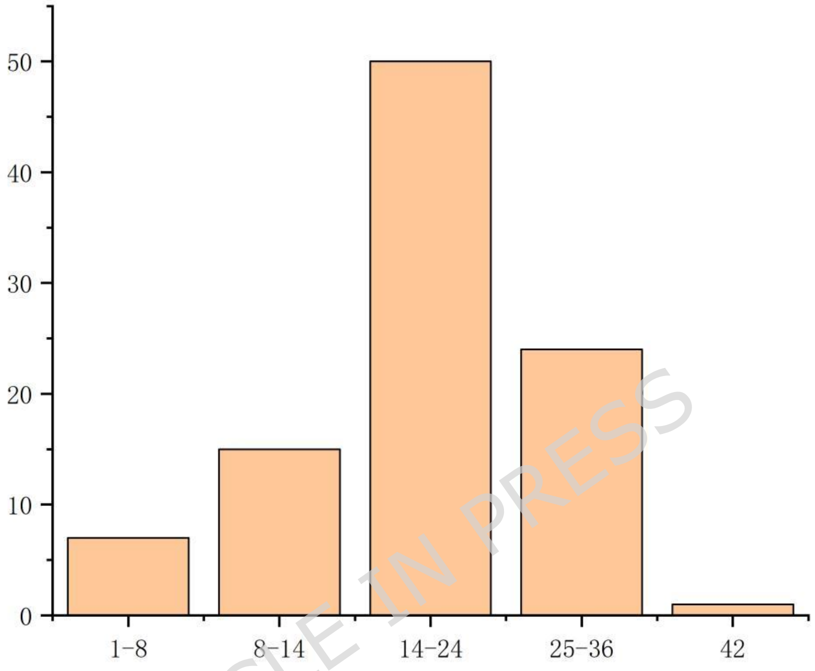

Fig. 11 Age-at-death distribution of domestic pigs from Erdaojingzi.

Generally, young pigs have a high growth potential for meat production, but the economic returns from slaughtering them are relatively low[115]. In many agricultural societies where pigs are typically raised for up to two years, there is therefore a tendency to avoid slaughtering piglets in favour of maximising economic efficiency[116]. The age-at-death pattern of pigs at Erdaojingzi, with slaughter occurring across a broad age range and including a non-negligible proportion of younger animals, suggests a relatively flexible management strategy rather than a narrow focus on optimising carcass weight. Such flexibility may in part reflect the integration of pig husbandry into a wider mixed farming and herding economy and the need to accommodate the ecological and economic conditions of a steppe environment.

In summary, the inhabitants of Erdaojingzi appear, on current evidence, to have adapted to a grassland setting by retaining core elements of an agricultural economy while expanding livestock herding and increasing the contribution of animal protein to their diet. After moving into the grassland zone, farming communities applied cultivation, animal management and possibly manuring practices familiar from agricultural regions, but also developed forms of pastoral exploitation suited to local ecological conditions. Their mixed farming and herding livelihood strategy thus illustrates an active process of adjustment to, and modification of, the surrounding environment.

5.2 A comparative study of differentiated subsistence strategies across geographic regions characterised by population genetic structure

We compiled data from archaeological sites in different regions of China dating to around 4000 BP, with a particular emphasis on sites where genetic profiles are dominated by ancestry related to agricultural populations. These include locations in the upper Yellow River region, such as Jinchankou, Lajia, Muzhuzhuliang and Shimao, as well as sites in the middle Yellow River region, including Wadian, Pingliangtai and Yangshaocun in Henan Province. In this section, we synthesise published ancient DNA (aDNA) results together with information on plant and animal resource use and human bone isotope ratios in order to explore regional similarities and differences in subsistence strategies.

5.2.1 aDNA reveals expansion patterns of YR-related populations

Previous research has shown that populations associated with millet farming in the Yellow River Basin of northern China expanded widely during the Neolithic period. Genetic and archaeological evidence indicate that ancestry related to these communities spread southeast along the coast towards Fujian and the Taiwan Strait, moved inland towards Guangxi in the south and extended along the "Tibetan–Yi Corridor" onto the Tibetan Plateau, often in parallel with the dispersal of millet agriculture. During the transition from the Yangshao Culture to the Longshan Culture in the Yellow River Basin, these farming populations also received continuous genetic input from southern groups, probably linked to the northward spread of rice cultivation[117][118][119][120][121][122].

In the post-Neolithic period, ancestry components associated with northern East Asian populations became increasingly prominent in many parts of East Asia, reflecting complex patterns of mobility and interaction, including southward movements of northern groups. Within this broader context, genome-wide analyses suggest that the two individuals from the Erdaojingzi site share close genetic affinities with farmers in the Yellow River Basin of the Central Plains. This indicates that farming communities carrying Yellow River–related ancestry had reached the West Liao River region in northeastern China by around 4000–3500 years before present.

Modelling of population structure at broadly contemporaneous sites using qpAdm reveals marked regional variation. As communities with Yellow River–related ancestry expanded southwards and towards the lower reaches of the Yellow River, they admixed with local groups, resulting in substantial southern East Asian–related components in the genetic profiles of sites such as Haojiatai, Pingliangtai and Sanlihe. In contrast, sites in the upper reaches of the Yellow River Basin, such as Lajia, Jinchankou and Shengedaliang, commonly require additional ancestry related to ancient northern East Asian populations (ANA) in order to obtain good-fitting models. Under the set of sources and outgroups tested in this study, the two Erdaojingzi individuals can be adequately modelled as deriving their ancestry from a single source related to Yellow River Middle Neolithic farmers, without the need to invoke extra ANA or southern East Asian components. Given the very small sample size, however, limited admixture with local groups cannot be excluded. This genetic pattern is consistent with archaeological observations that the material culture at Erdaojingzi shows strong similarities to contemporary Central Plains traditions and contrasts with that of neighbouring northern steppe-related cultures (Fig. 12a).

When viewed together with previously published data, the ancestry profiles of the Erdaojingzi individuals differ from those of Middle Neolithic populations in the West Liao River Basin that carried more pronounced ANA-related components. This suggests that the Erdaojingzi community was unlikely to have been a simple, direct continuation of earlier local groups. Possible demographic scenarios include the arrival of farming communities with Yellow River–related ancestry, admixture between such groups and resident populations, or more complex multi-phase processes. At present, the limited number of individuals available from Erdaojingzi and neighbouring sites does not allow these possibilities to be distinguished, and further sampling will be required to clarify the detailed population history of the region.

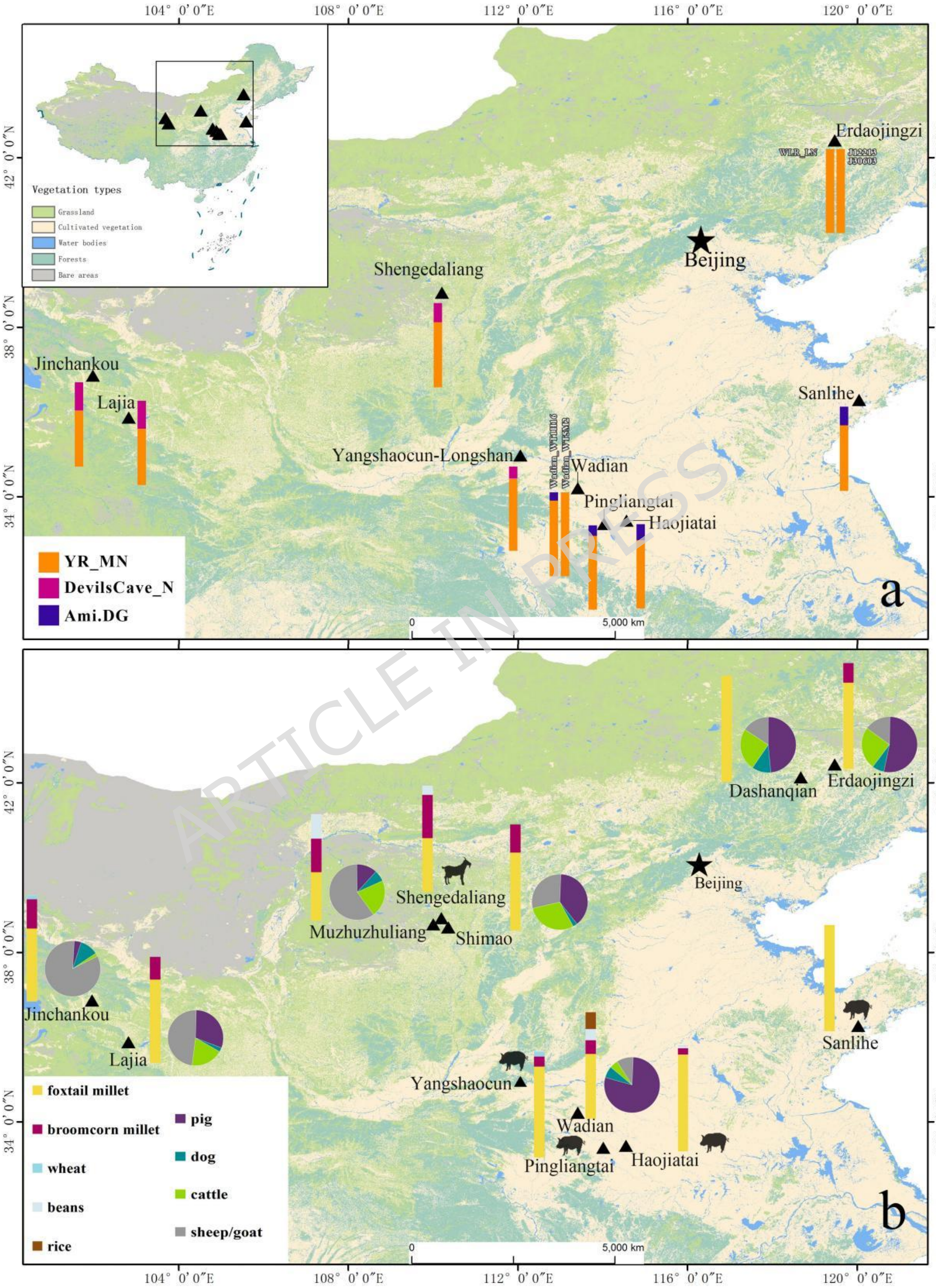

Fig. 12 a: Schematic representation of expansion patterns of Yellow River–related populations across different regions between 4.2 and 3.5 ka BP. **b**: Relative proportions of plant (left) and animal (right) resources used by agricultural populations at selected sites. Dark icons for pigs and sheep denote sites where these taxa dominate the assemblage, but detailed faunal quantification is not available. Base map derived from the Standard Map of the Ministry of Natural Resources of the People's Republic of China (Map Approval No. GS(2024)0650). Generated using ArcGIS 10.8 (ESRI, https://www.esri.com/). Archaeological site locations were added by the authors.

5.2.2 Utilization of animal and plant resources

We also compiled and analysed published research on patterns of plant and animal utilisation among agricultural communities in northern China, focusing on the agro-pastoral transition zone (Fig. 12b). This allows us to explore both shared features and regional contrasts in resource use.

Qualitative and quantitative analyses of animal bones indicate that pigs were the predominant domestic animal in the Central Plains, with pig bones significantly outnumbering those of other species[123] . In the Erdaojingzi area, the overall pattern of animal utilisation broadly resembles that of the Central Plains: pigs account for 49.9% of identified specimens (NISP), followed by cattle at 23.3% and sheep at 14.4%. A similar pattern is observed at the Dashanqian site. In contrast, at the Shengedaliang site, located in the upper reaches of the Yellow River in the Shaanxi–Gansu region, sheep are the primary domestic animals (56.7% of NISP), followed by cattle (20.6%) and pigs (11.3%)[124][125][126]. A comparable trend is seen at the Jinchankou site, where sheep account for 30% of the identified individuals (MNI = 20)[127]. These divergent patterns indicate differences in animal husbandry strategies among agricultural populations in different geographic units, with a stronger emphasis on grazing livestock in the upper Yellow River region and the Shaanxi–Gansu corridor, consistent with a greater degree of engagement with herding economies in the northwest.

Archaeobotanical analyses show that foxtail millet and broomcorn millet were the dominant crops across all sites; however, the Central Plains exhibit the greatest diversity of crop species[128]. Notably, the Wadian and Pingliangtai sites show the highest variety, including foxtail millet, broomcorn millet, beans, wheat and rice. Even so, the proportions of wheat and rice remain relatively low, and individual assemblages show some variability. For instance, at the Wadian site, rice accounts for 61.9% and wheat for 4.3% of identified grains, whereas at Pingliangtai wheat reaches 62.1%, underscoring spatial and contextual differences in the presence of these crops[129]. In contrast, the primary crops in Shaanxi, Gansu and Inner Mongolia are predominantly foxtail millet and broomcorn millet, with only occasional beans[130]. A closer examination of the ratios suggests that the ubiquity or relative proportions of foxtail and broomcorn millet at Shengedaliang (foxtail millet 36.2%, broomcorn millet 32.2%) and Muzhuzhuliang (foxtail millet 68.9%, broomcorn millet 67.4%) are lower than those in the Erdaojingzi region (foxtail millet 100%, broomcorn millet 92.2%). On this basis, millet cultivation at Erdaojingzi appears relatively well developed compared to other roughly contemporaneous sites in surrounding grassland regions[131][132][133].

These variations in crop types and animal-usage patterns illustrate the ways in which agricultural populations adjusted their subsistence systems to local environmental and social conditions. The adaptation of the Erdaojingzi community to a steppe environment provides one example of how agricultural societies could reorganise their economies following migration, and offers a useful comparative case for studying similar instances of environmental adaptation. Rather than endorsing environmental determinism, we seek to integrate natural geographical settings with archaeological and genetic evidence in order to highlight the flexibility and resilience of agricultural populations, as reflected in their diverse patterns of animal and plant resource utilisation across different regions.

5.2.3 Isotopic evidence from human bones

Due to the limited availability of human skeletal material from the Erdaojingzi site, we obtained only two reliable isotopic measurements (Table 1). Isotopic data from these two individuals, together with published results from related sites (Fig. 12), are summarised in Table 5 and plotted in Fig. 13.

Table 5 Summary of human bone collagen δ^{13}C and δ^{15}N values from Erdaojingzi and comparative sites.

site	n	δ^{13}C±SD(‰)	δ^{15}N±SD(‰)	Reference
Erdao	2	-6.3±0.4	9.8±0.3	This study
Dashanqian	9	-7±0.4	9.4±0.5	[134]
Shengedaliang	28	–8.5±1.8	8.8±1.4	[135]
Muzhuzhuliang	7	-8.2±1.5	7.7±0.8	[136]
Lajia	4	-7.9±0.4	9.99±0.17	[137]
Jinchankou	2	-10.3±1.2	8.9±0	[138]
Haojiatai	11	-13.1±4.6	9.3±1.1	[139]
Pingliangtai	8	-8.7±1.1	9±0.9	
Wadian1	9	-9.9±0.7	7.5±0.5	[140]
Wadian2	3	-14.3±0.8	10.2±0.3	
Taosi	17	-6.8±1.3	7.5±0.6	[141]
Xinzhai	11	-8.5±1.3	6.2±0.9	[142]
Erlitou	22	-10.4±2.7	7.3±1.2	[143]

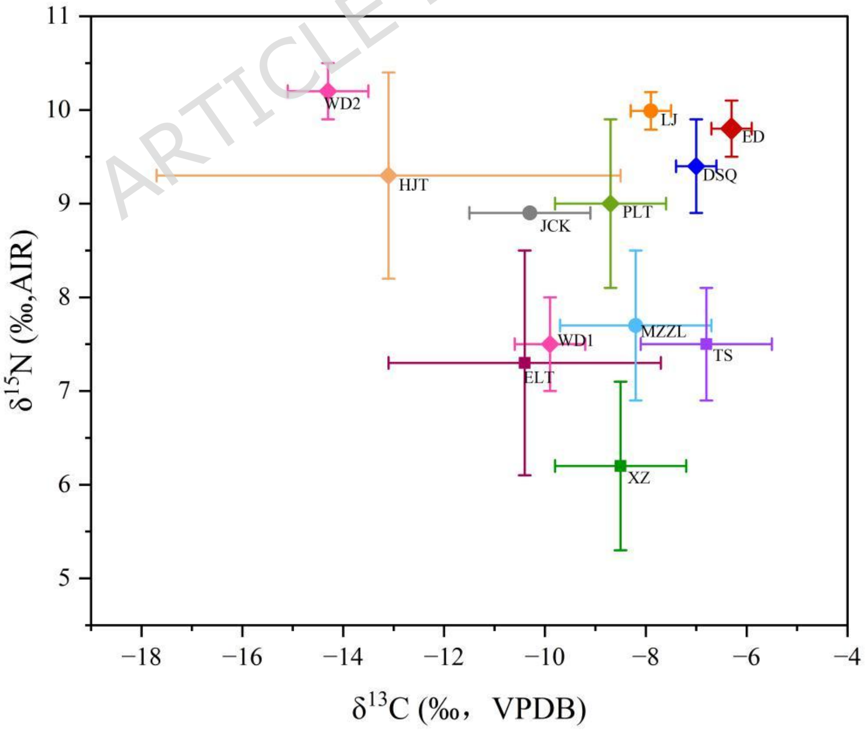

Fig. 13 Error-bar plot of human bone collagen δ^{13}C and δ^{15}N values from Erdaojingzi (ED) and comparative sites. Comparative sites include Dashanqian (DSQ), Shengedaliang (SGDL), Lajia (LJ),

Jinchankou (JCK), Muzhuzhuliang (MZZL), Haojiatai (HJT), Pingliangtai (PLT), Wadian (WD1, WD2), Taosi (TS), Xinzhai (XZ), and Erlitou (ELT). Abbreviations correspond to labels shown in the figure.

Overall, the sampled populations primarily consumed C_4 plants, consistent with diets based on millet agriculture, and relied mainly on terrestrial domestic animals as sources of animal protein (Fig. 13). Human isotopic data from Shaanxi, Gansu and Inner Mongolia cluster in a range suggesting a strong reliance on C_4 plants and relatively elevated $\delta^{15}N$ values, which may reflect higher intakes of animal protein[144]. In the Yellow River Basin, the presence of rice and wheat in archaeobotanical assemblages points to more varied and regionally complex dietary patterns[145]. For example, at the Wadian site, isotopic data suggest two broad dietary regimes: one group with a predominantly agricultural diet based almost entirely on C_4 plants (enriched $\delta^{13}C$ values and $\delta^{15}N < 7‰$), and another group with a mixed C_3–C_4 diet and higher $\delta^{15}N$ values ($> 10‰$), possibly reflecting differences in livelihood strategies or social roles[146][147]. At Jinchankou and Lajia in the upper Yellow River, isotopic variability may in part be related to the introduction of C_3 wheat into local cropping systems.

In summary, around 4000 years ago, populations with ancestry related to Yellow River farmers were distributed across the upper, middle and lower reaches of the river, as well as the West Liao River region. While there was a broad common pattern in plant and animal resource use, like foxtail millet and broomcorn millet forming the staple crops, and pigs, cattle and sheep constituting the main domestic animals, the relative proportions of these resources varied between geographic areas. Broomcorn millet, being more drought-tolerant, tended to be more important in the upper and some parts of the middle Yellow River, whereas foxtail millet was more commonly used in the lower reaches and in the West Liao River region. In terms of animal husbandry, cattle and sheep were relatively more prominent in the upper and some middle reaches, consistent with more extensive herding in the northwest. By contrast, in the West Liao River region and the traditional Central Plains of the middle Yellow River, pigs generally formed the primary livestock. These differentiated patterns of plant and animal use are reflected in human isotopic signatures and highlight the close relationship between resource utilisation strategies and the development of dietary practices. Together, they provide insights into how ancient populations organised their livelihoods and adapted to diverse landscapes within a broadly shared agricultural tradition.

6 CONCLUSIONS

Drawing on the available ancient DNA and stable isotope data from human and animal bones at the Erdaojingzi site, together with zooarchaeological and archaeobotanical evidence, we draw the following conclusions:

(1) Ancient DNA results suggest that the two individuals from Erdaojingzi are genetically closest to farming populations in the Yellow River Basin. This implies that farming communities carrying Yellow River–related ancestry had reached the agro-pastoral transition zone of the West Liao River region by ca. 3700–3330 cal BP. Stable isotope and zooarchaeological evidence is consistent with a millet-based mixed farming and herding economy at the site: pigs and dogs relied mainly on C_4 plants, whereas sheep and cattle made use of both C_3 and C_4 plants.

(2) After entering a steppe environment, the inhabitants of Erdaojingzi appear, on current evidence, to have maintained traditions of millet cultivation and pig husbandry while expanding the use of cattle and sheep. Archaeobotanical and isotopic results indicate that drought-tolerant millets such as broomcorn and foxtail millet remained important staple foods. Zooarchaeological and isotopic data further point to

differentiated management strategies for pigs, dogs, sheep and cattle, reflecting the integration of familiar agricultural practices with forms of livestock herding suited to local ecological conditions.

(3) From the upper, middle and lower reaches of the Yellow River Basin to the West Liao River region, there is a broad common pattern in plant and animal use, with millets such as broomcorn and foxtail millet and domestic pigs, cattle and sheep forming key resources. Regional differences lie chiefly in the relative importance of these resources and in specific management practices. Within this wider framework, Erdaojingzi provides a case study of how farming communities carrying Yellow River–related ancestry adjusted and reorganised their economic practices after entering an agro-pastoral frontier zone. At the same time, the limited and uneven nature of current datasets highlights the need for further aDNA, isotopic and archaeobotanical work in order to refine this comparative picture.

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DECLARATIONS OF INTEREST

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

DATA AVAILABILITY STATEMENT

The raw alignment file (in BAM format) can be accessed publicly at the Genome Warehouse in the National Genomics Data Center, Beijing Institute of Genomics (part of the China National Center for

Bioinformation), under the Chinese Academy of Sciences. The data set will be catalogued under the Accession Number: HRA010456 and can be retrieved from https://bigd.big.ac.cn/gsa-human/. The other original contributions presented in the study are included in the article.

AUTHOR CONTRIBUTIONS

Xiaohong Lv: Formal analysis, Methodology, Data curation, Visualization, Writing - original draft, Writing - review & editing. **Yao Yu:** Formal analysis, Methodology, Data curation, Visualization, Writing - original draft, Writing - review & editing. **Lin Ban:** Formal analysis, Methodology, Data curation, Visualization, Writing - original draft, Writing - review & editing. **Panxin Du:** Formal analysis, Data curation, Visualization, Supervision, Writing - review & editing. **Jianxue Xiong** Validation**, Xin Chang:** Validation. **Baoshuai Zhang:** Validation. **Bangyan Wang:** Validation. **Yiran Xu:** Validation. **Chunxue Wang:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Writing - original draft, Writing - review & editing. **Jianen Cao:** Investigation, Methodology, Resources, Writing - review & editing. **Shaoqing Wen:** Conceptualization, Formal analysis, Methodology, Visualization, Validation, Writing - review & editing.

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