AGRICULTURE

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Discontinuous spread of millet agriculture in eastern Asia and prehistoric population dynamics

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Although broomcorn and foxtail millet are among the earliest staple crop domesticates, their spread and impacts on demography remain controversial, mainly because of the use of indirect evidence. Bayesian modeling applied to a dataset of new and published radiocarbon dates derived from domesticated millet grains suggests that after their initial cultivation in the crescent around the Bohai Sea ca. 5800 BCE, the crops spread discontinuously across eastern Asia. Our findings on the spread of millet that intensified during the fourth millennium BCE coincide with published dates of the expansion of the Sino-Tibetan languages from the Yellow River basin. In northern China, the spread of millet-based agriculture supported a quasi-exponential population growth from 6000 to 2000 BCE. While growth continued in northeastern China after 2000 BCE, the Upper/Middle Yellow River experienced decline. We propose that this pattern of regional divergence is mainly the result of internal and external anthropogenic factors.

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INTRODUCTION

Broomcorn (*Panicum miliaceum*) and foxtail (*Setaria italica*) millet, often summarized as the East Asian millet cultigens, are two of the world's oldest crops. Both were important in many prehistoric food production systems across Asia and other parts of the world over several millennia (*1*). Especially in northern China, where they were domesticated, broomcorn and foxtail millet played a fundamental role in the formation of one of the world's early agricultural systems and civilizations (*2*). Although having largely lost significance in worldwide agriculture over the last century, they are currently regaining attention in developing strategies for global food security in light of advancing global warming and a growing world population (*3*).

Despite their significance as a food source in the ancient Old World, the process and timing of millet domestication and the transition to agriculture in northern China remain unclear (*4*). Records of directly ^{14}C-dated carbonized caryopses suggest that cultivation of domesticated millet first occurred more or less contemporaneously during the sixth millennium BCE in the regions of three different Early Neolithic cultural complexes (Peiligang, Houli, and Xinglongwa) (*2*) in the fertile crescent surrounding the Bohai Sea, i.e., stretching across the Lower Yellow River and Liao River region. The claim that the Upper Wei River is also a center of early millet domestication exists (*5*). This claim relies on eight undated broomcorn millet grains collected at the Dadiwan site from a single pit assigned to the occupation phase 1 (5800 to 5300 BCE). All other archaeological remains, however, point to a hunter-gatherer subsistence rather than food production (*5*). This and the fact that Dadiwan is known for intensive millet cultivation during the fourth millennium BCE makes contamination from younger layers highly probable.

Studies based on phytolith (*6*) and starch grain (*7*) analyses claim a much earlier appearance at, respectively, ca. 8500 to 7500 BCE (broomcorn millet) and 9500 BCE (foxtail millet) within the Lower Yellow River and Liao River region. However, this evidence is controversial because of methodological limitations and/or ambiguous chronologies (*8*). Recent studies indicate an early onset of wild grasses (Paniceae) use and thus a long-term shift to agricultural lifeways that might have already started around 20,000 years ago (*8*). This incomplete knowledge is mainly due to the absence of documents of a continuous in situ foraging-farming trajectory and limited insights into pre-Neolithic societies owing to a scarce archaeological record (*4*). Uncertainty about the spatiotemporal spread of millet cultivation across eastern Asia also exists. Existing studies only focus on certain regions and/or are based, at least partly, on ambiguous evidence (*1*, *9*).

It has been recognized that plant domestication was a cornerstone for the Neolithic agricultural revolution (*10*), which led to major transformations in human societies (*11*), particularly linked with population growth (*12*), and disturbance of natural environments (*13*). However, there are ongoing debates, on the one hand, about the pattern of this population growth including whether it was accelerated and whether it was different from those of foraging societies (*12*, *14*) and, on the other hand, about the intensity of early agricultural activities and whether they had a global-scale impact on environments, which induced the Anthropocene era (*15*). Previous studies have shown that China, especially the northern part, was already a dynamic global population hot spot since the Neolithic era (*16*). Although agricultural practices based on domesticated millet and pigs have been identified as a major control on population dynamics in this region (*4*, *17*), systematic knowledge about their spatiotemporal relationship remains poor.

To address these issues, we compiled a set of ^{14}C dates directly derived from remains of domesticated millet (Fig. 1). Available datings extracted from the literature (n = 170; table S1) were supplemented by a set of newly obtained data (table S2) from the Khanka-Ussuri region between China and Russia (n = 7), one of the less well-represented regions in far-eastern continental Asia, and from the Chinese province of Shandong (n = 7), one of the centers of millet domestication (*8*). This dataset was subdivided into eight geographical regions from eastern central Asia to the Japanese archipelago (see Materials and

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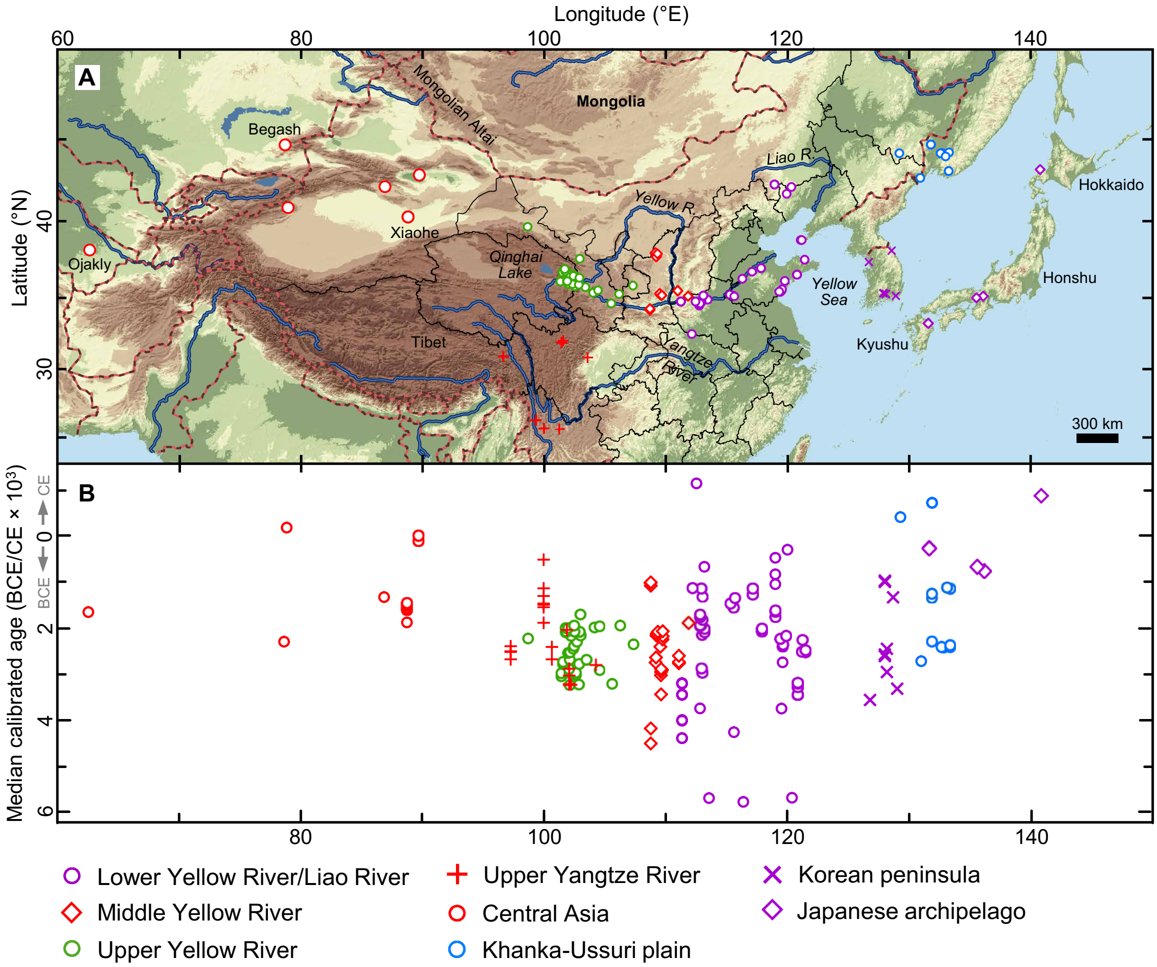

Fig. 1. Spatiotemporal distribution of directly dated millet remains from central and eastern Asia. (**A**) Topographic map with the locations of directly ^{14}C-dated foxtail and broomcorn millet remains (n = 184) contained in the compiled datasets (tables S1 and S2) organized into eight geographical regions (see Materials and Methods). (**B**) Longitudinal distribution of calibrated median millet ages.

Methods) and analyzed using Bayesian modeling to reconstruct the spatiotemporal pattern of millet dispersal across eastern Asia. To test the effect of millet-pig–based agricultural activities on the development of population size, we compiled and reanalyzed a subset (n = 40,696) of an archaeological site distribution database (*16*) covering 13 provinces in northern China (see Materials and Methods) from the Early Neolithic to early Iron Age (ca. 8000 to 500 BCE).

RESULTS AND DISCUSSION

Millet spread across eastern Asia

The results of Bayesian modeling (Fig. 2 and fig. S2) applied to the compiled set of published and newly obtained millet ^{14}C dates suggest that the crop first appeared in the fertile region stretching from the Lower Yellow River in the south to the Liao River in the north around 6100–5700 BCE (95% probability range, as for all time intervals for the defined regions presented in the following) with a median age of 5800 BCE. This provides robust support for the common assumption of earliest domesticated millet appearance in different sedentary cultures within this region around the beginning of the sixth millennium BCE (*1*). From this domestication core zone, millet spread mainly to eastern and western directions (Figs. 1 and 2). Spreading toward the west and southwest, the crops arrived in the Middle Yellow River region 5000–4400 BCE (median, 4600 BCE), but it took another thousand years or more for establishing in the higher elevated regions along the Upper Yangtze River (3700–3100 BCE; median, 3400 BCE) and the Upper Yellow River (3400–3000 BCE; median, 3200 BCE). For the region of central Asia, which includes the data from Xinjiang in the east and from Kazakhstan and Turkmenistan in the west, the model suggests appearance of millet since 3200–2100 BCE (median, 2400 BCE). However, the 95% probability ranges of the earliest available millet-based date from the archaeological site of Begash (2461–2154 BCE; median, 2304 BCE) in southeastern Kazakhstan (Fig. 1) indicate that millet likely appeared in the western central Asian steppes before it was introduced into the Xinjiang region, where the earliest date comes from the Xiaohe site (2011–1756 BCE; median, 1886 BCE).

The reversal in the east-west spread of millet suggested by the data in hand deserves a discussion. The most probable route connecting the Upper Yellow River and the western central Asian steppes runs along the southwestern slopes of the Mongolian Altai and the southern Mongolian Plateau. This agrees with suggested routes for

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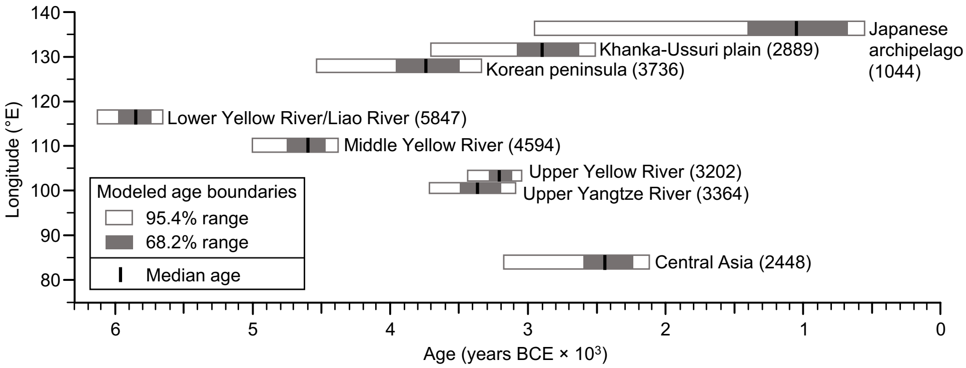

Fig. 2. The modeled age ranges and medians for the appearance of millet in different regions of central and eastern Asia. Numbers in parentheses show modeled calibrated median ages BCE. The longitudinal position of a defined region represents the center of the longitudinal range of all dated millet remains contained in the respective dataset.

the dispersal of West Asian crops such as wheat and barley and animal domesticates (sheep/goat, cattle, and horse) into eastern Asia (*18*, *19*), linked to the spread of agropastoral populations from the central Asian steppe (*20*). We propose that it was also these populations moving into Xinjiang oases along the Tarim, Ili, and other rivers, that introduced not only wheat and barley, which simultaneously appeared there around 1900 BCE (i.e., several centuries later than in the eastern part of China) (*18*), but also millet. The recorded use of both western and eastern domesticates including wheat, millet, sheep/goat, and cattle (*21*) and assemblages of Andronovo culture origin or at least affinity (*22*) since the early second millennium BCE in different parts of Xinjiang provides evidence for the presence of central Asian steppe agropastoral populations in this currently extremely arid region. In addition, increased population numbers are also indicated by the substantial rise in archaeological site numbers in Xinjiang from 44 to 153 between the two time slices 2350 and 1750 BCE (*16*), which may point to immigration and/or intensified food production as a result of changes in subsistence economy.

Spreading toward the east, millet appeared on the Korean Peninsula 4500–3300 BCE (median, 3700 BCE) during the late Early Neolithic (6000 to 3500 BCE) associated with the Chulmun culture. Recent evidence from seed impressions on pottery suggests an earlier existence since the Initial Neolithic (6000 to 5000/4500 BCE), although no direct dates are available for the related sherds (*23*). Archaeological findings suggest that millet was adopted by existing populations rather than introduced by immigration and did not play a substantial role until the Middle Neolithic (3500 to 3000/2700 BCE) (*23*) when millet cultivation as part of the mixed (foraging-farming) subsistence economy was enhanced. Full-scale agriculture is documented only since the Bronze Age associated with the Mumun culture (1500 to 800 BCE), during which rice, wheat, and barley were also cultivated.

The earliest presence of millet in the agriculturally fertile Khanka-Ussuri region is suggested to be ca. 3700–2500 BCE (median, 2900 BCE) and is related to the Late Neolithic Zaisanovka culture (3300/3200 to 1400 BCE), which seems to have spread into the region in several waves bringing along millet cultivation (*24*). A broad cultural interaction sphere ("south Manchurian Neolithic sphere") comprising the regions of the Liao River/Liaoning, Korean Peninsula, and Khanka-Ussuri has been identified on the basis of conformity in pottery styles (*25*). There is evidence for a rise in the number of settlement sites in the western Korean Peninsula by 3000 BCE due to increased farming productivity, which was followed by a decrease in site numbers and extent during the Late Neolithic (3000/2700 to 1500 BCE) (*23*). Currently discussed reasons for this decrease in Chulmun populations, whose subsistence economy was largely based on foraging, are declining natural resources related to overexploitation or pressure from immigrating farmers related to the early Bronze Age Mumun culture (1500 to 800 BCE), which could have pushed parts of the population to northern regions, such as the fertile and less populated Khanka-Ussuri region (*23*, *26*).

Because of the limited number ($n = 4$) of available direct ^{14}C millet datings, the 95% probability range (2900–500 BCE) for the earliest presence of the crop in the Japanese archipelago comprises a comparatively long time interval. The derived median age of 1000 BCE is thus more useful for discussion. It is believed that foxtail and broomcorn millet were introduced to Japan together with rice around the Final Jomon–Initial Yayoi transition (ca. 1000 BCE) and spread northeastward after arriving on Kyushu Island from the Korean Peninsula (*27*). The Yayoi period (ca. 1000 BCE to 300 CE) is characterized by the mixing of immigrants from China and/or the Korean Peninsula and the indigenous Jomon population. It seems that the introduction of rice and millet into the Japanese archipelago reflects a continuation of the spread of both crops to the Korean Peninsula, where they were intensively cultivated since the Bronze Age (Mumun culture).

Although millet seems to have appeared in northern Japan (i.e., the Hokkaido region) relatively late around 689–1015 CE (95% probability range of calibrated direct date TO-1998; median, 862 CE), there is evidence for an earlier presence by carbonized seed assemblages from Epi-Jomon cultural (300 BCE to 700 CE) layers in Hokkaido (*28*) and Late Jomon layers in northern Honshu (*29*). A rice grain associated with the latter millet assemblage, which was dated (*29*) and recalibrated (95% probability range, 1683–382 BCE; median, 1018 BCE), indicates a Late–Final Jomon context. Nondirectly dated foxtail and broomcorn millet grains were also found in Okhotsk cultural layers (ca. 500 to 1000 CE) of six archaeological sites on the Hokkaido island (*30*). This culture has also used other domesticated crops like naked barley, which was not introduced from southern Japan but from the Russian Far East (*30*). The so far oldest well-documented use of naked barley in the Hokkaido region dates between 375 and 203 BCE (95% probability range; median, 279 BCE) (*31*). It is conceivable that, like naked barley, millet spread into northern Japan from the Russian Far East. This hypothesis is supported by evidence from DNA analysis of modern landraces, which suggests

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that barley and broomcorn millet spread to Japan from two different directions, including a southern route via Kyushu and a northern route via Hokkaido (*32*).

The Bayesian modeling results demonstrate a discontinuous westward spread of millet, with an interval of ca. 1200 years (on average) between its appearance in the neighboring regions (Fig. 2). However, no clear temporal pattern can be found for its eastward dispersal. Although the Korean Peninsula is geographically close to the Lower Yellow River and Liao River regions, millet did not appear there until ca. 2100 years later, followed by the Khanka-Ussuri and Japan regions (another ca. 800 and 2700 years, respectively). This shows that adoption of agriculture by prehistoric populations is a complex process. Similar complexity appears in the dispersal of early agriculture from West Asia to Europe along the Danube valley (*33*). After appearance in southeast Europe (6500–6000 BCE), agriculture spread relatively quickly across the fertile central European loess regions (5500–5000 BCE) but subsequently paused on its way to Scandinavia and the British Isles, where it did not arrive before ca. 4000 BCE (*33*).

Further evidence against the long-standing hypothesis of a progressive spread of agriculture (and thus, "civilization") from the region of the Middle Yellow River, traditionally seen as the core area of Chinese Neolithic tradition and Chinese civilization (*7*), is provided by the modeled spread of agriculture across Britain and Ireland (*34*). Starting in southeast England, it reached northwest Scotland earlier than south Scotland. The latter region, for a complex of reasons, did not become the first choice for agriculture spread to the north, as did Xinjiang not become for the millet spread to the west (Fig. 2) and for the wheat spread to the east (*18*).

Disregarding its mode, the inferred long-term spread of millet agriculture and associated population dynamics adds to ongoing debates about the evolutionary history and divergence of the Sino-Tibetan language family (*35*). The reconstructed patterns of millet spread in China that intensified during the fourth millennium BCE concur with results of a recent Bayesian phylogenetic modeling study (*35*), which dates the major dispersal of the Sino-Tibetan language populations from their core area in the Yellow River basin between ca. 5850 and 2250 BCE (average value, 3950 BCE). Further progress in assessing the relationship (that is, coincidence or causality) between the spread of millet farming and dispersal of languages in northern China and eastern Asia can be achieved through interdisciplinary projects, including phylogenetic modeling and a systematic analysis of archaeological and paleoenvironmental records.

Population dynamics in millet-based farming societies of northern China

Changes in archaeological site numbers contained in a dataset from China were interpreted as qualitative estimates for changes in population size (*16*). Here, we reanalyze this dataset to address large-scale changes in the core area of millet-based agriculture and Chinese civilization (see Materials and Methods). The results (Fig. 3A) show the following trends: an increasing growth from 21 to 2220 sites per century from 6400 to 1900 BCE, best explained by an exponential regression curve; a period of decreased site numbers (to 1195 sites per century, 1900 to 1600 BCE); and a period of discontinuous reincrease to 2420 sites per century until 1000 BCE. The calibrated probability distribution of the millet-based datings (Fig. 3B) stretching from the Upper Yellow River region to the Khanka-Ussuri region (ca. 98°E to 133°E) corroborates this trend.

This suggests that substantial population growth in Neolithic northern China started in the late seventh millennium BCE, which was likely initiated by the onset (ca. 6100–5700 BCE) of millet-based agriculture. Our results demonstrate that the population growth controlled by millet cultivation was exponential and accompanied by the spread of millet across the northern part of China from the Upper Yellow River in the west to the Khanka-Ussuri region in the east. The temporal millet dispersal suggests that population growth was, until 2900 BCE, driven by both intensification and spread of millet cultivation and, between 2900 and 1900 BCE, controlled exclusively by intensification of agricultural activities. The site number curve, which shows stable low values between 6000 and 5000 BCE, suggests that the temporal gap in millet datings (ca. 5700 to 4500 BCE; Fig. 1B) and its associated minimum in the estimated probability distributions (Fig. 3B) may be an artifact caused by a general scarcity of millet cultivation sites and relatively little direct-dated archaeological information available for this period (*4*). It seems plausible that this period represents the early stage of the transition to agriculture, which is often attributed to deteriorating health conditions and declining life expectancy (*36*). These unfavorable conditions at the onset of a fully agricultural lifestyle may have also constrained population growth and millet spread in northern China.

The decrease in probability density of millet datings at the turn of the third and second millennium BCE indicates reduced millet cultivation, which may explain the apparently rapid and substantial depopulation by 1900 BCE (Fig. 3). Both curves suggest that diminished site numbers prevailed until the middle second millennium when agricultural activities and population size started to reincrease. We demonstrate, however, that this trend was not universal throughout northern China (*16*). The archaeological site dataset shows (Fig. 4) that it was mainly bounded to the region between 94°E and 115°E and associated with the coeval decline of several Late Neolithic cultures (Majiayao, Longshan, Qijia, and Laohushan) flourishing in the Middle and Upper Yellow River regions. At the same time, the region between 115°E and 131°E demonstrates a generally steady population growth interrupted by only a weak reduction in population size around 2000 BCE.

Numerous studies have tried to identify the driving forces behind this population/cultural decline at the Neolithic–Bronze Age transition in different parts of northern China. The most frequently argued causes are changing climate conditions characterized by higher variability leading to more unstable environments and an enhanced trend toward lower temperatures and moisture availability related to the 4.2-kiloyear event and/or the continuous middle-late Holocene decline in Asian summer monsoon intensity (*37*–*40*). Although the importance of climatic conditions in the life of prehistoric farmers in China is frequently acknowledged (*5*, *16*, *40*), geoscientists and archaeologists still have difficulties in determining where, when, and how changes in climate affected the ancient population (*41*). Many of the published archaeological and paleoclimatic records often allow controversial interpretations due to the lack of high enough resolution and accurate dating (*16*). Recent high-resolution studies also reveal a rather complex and even asynchronous precipitation/humidity trends in different parts of China (*42*). This further complicates the assessment of the potential impact of Holocene climate change on China's population, agricultural development, and subsistence strategies and requires the highest standards of proof in each particular case.

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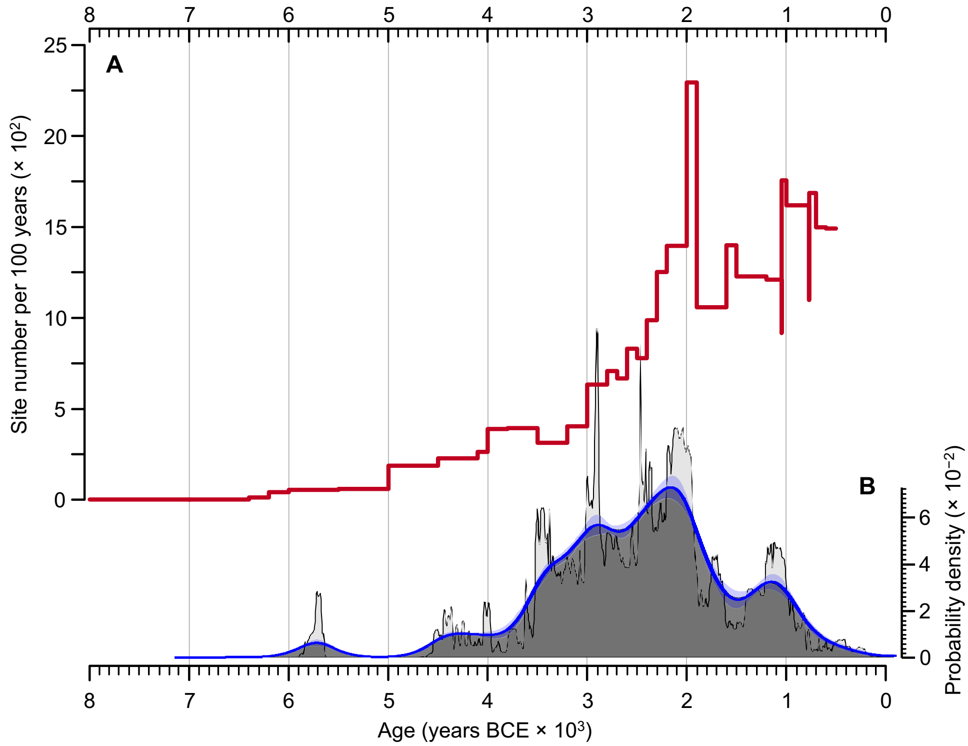

Fig. 3. Archaeological site numbers in northern China, longitudinal spread of millet in eastern Asia, and probability distribution of available millet datings. (**A**) Development of archaeological site numbers per 100 years in northern China (ca. 94°E to 131°E) between 8000 and 500 BCE. (**B**) Probability density distribution of direct millet radiocarbon datings located between 98°E and 133°E based on kernel density estimation (KDE) modeling using the KDE_Model approach implemented in OxCal v4.3.2. The dark gray silhouette is the sampled KDE estimated distribution. The blue line and lighter blue band show the mean ± 1σ for snapshots of the KDE distribution generated during the Markov chain Monte Carlo process. The light gray silhouette represents the stacked (summed) distribution of all datings plotted using the Sum function in OxCal v4.3.2 (see Materials and Methods).

The results summarized in Fig. 4 also require careful consideration before giving priority to climatic or nonclimatic factors. Both the Middle and Upper Yellow River regions west of 115°E and northeastern regions east of 115°E are located at the modern limits of the Asian summer monsoon (*42*). Thus, the environments there must have been similarly vulnerable to precipitation change. Moreover, climate instability would be even more pronounced in the generally colder northeast. Compared to other cereals, millet is well adapted to short growing seasons, dry and infertile soils with poor water-holding capacity, irregular precipitation, and droughts (*1*), making aridification and/or shorter summers less likely a main driver of the rapid and strong agriculture/population decline. A recent review of evidence from paleoenvironmental reconstructions illustrated the complex signature of the 4.2-kiloyear event across the Northern Hemisphere, showing variations in timing and intensity among the different regions (*43*). Regarding eastern Asia, several authors argued that a century-scale oscillation toward colder/drier climate around 4200 years ago strongly affected large parts of China. However, more recent high-resolution and well-dated records from northeastern and southern China (*42*) and from northern Japan (*31*) corroborate only a short-term phase of weak cooling accompanied by a slight decrease in generally high precipitation values. In line with this finding, it seems that the 4.2-kiloyear event had no (or very little) impact on the archaeological site and millet data presented in Fig. 4.

A crop niche modeling study (*41*) demonstrates that in parts of the Tibetan Plateau and in higher-elevated regions of central Asia, climate cooling enhanced after 2000 BCE had a negative impact on the yields of millet and led agropastoralists to diversify their crops, introducing more cold-resistant wheat and barley. Although crop diversification after 2000 BCE is also documented in the archaeological record from northeastern China (*5*, *18*), the probability density of millet-based ^{14}C dates does not indicate a decrease in millet cultivation but suggests that millet continued to be a staple in the region during the second millennium BCE (Fig. 4B).

The drop in archaeological site numbers and in the probability density of millet-based ^{14}C dates in north-central China (Fig. 4A) and the synchronous increase in site numbers in the northeastern region (Fig. 4B) during the early second millennium BCE, only at first glance, appear to be the retreat of farmers from the Middle Yellow River catchment that became progressively drier compared to the relatively humid Liao River region. However, such a straightforward climatic interpretation cannot explain why the still warm and humid middle and lower reaches of the Yangtze River shared the same fate (i.e., habitation collapse and emigration of agricultural population) as the Middle Yellow River region between ca. 2350 and 1750 BCE (*16*).

We suggest that not climate change but economic development and associated social stratification, high population density, and concentration in the growing settlements and their intensified contacts with the Asian steppes could have played a major role in the population and cultural decline at the end of the third millennium BCE. Hosner *et al.* (*16*) were the first who argued for this relationship and discussed as the possible main cause the spread of plagues by

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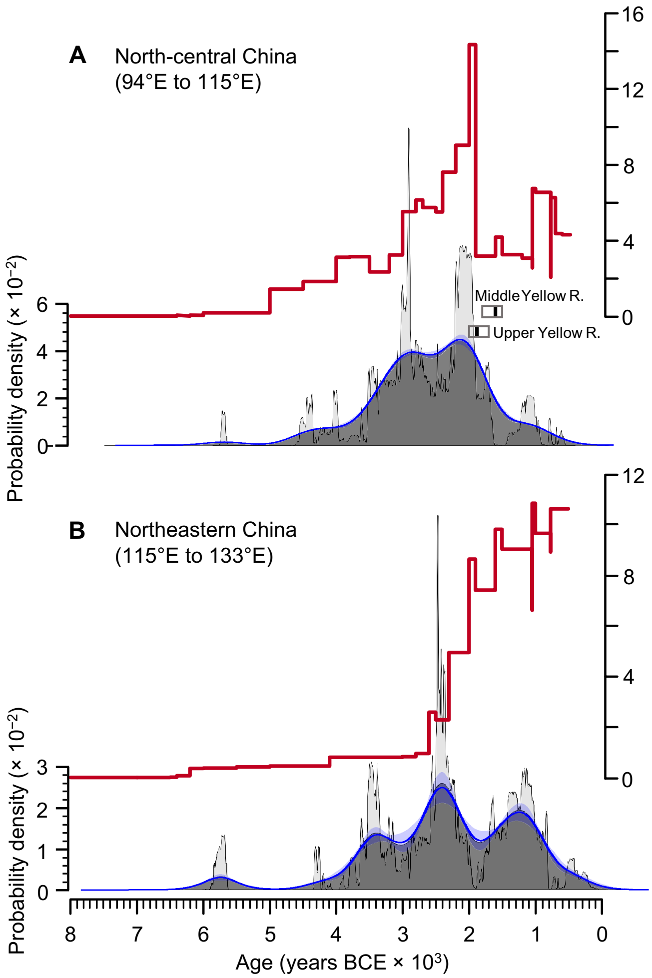

Fig. 4. Archaeological site numbers and probability distribution of available millet datings for north-central and northeastern China. (**A**) Development of archaeological site numbers per 100 years in north-central China between 8000 and 500 BCE and KDE probability density distribution of direct millet radiocarbon datings (west of 115°E). (**B**) As in (A) for northeastern China (east of 115°E). Error bars and vertical black strokes in (A) indicate, respectively, the 95% probability range and median age of the estimated onset of wheat cultivation in the Middle and Upper Yellow River regions (*18*). See caption of Fig. 3 for further details.

Afanasievo and/or Andronovo cultural populations and its possible impact on the densely populated village clusters and fortified centers along the Yellow River and possibly also in the Middle and Low Yangtze River regions. It seems conceivable that expansion of semisedentary agropastoral populations may have involved both increasing cultural pressure in the form of competition for natural resources (e.g., copper and pastoral grounds) as well as the introduction and spread of plague epidemics. The advance of steppe cultural elements is documented during the Late Neolithic by the appearance of domesticates (such as sheep/goat, cattle, barley, and wheat) and technologies (such as metallurgy) of West Asian origin. The estimated (95% probability range) onset of wheat cultivation in the Upper and Middle Yellow River regions ca. 2000–1700 BCE and ca. 1800 –1500 BCE, respectively (*18*), is contemporaneous with the observed population gap there (Fig. 4A). This population decrease in the "core areas of Chinese civilization" (*5*) along the Yellow River might also reflect rising tensions and conflicts between indigenous farmers and western pastoralists. Further support for competition and conflict lies in the replacement of different agricultural societies by agropastoralists in the eastern Gansu-Qinghai region (Upper Yellow River) and southern central Inner Mongolia (Middle Yellow River) (*40*). This context provides an alternative explanation for the increasing number of fortifications and site clustering since the Late Neolithic and the development of urbanism and formation of early states during the Bronze Age. Instead of marked climate changes (*40*), which are most widely considered as main and often the only triggers (*5*), we suggest that it might have been pressure from internal population growth and external anthropogenic forcing that initialized the changes in the cultural landscape expressed by the development of centralized, hierarchical settlement systems. There is increasing evidence for broad expansion processes of Eurasian steppe populations during the third millennium BCE toward the west and east from archaeological records and genetic studies (*44*–*46*). Westward migration of so-called Yamnaya steppe herders from eastern Europe in the early Bronze Age (around 2500 BCE) was even so massive that it led to the large-scale replacement of populations in central Europe (*47*). Our study argues that a similar scenario could be applied to northern China.

For northeastern China, our results suggest prolonged population growth underpinned by continued millet-based agriculture beyond the end of the Neolithic period ca. 2000 BCE (Fig. 4B), which might have been augmented by immigration from the Yellow River region. A population shift is also indicated by the appearance of massive fortifications after 2000 BCE, which originated in the Middle Yellow River region (*48*). Our findings contradict claims of a Late Neolithic (third millennium BCE) population decline in northeastern China and the perception of a general transformation from sedentary agriculture to pastoral nomadism around 2000 BCE (*40*, *49*).

CONCLUDING REMARKS

The results presented in this study shed new light on the relationship among millet-based agricultural activities, the spread of crops and technologies, and population dynamics in large parts of Neolithic and Bronze Age eastern Asia. Our findings suggest that millet-based agricultural systems appeared around 6000 BCE in different parts of the Lower Yellow River and Liao River reaches and do not provide evidence for early millet cultivation in the Wei River region traditionally seen as one of the core areas of Chinese civilization. Comparable with the dispersal of West Asian crops across Europe and China, millet spread was discontinuous across eastern Asia. This suggests that adaptation of agriculture by prehistoric populations is a nonlinear process depending on the interaction of various anthropogenic and environmental factors.

The shift to agricultural practices induced an exponential population growth in northern China, which continued until ca. 2000 BCE. We hypothesize that the following decline in millet cultivation and population size in north-central China is mainly the result of enhanced expansion of agropastoralists leading to competition with indigenous farmers for natural resources (e.g., copper and pastoral grounds) likely in combination with the spread of plague epidemics. It seems plausible that the Neolithic farmers of northern China faced similar profound immigration pressure at about the same time as their counterparts in central Europe, who were largely replaced by expanding eastern European pastoralists in the early Bronze Age around 2500 BCE

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(*45*, *47*). These migration processes exemplify the important role of the steppe cultural sphere in Eurasian prehistory at least since the third millennium BCE. The recognized expansion of agropastoral population might have been promoted by improving moisture availability in the central Asian and eastern European steppe regions over the middle and late Holocene (*50*). One reason for the construction of massive fortifications by populations in northern China may be the need for protection from this "migration threat." If this hypothesis is true, these defense works might represent precursors of the walls built some 2000 years later by early feudal states during the pre-imperial late Eastern Zhou dynasty, also called the "Warring States" period (475 to 221 BCE), in response to interstate conflict and for protecting against hostile nomadic societies, which later developed into what is today known as the Great Wall of China, the largest military structure in world history.

MATERIALS AND METHODS

Calibration of radiocarbon dates

Newly obtained ^{14}C dates and the reported ^{14}C date of a rice grain from northern Honshu (*29*) were calibrated to calendar ages using OxCal v4.2.3 (https://c14.arch.ox.ac.uk/oxcal.html) and the IntCal13 curve (*51*).

Compilation of millet-based ^{14}C dates

In addition to the newly obtained datings from millet caryopses ($n = 14$), we compiled 170 directly dated millet-based ^{14}C dates from available publications. Reported millet finds with ages derived from typologies or stratigraphically correlated material (e.g., carbon-rich soil and charcoal) were not included in the dataset. These correlations may introduce additional errors, including those resulting from postdepositional processes or the "old wood effect," which may lead to age shifts of hundreds or even thousands of years (*18*). Additional care should be taken when equating radiocarbon dates with demography. The decreasing numbers of millet-based ^{14}C dates in the Middle and Upper Yellow River regions of north-central China after 2000 BCE (Fig. 4A) could reflect a decrease in site numbers and population densities or could be an artifact of sampling strategy, for example, preferentially selecting for dating grains of wheat and barley when they begin to appear in cultural layers during this period of time. Such a bias, if it exists, should more or less equally affect the probability density of millet-based ^{14}C dates in both parts of northern China shown in Fig. 4 and would contradict the independently collected archaeological site dataset (*16*) and interpretations based on archaeological materials (*5*). Since this is not the case, we assume that the data used in this study are suitable for qualitative interpretation and justify the reliability of our conclusions.

Bayesian chronological modeling

We constructed a Bayesian chronological model (fig. S1) to estimate the appearance of millet in different parts of eastern Asia. Our approach generally follows the one used by Long *et al.* (*18*), which the reader is referred to for further references. The employed model uses the overlapping multiphase model for the overall structure and the phase model as a building block (i.e., a submodel) implemented in OxCal v4.3.2. The compiled millet-based ^{14}C datings ($n = 184$) were organized into eight geographical regions (listed in Fig. 1), each of which is represented by a submodel. Each submodel conceptually represents the archaeological phase during which millet appeared in the respective region, and the lower boundary of that modeled phase (*18*) was adopted as its age estimate. Outliers were detected on the basis of the OxCal agreement index calculation. The modeled ages are presented as both 95% probability range and median (point estimate).

^{14}C probability distribution

Probability density distribution was calculated based on a selection ($n = 144$) of the compiled set ($n = 184$) of millet-based ^{14}C datings representing five of the defined geographical regions (ca. 98°E to 133°E) including the Upper Yellow River, Middle Yellow River, Lower Yellow River and Liao River, Korean Peninsula, and Khanka-Ussuri, roughly representing the region covered by the archaeological site dataset used. For analyzing spatial differences, the subset of ^{14}C dates was divided along 115°E, resulting in a western ($n = 90$), representing north-central China, and eastern ($n = 54$), representing northeastern China, dataset. ^{14}C dates <2000 uncalibrated years before the present were not considered. The probability density distribution and stacked (summed) distribution were derived from kernel density estimation (KDE) modeling using the KDE_Model approach (*52*) implemented in OxCal v4.3.2.

Archaeological site data

We used archaeological site data extracted from an existing database (*16*) to estimate the Neolithic–Bronze Age population development in the core region of early millet-based (dry-land) agriculture and Chinese civilization in northern China. The original database contains a total of 51,074 archaeological sites from the Early Neolithic to the early Iron Age (ca. 8000 to 500 BCE) and covers most regions of China (i.e., site data from 25 Chinese provinces, autonomous regions, and municipalities, published in the series *Atlas of Chinese Cultural Relics*). The entire dataset is also available in the open access database PANGAEA Data Publisher for Earth & Environmental Science (https://doi.pangaea.de/10.1594/PANGAEA.860072). It should be acknowledged that overreliance on archaeological site numbers as population proxy can be critical, given the heterogeneous nature of the base data (*16*). This issue was addressed in detail by Hosner *et al.* (*16*), to which the reader is referred to for further discussion and references. They also performed a comparison of the estimated population (*53*) with the archaeological site numbers obtained in their study and reported rather similar trends in both curves, thus suggesting a reasonably good correlation between number/density of archaeological sites and prehistoric population estimates in China. Being aware of the existing biases in data collection, we put accent in the discussion not on the absolute values but on the major trends (i.e., on qualitative rather than quantitative parameters).

The compiled subset of 40,696 sites represents 13 Chinese provinces including Beijing, Gansu, Hebei, Henan, Inner Mongolia Autonomous Region, Jilin, Liaoning, Ningxia Hui Autonomous Region, Qinghai, Shaanxi, Shandong, Shanxi, and Tianjin (ca. 32°N to 51°N, 90°E to 131°E), covering the period 8000 to 500 BCE. The subset represents the areas with directly dated millet grains that originate from a clearly millet-based agricultural context. Each contained archaeological site in this subset is assigned to one or more well-dated cultural periods. This implies that the sites represent different time ranges, which vary between 100 and 6000 years. To temporally normalize the site data eliminating influence of the length of the defined cultural periods, the site numbers are presented by time intervals of equal length, which we randomly set to 100 years. In addition, to allow determination of

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longitudinal differences in site number development in response to the evolution of millet-based agriculture, the compiled dataset was divided in concert with the set of millet ^{14}C datings into two subsets along 115°E representing north-central China and northeastern China, respectively. It should be mentioned that we are only relying on radiocarbon dating when discussing the probability density of directly dated millet remains, while the age determinations in the archaeological site database are made by the respective regional teams of Chinese archaeologists, who used all available dating approaches (e.g., absolute dates, pottery typology, and other sources of information), which makes the two datasets involved in the analysis (Figs. 3 and 4) independently and securely dated. This is particularly important, keeping in mind the tendency of Chinese archaeologists to have more confidence in the chronological usefulness of ceramics and other chronologically sensitive materials when dating sites and cultural layers from first millennium BCE contexts.

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at http://advances.sciencemag.org/cgi/content/full/5/9/eaax6225/DC1

Fig. S1. Bayesian model structure and OxCal coding.

Fig. S2. OxCal modeling results.

Table S1. Available ^{14}C dates directly derived from remains of domesticated millet extracted from the literature.

Table S2. Newly obtained ^{14}C dates directly derived from remains of domesticated millet from prehistoric cultural layers in the Khanka-Ussuri region and the Chinese province of Shandong.

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Acknowledgments: The current study contributes to the PAGES-sponsored program "LandCover6k: Global anthropogenic land-cover change and its role in past climate" and to the MEXT Grant-in-Aid project "Cultural History of PaleoAsia" (MEXT Grant-in-Aid no. 1802). We express our special thanks to G. Jin (Shandong University, China and Reading University, UK), T. Goslar (Poznan Radiocarbon Laboratory), and the Russian archaeologists N. A. Klyuev and A. V. Garkovik (Institute of History, Archaeology and Ethnography, Russian Academy of Sciences, Far Eastern Branch, Vladivostok, Russia), E. V. Krutykh (Scientific and Production Centre of Historical and Cultural Expertise, Vladivostok, Russia), and S. A. Kolomiets (Pacific State Medical University, Vladivostok, Russia) for providing various help in collecting the ^{14}C-dated plant remains from archaeological sites in the Russian Far East. We also extend our thanks to the anonymous reviewers who made valuable suggestions, which allowed the improvement of the manuscript. **Funding:** Obtaining the dated plant remains from archaeological sites in the Russian Far East was possible because of the financial support of the Russian Foundation for Basic Research (project no. 13-06-12027-офи-м). C.L. acknowledges financial support by a long-term Research Fellowship (grant LE3508/2-1) granted by the German Research Foundation. The work of T.L. was supported by the FoSE New Researchers Grant by the University of Nottingham Ningbo China. **Author contributions:** C.L., E.A.S., M.W., and P.E.T. designed the research. E.A.S. performed botanical identification and contributed millet samples from field campaigns for ^{14}C dating. C.L., T.L., M.W., and P.E.T. constructed the ^{14}C dataset. T.L. and P.E.T. designed the Bayesian chronological model. C.L. modeled the probability density distribution of the ^{14}C dates and reanalyzed the archaeological site data. T.L., E.A.S., and M.W. contributed to the Introduction and Results and Discussion sections. C.L. and P.E.T. wrote the manuscript and compiled the figures. **Competing interests:** The authors declare that they have no competing interests. **Data and materials availability:** All data needed to evaluate the conclusions in the paper are present in the paper and/or the Supplementary Materials. Additional data related to this paper may be requested from the authors.

Submitted 8 April 2019
Accepted 28 August 2019
Published 25 September 2019
10.1126/sciadv.aax6225

Citation: C. Leipe, T. Long, E. A. Sergusheva, M. Wagner, P. E. Tarasov, Discontinuous spread of millet agriculture in eastern Asia and prehistoric population dynamics. *Sci. Adv.* **5**, eaax6225 (2019).

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Sci Adv **5** (9), eaax6225.
DOI: 10.1126/sciadv.aax6225

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