SRYAHWA PUBLICATIONS

Annals of Archaeology
ISSN: 2639-3662 | Volume 5, Issue 1, 2023
https://doi.org/10.22259/2639-3662.0501003

RESEARCH ARTICLE

Millet Diffusion and Subsistence Diversification in Late Neolithic Central China: Perspective from Archaeological, Archaeobotanical, Stable Isotopic and Genetic Evidences

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Received: 10 May 2023 Accepted: 20 May 2023 Published: 29 May 2023

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Abstract

The origin and spread of agriculture, accompanied with development and movement of populations, played an important role in human prehistory. China is one of the earliest centers for the origins of agriculture parallel to the Near East, with millets in the north and rice in the south. Recent studies showed the spread and intensification of millet not only made a significant role for the occurrence of the early civilizations in the Yellow River (YR) regions of northern China, but also left extensive impact on nearby islands as well as the Eurasia steppe. Here we trace the dispersal of millets farming in the Central Plains of the YR by using interdisciplinary research combing the archaeological, archaeobotanical, stable isotopic and genetic evidences in the literature. Two stages of millets subsistence were identified with broomcorn millet first appeared almost simultaneously across a wide range of northern China, by around 6,000 years ago (during the Yangshao period) foxtail millet gradually replaced broomcorn millet and finally became the dominant cereal food there. Our results also suggest that the dispersal and intensification of foxtail millets might be driven by large-scale population expansions from the YR, and that the growing proportion and intensification of rice farming in the Late Neolithic Longshan populations in the YR regions was in parallel with population genetic contribution from South China, showing that the northward dispersal of rice farming was combined with population movement.

Keywords: Foxtail millet, Ancient DNA, Archaeobotanical, Agricultural Dispersals

1. Introduction

China is one of the main centers in the world for the earliest cultivation of cereal crops, including millets in the YR and rice in the Yangtze River,both of which were first domesticated at around 9,000-10,000 years before present (BP) and then spread across most part of China during the past millenniums. The Central

Citation: Hai Zhang, et al. Millet Diffusion and Subsistence Diversification in Late Neolithic Central China: Perspective from Archaeological, Archaeobotanical, Stable Isotopic and Genetic Evidences. Annals of Archaeology. 2023; 5(1): 18-27.

Plains of China (CPC), including areas surrounding the Songshan Mountains in Henan province, the southern part of the Shannxi province as well as the Guanzhong basin in Shanxi province were the areas where the two types of crops coexisted and were traditionally considered as a mixed farming zone of millet and rice[1–4] (Figure 1A). The up-to-now earliest known evidence of foxtail (Setaria italica) and broomcorn (Panicum miliaceum) millets cultivations were discovered in northern China (e.g. Donghulin in Beijing [5], Xionglongwa in Inner Mongolia[6,7], which the former is more prevalent in present-day northern China and with a better taste. In contrast, the latter is more adaptive to dry and cool environment and is geographically distributed in higher latitude areas nowadays.

Figure 1. *The distribution of rice and millets agriculture and potteries in China during the Neolithic.A) The distribution of rice and millets in China during the Neolithic; B) Earliest archaeological sites where the earliest millet was discovered; C) A comparison of archaeological excavations from different archaeological cultures.*

The earliest domestication of millet from wild foxtail seed was originated from the gathering of Gramineae plant seeds in the Late Paleolithic since the last glacial period as a supplement to the hunting and gathering subsistence. Archaeologically, both phytolith and starch grain evidences indicated a wide range of Gramineae plant seed gatherings as a broad spectrum of subsistence in northern China[8]. At about 9,000 to 8,500 BP, millet (including both foxtail and broomcorn) was discovered almost simultaneously at several Neolithic archaeological sites in northern China, including Dadiwan in the upper reach of the YR, Peiligang/Cishan in the CPC and the Xinglongwa in northeastern China. Geographically, these sites are mainly located at the edge of East Asian Monsoon, which suggests that those first or maybe the earliest domestication of millet might be the result of global environmental change to a warmer weather since the transition from the early to the mid-Holocene[9].

The earliest cultivation of millet was mainly broomcorn millets with little or no foxtail millet discovered, probably reflect the unmatured millets farming systems at the early stage of domestication. Both archaeobotanical and faunal evidences showed that millet cultivation was just served as a supplementary to their main hunting-gathering way of life[10]. This is also the case for the early rice cultivation, such as in Jiahu site diverse food resources were found coexisted with primitive rice farming[11]. However, roughly two or three millenniums later, a significant shift of millet cultivation from the low-level productive of broomcorn millet to a more intensive foxtail millet as the staple cereal crop[12]. Faunal records in the upper and middle reaches of YR all revealed a similar stable isotopic pattern of animal foxtail millet consumptions, which the majority of live stock domesticated were pigs and dogs, with a certain numbers of hunting deer[13]. Although the process, mechanism and accurate time on when this shift or new stage of millet domestication indeed happened are still opaque in archaeology now, such great shift with the wide spread of foxtail millet subsistence had left significant impact on development of the Chinese prehistoric cultures. Particularly in the YR from the Late Neolithic Yangshao to Longshan Periods[9,14].

In addition to the change of crops associated with the spread of foxtail millets, painted pottery, the main character of the Yangshao Culture, were well developed almost simultaneously. It is also noticeable that the Yangshao painted pottery elements including the decoration motifs and patterns spread rapidly to the eastern and northeastern part of China by around 6,000 BP, contributing to pottery making in the Dawenkou and Hongshan Cultures[15–19]. Recent archaeobotanical studies revealed potential correlation between millet crop patterns and Yangshao-style painted potteries. In some archaeological sites associated with the Hongshan culture, such as in Weijiawopu, both painted potteries and high proportion of foxtail millet were discovered[20]. Whereas, in some other archaeological sites, such as Haminmangha, where no painted pottery was discovered, but instead a relatively low percent of foxtail millet was characterized[21]. Since about 6,000 BP, it seems that foxtail millets was more adapted to the diverse environments so as to be quickly spread across most part of China, the Korean Peninsula via northeastern China as well as Taiwan and southeast Asia at about 4,000BP[22]. In this sense, the change of broomcorn to foxtail millet might actually promoted the development of the Neolithic societies in China.

2. Results and Discussions

The CPC is a key area to accept foxtail millet as well as the rice since 6,000BP, where the first state-level society, namely Erlitou appeared at 3,800BP in the northwestern of the Songshan Mountains. The various landforms of the CPC may contribute to the diverse mode of subsistence associated with the spread of both millet and rice. In this study, we try to depict how millet were dispersed and whether the spread of millet was combined with or driven by large scale population movements by combining evidences from archaeology, archaeobotanical, stable isotope and genes.

2.1 Archaeological Evidences

The assemblages of potteries with stone/bone tools could be identified to represent different subsistence and culture. In the CPC, between 9,000 and 6,000 BP, the reddish potteries were discovered in Peiligang and Jiahu cultures that were burned in an oxidizing environment, reflecting a primitive stage of pottery makings at this time period. The stone sickles, however were mainly used as harvesting tools to get both the stems and seeds. A large number of millstones were discovered and were suggested to be used to process the tubers given the fact that starch grains were identified from them. There were also music or divination tools made from wild animals such as crane bones for flutes and tortoise shell for divination, suggesting the hunting-gathering subsistence together with primitive farming[11,23](Figure1B).

From 6,000BP onwards, with the spread of foxtail millet and painted potteries, stone knives instead of sickles were used as harvesting tools. This shift is considered be associated with the special harvesting method of millets as only the spikes of millets are edible[24–26]. Almost at the same time, music tools materials were changed to ceramic styles such as ocarina and bell[27,28]. All these changes indicate an overwhelming change to mature millet subsistence. Starting from 4,500BP, a noticeable development of pottery making techniques was witnessed. The invention of fast wheels and reducing atmospheres in kilns made it possible to produce more elegant potteries whose thinnest point of its body was only 1 millimeter and weigh less than 40 grams. The emergence of this advanced techniques represents the development of residential societies and also corresponding to the intensification of foxtail millet agriculture[29](Figure1C). The change of settlement patterns, especially their quantities, could also reflect population fluctuation and the spread of millet agriculture in Central China[30]. Some systematic surveys in Central China revealed the rapid growth of population size during the Yangshao period(6,000-4,000BP) and then reached its peak duringthe Longshan period (4,000-3,800BP)[31–33]. This could also be related to the diffusions of both millet and rice in China. 8,500-6,000 BP is the period for the early spread of rice from south to north China. But the CPC was only in the stage of primitive rice cultivation or low-level food production[34]. The settlement size and number were limited. However, after 6,000 BP, there was a fast spread of foxtail millet perhaps from the middle reaches of YR. It was evident that populations in CPC widely accepted this mature millet subsistence and the population size increased sustainability since then[35,36]. More detailed systematic surveys in Central China revealed that Yangshao archaeological sites were first developed in the western part of Central China. Then during the Longshan period, there was a sharp increase both in site size and number in eastern and southeastern part of Central China. This spatial and temporal change of settlement pattern in Central China could be regarded as another evidence for the potential diffusions of millet subsistence from west to east[37].

2.2 Archaeobotanical Evidences

Archaeobotanical evidences, mainly the charred seeds from soil floatation of different archaeological sites, could provide intuitive understanding on the farming crop structures. The total amount of charred seeds from archaeological remains of the Sha-Ying floodplain in the eastern part of Central China revealed that before 7,000 BP, a diverse of plant remains excavated, although rice harbored the highest proportion, it only took up a small part of all plant cereals discovered. Wild food collecting still constituted a large proportion of their daily life [11]. After 6,000 BP, the intensive foxtail millet subsistence emerged, that foxtail millet consists of most of the crops with relatively small proportion of broomcorn millet, even lesser soybeans and seldom rice. This crucial change of farming subsistence cannot be explained by the local domestication. But instead introduced from elsewhere or more specifically most probably from some sites in the middle reaches of YR, such as Banpo[38–40]. As is illustrated in Figure2 that the ubiquities of the main crops including foxtail/broomcorn millets, rice and soybean that were floated from charred archaeobotanical remains in the sites between 4,500 and 3,800BCin the Central Plain of China. Although foxtail millet still served as the dominant cereal food in almost all sites surveyed, a high proportion of rice was also found in some sites[41]. Figure 2 is the map with illustrated charts for an archaeobotanical survey in Ying River valley, in the middle Central Plain.Wadian, the largest archaeological site in local region, is different from the others on the patterns of crops proportion. The main remains excavated from Wadian were dated between 4,300 BP and 3,800 BP, where cereal crops consisting both foxtail millet and rice was discovered. Therefore, it may represent a kind of mixed cultivation subsistence. Archaeological surveys and excavations revealed that Wadian is located in a region that served as cross roads in Late Neolithic CPC, where large settlement size and various pottery styles and jade types were discovered. It is most likely that different populations from various regions might meet with each other in this region and took with them their own cultures [37].

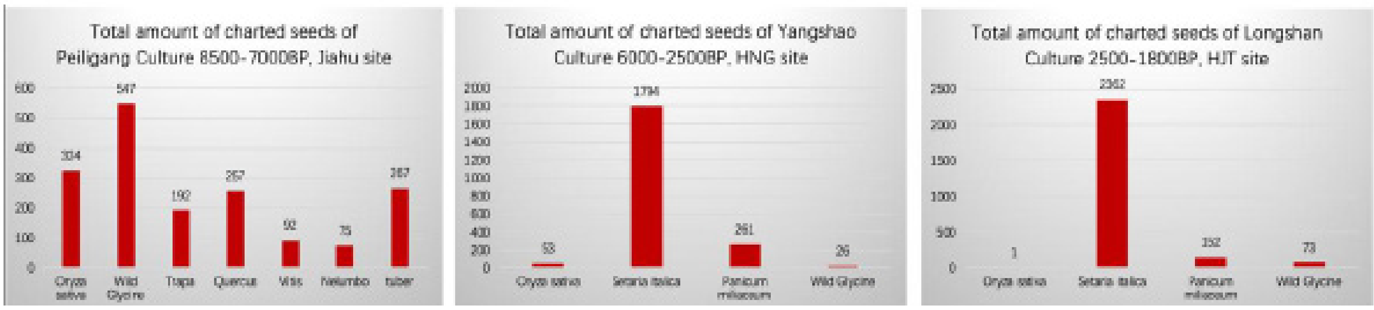
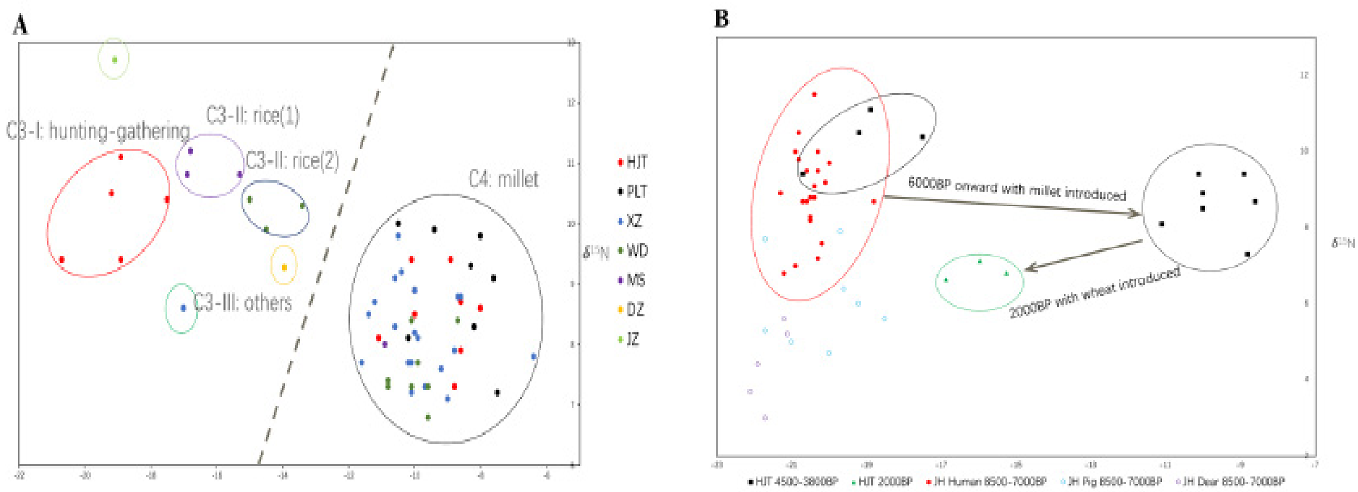


Figure 2. *Number of charred seeds from different time period.*

2.3 Stable Isotope Evidences

The aggregation of populations in Central China who came from different culture background with various subsistence and dietary strategies can also be well identified by using stable isotopic analyses. Stable isotopic testing of human bones and teeth could provide circumstantial evidences on human's diets. This kind of method is based on the basic photosynthesis type of plant, the fractionation of animal/human on digestion. On the one hand, where there is a higher trophic level, there is a more intake of proteins and therefore resulted in a higher value of nitrogen in their body. On the other hand, the animal/human taking C3 or C4 plants as staple food, could be well distinguished according to the carbon value[42]. It is obvious that the main isotopic data from the Longshan period of Central China could be divided into four groups[43–45](Figure 3A). (1) C4 group: Farmers, who ate millet as staple food crops, might migrated into Central China after 6,000BC. The plots on the isotopic chart could not be well distinguished among each other. (2) C3-I group: The hunter-gather, might be the descendants of the local people. (3) C3-II group: The farmers, who ate rice as the main crop, may be migrated into Central China after 6,000BC or earlier. The isotopic plot could be clearly distinguished on the chart between sites. (4) C3-III group: This group is undefined, who might be related with their specific social statues, such as samples with extraordinary high nitrogen value. Figure 3B is the stable isotopic data from the floodplain of Central China, where we can see clearly a shift of diet and subsistence from hunting-gathering to millet cultivation since 6,000BP and then to wheat cultivation after 2,000BP. Stable isotopic data from the Haojiatai archaeological site associated with the Longshan culture (4,500-3,800BP), we observe two groups of people with distinctive diet strategies (millets farmers and hunter-gatherers) co-exist at the same community[45] (Figure 3C).



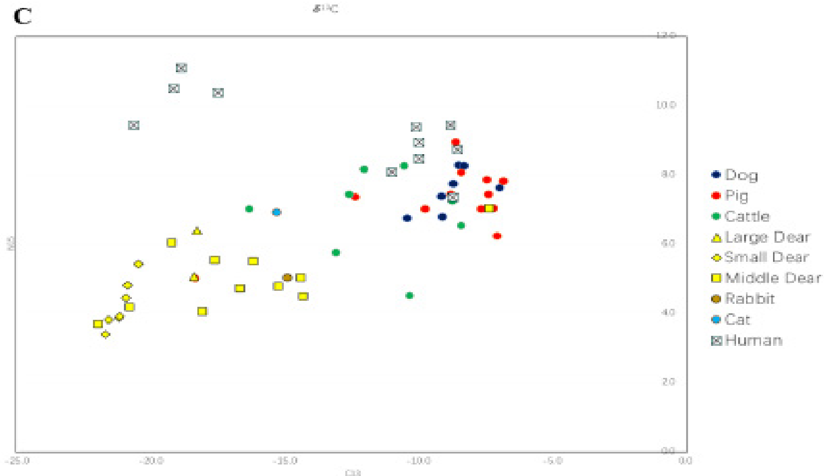


Figure 3. *Stable isotopic analysis of ancient populations in Central China that are dated to the Longshan period. A) Stable isotopic data from the Late Neolithic populations in Central China; B) Introduction of millet from 6000 BP onwards; C) Stable isotopic of skeletons excavated from Haojiatai archaeological site.*

2.4. Genetic Evidences

Previous studies had proved that genetics serves as a powerful tool in tracing population migrations and admixtures [46]. Especially those from ancient DNA, which provide a time transect observation on what happened at a certain time period. By comparing the genetic profile of time series populations, we can directly tell whether population replacement or admixture once occurred and if so whether this process also combined with cultural changes and/or linguistic dispersals [47].

Recent ancient genomic studies in China have shown that the genetic separation between southern and northern populations in China had already been well distinguished at least 8,300 BP [48]. By around 6000 BP, populations associated with the Yangshao culture expanded from the CPC and left great genetic contribution to populations in the West Liao Rive region, for example, they contributed around 60% of their genes to the Hongshan culture populations, such a number even reached 90% in the sequent Lower Xiajiadian populations, suggesting growing genetic contribution from the YR to the West Liao River regions [49]. By the Late Neolithic, populations associated with the Longshan culture in the YR region inherited around 90% of their genes from the preceding Yangshao with the rest from further south of China, more probably from the Yangtze River regions, despite that no ancient genomes from the region have yet published. Such an observation is in parallel to the abrupt growing of rice farming in the YR regions suggesting that populations from the Yangtze River region migrated in the YR regions and took with them rice farming[49]. Long term genetic continuity from Longshan to the Iron Age was also attested by genetics, but with a further northward population migration and admixture into the YR to form the present-day Han Chinese. Great genetic contribution of Yangshao to Qijia culture individuals in the Upper YR has also been observed with the representative of the Late Neolithic Lajia and Dacaozi individuals harbor nearly 80% of their genes from populations associated with Yangshao.Evidence from the paternal Y chromosomal high throughput sequencing showed that about 40% of present-day Chinese were patrilineal descended from three “super-grandfathers” and all of which experienced a strong population expansion approximately 6,000 years ago [50] (Figure 4). In sum, both genomics and Y chromosome studies agrees with what we have observed in the above mentioned the shift from broomcorn millet- to foxtail millet-based subsistence in northern China and may further suggests that the dispersal and the intensification of foxtail millet provide enough food resources and finally contributed to the population expansions in a large scale.

However, we have to admit that the actual scenarios of population prehistory are much more complex than we had anticipated and given the fact that frequent populations replacement and admixture occurred, analyzing modern DNA sometimes cannot fully reflect the true human prehistory. Despite that several projects had been published in China[49,51–54], the number of ancient genomes in China are still limited and that the framework of population movement and admixture has not yet established in China.Although that extensive sampling and sequencing of ancient individuals from Yangshao and Longshan cultures, the earliest Yangshao culture individuals were dated only at 6000 BP. Because of a lack of samples from Yangtze River regions, we can't tell in details whether Yangshao people moved southward to the Yangtze River or vice versa.

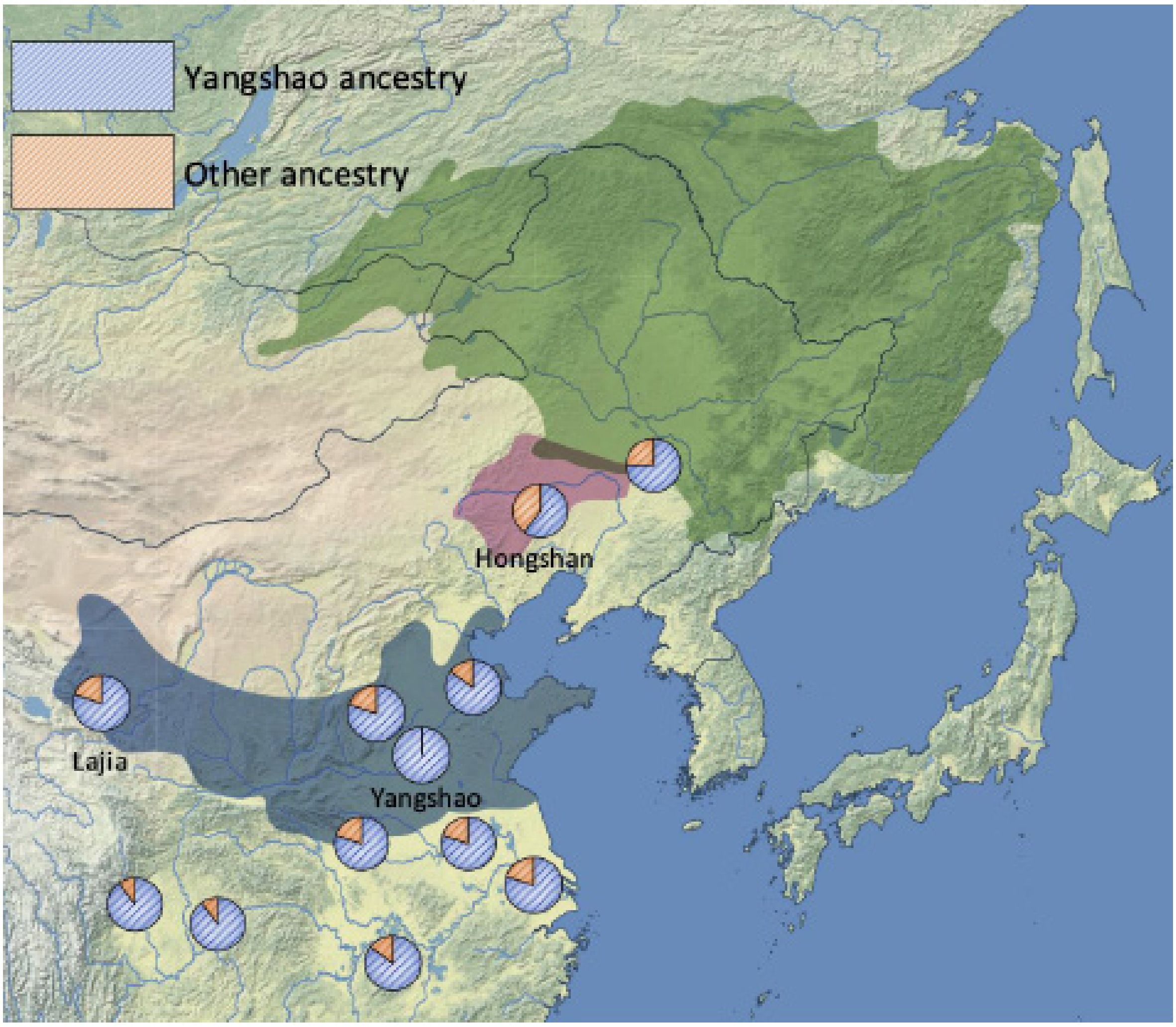


Figure 4. *Genetic contribution of Yangshao-related population to the surrounding ancient and present-day Han Chinese populations.*

3. Conclusions

Archaeological evidences had suggested major cultural and technological changes during the Yangshao period with a rapid population growth at some time around 6000 years ago, from which time period on, intensive millet farming was established, foxtail overtakes broomcorn millet and became the dominant cereal food. The spread of foxtail millet to Central China some 6,000 years ago dramatically shifted the local subsistence from hunting-gathering societies to millet based multi-crops agriculture, supplement with a minor rice consumption. The same pattern could be perceived in the northeastern China, such as from Houtaomuga hunter-gatherers to Hongshan millet farmers. Genetic evidence on Xiaowu individual, the earliest individual sequenced in the YR showed an extensive expansion of populations expansion from the YR regions starting roughly 6000 years and left great genetic fingerprint to surrounding populations and their successors, for example, to Hongshan individuals in the West Liao River and Qijia individuals in the Upper YR regions. In sum, all four lines of evidences had pointed point out major changes occurred roughly 6000 BP, the dispersal of foxtail millet is in parallel with population expansion from the YR suggesting that population expansion might be one of the dynamics for foxtail expansion. We recognize that our focus in this study is only on the central and northeastern part of China. Since the diverse terrain of China, other part of China may show different cereal subsistence pattern.

4. Author Contributions

H.Z and C.N. conceived and wrote the manuscript with input from all co-authors. C. N. and X.T. W. supervised this study.

5. Funding

This work was supported by the National Natural Science Foundation of China (Grant No. T2192953, 41971251); Special Major Foundation for Philosophy Social Science (2022JZDZ022); Major project of Mt. Songshan Civilizations Research Association (2021ZH).

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Data Availability Statement: No new data were created or analyzed in this study. Data sharing is not applicable to this article.

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