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Triangulation supports agricultural spread of the Transeurasian languages

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Triangulation supports agricultural spread of the Transeurasian languages

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The origin and early dispersal of speakers of Transeurasian languages, i.e., Japanese, Korean, Tungusic, Mongolic and Turkic, is among the most disputed issues of Eurasian population history. A key problem is the relationship between linguistic dispersals, agricultural expansions and population movements. Here we address this question through 'triangulating' genetics, archaeology and linguistics in a unified perspective. We report new, wide-ranging datasets from these disciplines, including the most comprehensive Transeurasian agropastoral and basic vocabulary presented to date, an archaeological database of 255 Neolithic and Bronze Age sites from Northeast Asia, and the first collection of ancient genomes from Korea, the Ryukyu islands and early cereal farmers in Japan, complementing previously published genomes from East Asia. Challenging the traditional 'Pastoralist Hypothesis', we show that the common ancestry and primary dispersals of Transeurasian languages can be traced back to the first farmers moving across Northeast Asia from the Early Neolithic onwards, but that this shared heritage has been masked by extensive cultural interaction since the Bronze Age. As well as marking significant progress in the three individual disciplines, by combining their converging evidence, we show that the early spread of Transeurasian speakers was driven by agriculture.

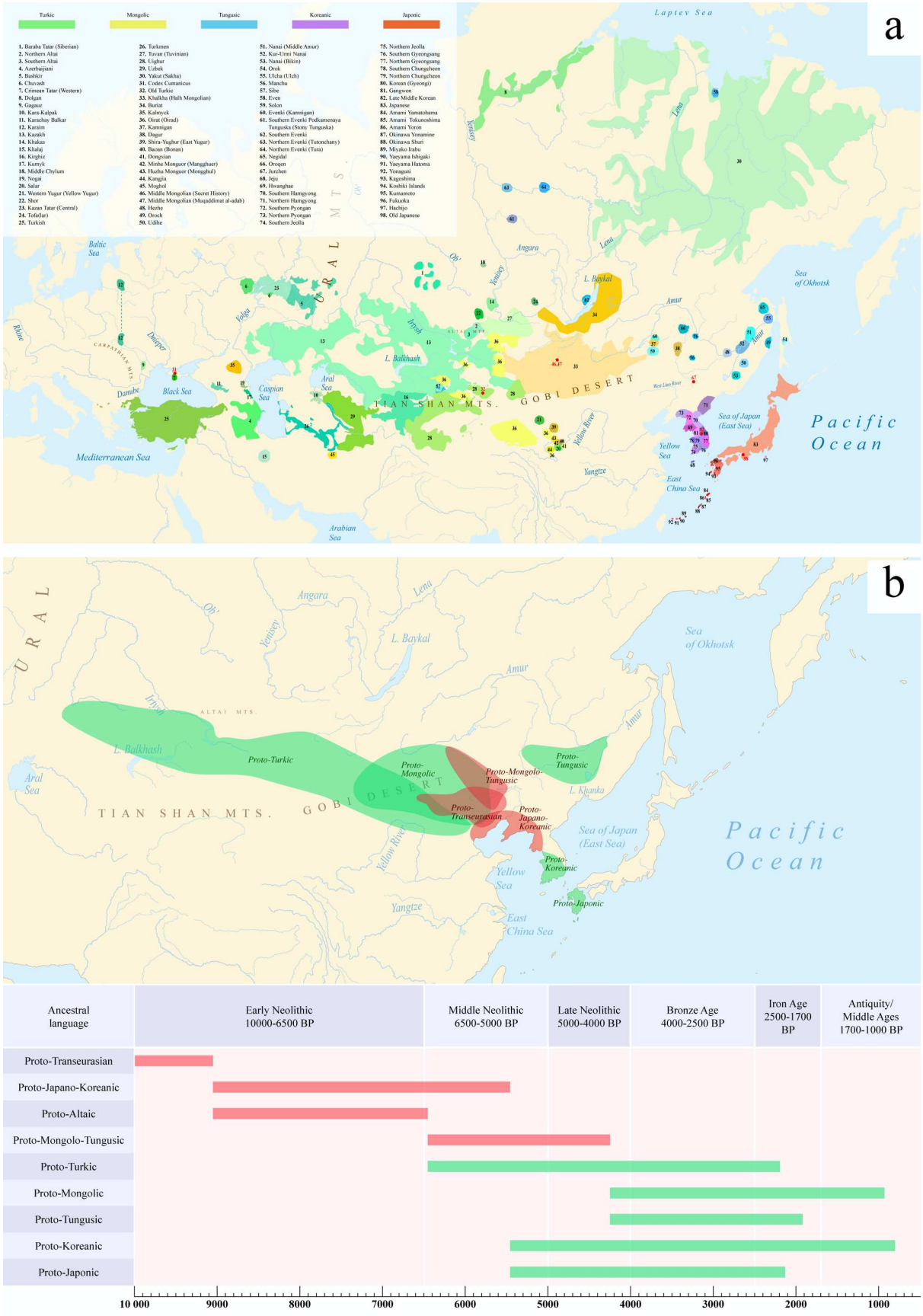
Introduction

Recent breakthroughs in ancient DNA sequencing have made us rethink the connections between human, linguistic and cultural expansions across Eurasia. Compared to western Eurasia[1,2,3,4], however, the dynamics in eastern Eurasia remain poorly understood. Northeast Asia, the vast region encompassing Inner Mongolia, the Yellow, Liao and Amur River basins, the Russian Far East, the Korean peninsula and the Japanese Islands, remains especially under-represented in the recent literature. With a few exceptions that are heavily focused on genetics[5,6,7,8], truly interdisciplinary approaches to Northeast Asia are scarce.

The linguistic relatedness of the Transeurasian languages — also known as 'Altaic' — is among the most disputed issues in linguistic prehistory. Transeurasian denotes a large group of geographically adjacent languages, stretching across Europe and northern Asia and includes five uncontroversial linguistic families: Japonic, Koreanic, Tungusic, Mongolic, and Turkic (Fig. 1a). The question of whether these five groups descend from a single common ancestor has been the topic of a longstanding debate between supporters of inheritance and borrowing. Recent assessments show that even if many common properties between these languages are indeed due to borrowing[9,10,11], there is nonetheless a core of reliable evidence for the classification of Transeurasian as a valid genealogical group[12,13,14,15].

Accepting this classification, however, gives rise to new questions about the time-depth, location, cultural identity and dispersal routes of ancestral Transeurasian speech communities. Here we challenge the traditional 'Pastoralist Hypothesis' that identifies the primary dispersals of the Transeurasian languages with nomadic expansions starting in the eastern Steppe in the fourth millennium BP[16,17,18], by proposing a new 'Farming Hypothesis', which places those dispersals within the scope of the 'Farming Language Dispersal Hypothesis'[19,43,44]. As these issues reach far beyond linguistics, we address them here by integrating other scientific disciplines such as archaeology and genetics in a single approach termed 'triangulation'.

Fig. 1a. Geographical distribution of the 98 Transeurasian language varieties included in this study. Contemporary languages are represented by coloured surfaces, historical varieties by red dots. Fig. 1b. Transeurasian ancestral languages spoken during the Neolithic (red) and Bronze Age and later (green).


a
Turkic
Mongolic
Tungusic
Koreanic
Japonic
1. Baraba Tatar (Siberian)
2. Northern Altai
3. Southern Altai
4. Azerbaijani
5. Bashkir
6. Chuvash
7. Crimean Tatar (Western)
8. Dolgan
9. Gagauz
10. Kara-Kalpak
11. Karachay Balkar
12. Karaim
13. Kazakh
14. Khakas
15. Khalaj
16. Kirghiz
17. Kumyk
18. Middle Chylum
19. Nogai
20. Salar
21. Western Yugur (Yellow Yugur)
22. Shor
23. Kazan Tatar (Central)
24. Tofa(lar)
25. Turkish
26. Turkmen
27. Tuvan (Tuvinian)
28. Uighur
29. Uzbek
30. Yakut (Sakha)
31. Codex Cumanicus
32. Old Turkic
33. Khalkha (Halh Mongolian)
34. Buriat
35. Kalmyck
36. Oirat (Oirad)
37. Kamnigan
38. Dagur
39. Shira-Yughur (East Yugur)
40. Bacon (Bonan)
41. Dongxian
42. Minhe Monguor (Mangghuer)
43. Huzhu Monguor (Mongghul)
44. Kangjia
45. Moghol
46. Middle Mongolian (Secret History)
47. Middle Mongolian (Muqaddimat al-adab)
48. Hezhe
49. Oroch
50. Udihe
51. Nanai (Middle Amur)
52. Kur-Urmi Nanai
53. Nanai (Bikin)
54. Orok
55. Ulcha (Ulch)
56. Manchu
57. Sibe
58. Even
59. Solon
60. Evenki (Kamnigan)
61. Southern Evenki Podkamenaya Tunguska (Stony Tunguska)
62. Southern Evenki
63. Northern Evenki (Tutonchany)
64. Northern Evenki (Tura)
65. Negidal
66. Oroqen
67. Jurchen
68. Jeju
69. Hwanghae
70. Southern Hamgyong
71. Northern Hamgyong
72. Southern Pyongan
73. Northern Pyongan
74. Southern Jeolla
75. Northern Jeolla
76. Southern Gyeongsang
77. Northern Gyeongsang
78. Southern Chungcheon
79. Northern Chungcheon
80. Korean (Gyeongi)
81. Gangwon
82. Late Middle Korean
83. Japanese
84. Amami Yamatohama
85. Amami Tokunoshima
86. Amami Yoron
87. Okinawa Yonamine
88. Okinawa Shuri
89. Miyako Irabu
90. Yaeyama Ishigaki
91. Yaeyama Hatoma
92. Yonaguni
93. Kagoshima
94. Koshiki Islands
95. Kumamoto
96. Fukuoka
97. Hachijo
98. Old Japanese
Laptev Sea
Lena
Yenisey
Angara
L. Baykal
Sea of Okhotsk
Amur
Baltic Sea
Oh'
URAL MTS
Volga
Irtysh
L. Balkhash
Dnieper
Rhine
CARPATHIAN MTS
Danube
Black Sea
Caspian Sea
Aral Sea
TIAN SHAN MTS.
GOBI DESERT
West Liao River
Yellow River
Sea of Japan (East Sea)
Pacific Ocean
Yellow Sea
Yangtze
East China Sea
Mediterranean Sea
Arabian Sea
b
Proto-Turkic
Proto-Mongolic
Proto-Tungusic
Proto-Mongolo-Tungusic
Proto-Transeurasian
Proto-Japano-Koreanic
Proto-Koreanic
Proto-Japonic
L. Khanka
Ancestral language
Early Neolithic 10000-6500 BP
Middle Neolithic 6500-5000 BP
Late Neolithic 5000-4000 BP
Bronze Age 4000-2500 BP
Iron Age 2500-1700 BP
Antiquity/ Middle Ages 1700-1000 BP
Proto-Transeurasian
Proto-Japano-Koreanic
Proto-Altaic
Proto-Mongolo-Tungusic
Proto-Turkic
Proto-Mongolic
Proto-Tungusic
Proto-Koreanic
Proto-Japonic
10 000
9000
8000
7000
6000
5000
4000
3000
2000
1000

Linguistics

We collected a new dataset of 3193 datapoints representing 254 basic vocabulary concepts for 98 Transeurasian languages, including dialects and historical varieties (SI 1). We applied Bayesian methods to infer a dated phylogeny of the Transeurasian languages (Extended data Fig. 1). Our results indicate a time-depth of 9181 BP (5595 -12793 95%HPD) for the Proto-Transeurasian root of the family, 6811 BP (4404-10166 95%HPD) for Proto-Altaic, the unity of Turkic, Mongolic and Tungusic languages, 4491 BP (2599-6373 95%HPD) for Mongolo-Tungusic, and 5458 BP (3335-8024 95%HPD) for Japano-Koreanic (Fig. 1b). These dates estimate the time depth of the break-up of a given language family into its subfamilies.

We used our lexical dataset to model the expansion of Transeurasian languages in space (SI 3 and 4). As classical methods such as lexicostatistics, the diversity hotspot principle and cultural reconstruction can be impressionistic[5,12,13,20], we applied Bayesian phylogeography for the first time to complement previous approaches.

In contrast to previously proposed homelands, which range from the Altai[16,17,18] to the Yellow River[21] to the Greater Khingan Mountains[22] to the Amur basin[23], we find support for a Transeurasian origin in the West Liao River region in the Early Neolithic. After a primary break-up of the family in the Neolithic, further dispersals took place in the Bronze Age. The ancestor of the Mongolic languages expanded northwards to the Mongolian Plateau, Proto-Turkic moved westwards over the Eastern Steppe and the other branches moved eastwards: Proto-Tungusic to the Amur-Ussuri-Khanka region, Proto-Koreanic to the Korean Peninsula and Proto-Japonic over Korea to the Japanese Islands (Fig. 1b).

Through a qualitative analysis, examining agropastoral words revealed in the reconstructed vocabulary of the proto-languages (SI 5), we further identified items that are culturally diagnostic for ancestral speech communities in a particular region at a particular time. Common ancestral languages that separated in the Neolithic, such as Proto-

Transeurasian, Proto-Altaic, Proto-Mongolo-Tungusic and Proto-Japano-Koreanic reflect a small core of inherited words relating to cultivation ('field', 'sow', 'plant', 'grow', 'cultivate', 'spade'), millets but not rice or other crops ('millet seed', 'millet gruel'), food production and preservation ('ferment', 'grind', 'crush to pulp', 'brew'), wild foods suggestive of sedentism ('walnut', 'acorn', 'chestnut'), textile production ('sew', 'weave cloth', 'weave with a loom', 'spin', 'cut cloth', 'ramie', 'hemp'), and pigs and dogs as the only domesticated animals.

By contrast, individual subfamilies that separated in the Bronze Age, such as Turkic, Mongolic, Tungusic, Koreanic and Japonic, inserted new subsistence terms relating to the cultivation of rice, wheat and barley, dairying, domesticated animals such as cattle, sheep, and horses, farming or kitchen tools, and textiles such as silk (SI 5). These words are borrowings resulting from linguistic interaction between Bronze Age populations speaking various Transeurasian and non-Transeurasian languages.

In sum, the age, homeland, original agricultural vocabulary and contact profile of the Transeurasian family support the 'Farming Hypothesis' and exclude the 'Pastoralist Hypothesis'.

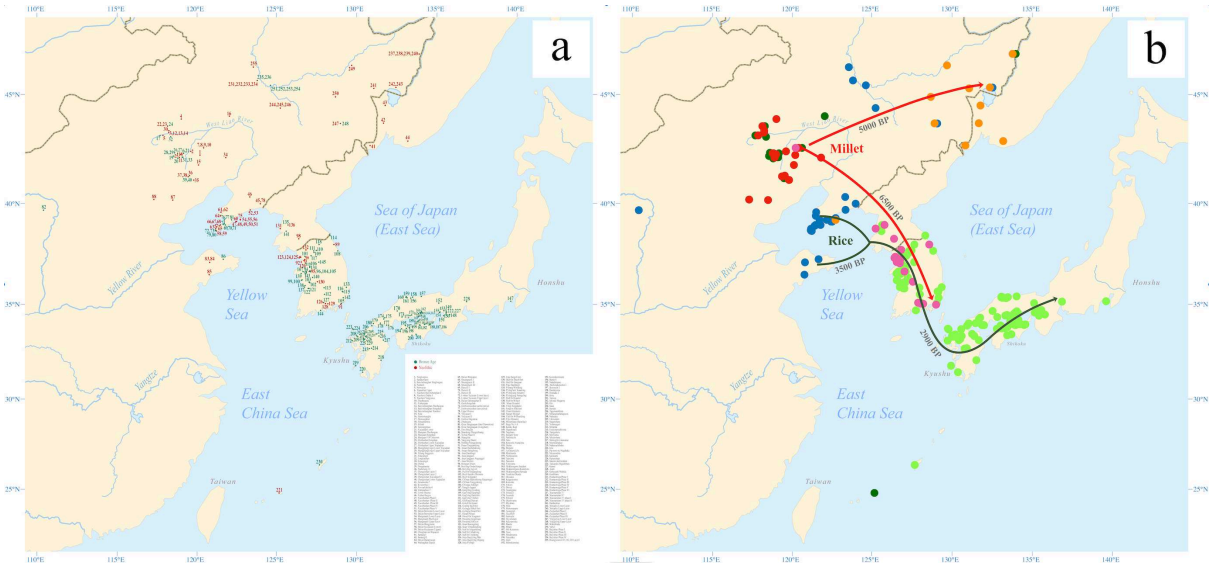
Archaeology

While Neolithic Northeast Asia was characterised by widespread plant cultivation[24], cereal farming expanded from several centres of domestication, the most important of which for Transeurasian was the West Liao basin where cultivation of broomcorn millet started by 9000 BP[25,26,27,28] Extracting data from the published literature, we scored 172 archaeological features for 255 Neolithic and Bronze Age sites in northern China, the Primorye, Korea and Japan. (SI 6; Fig. 2a) and compiled an inventory of early cereal remains with direct radiocarbon dates (SI 9) in northern China, the Primorye, Korea and Japan.

156 The main results of our Bayesian analysis (Extended data Fig. 2), which clusters the 255
157 sites according to cultural similarity are visualized in Fig. 2b. We find a cluster of Neolithic
158 cultures in the West Liao basin, from which two branches associated with millet farming
159 separate, a Korean Chulmun branch and a branch of Neolithic cultures covering the Amur,
160 Primorye and Liaodong. This confirms earlier findings about the dispersal of millet
161 agriculture to Korea by 5500 BP and via the Amur to the Primorye by 5000 BP.[29,30]
162 Our analysis further clusters Bronze Age sites in the West Liao area with Mumun sites in
163 Korea and Yayoi sites in Japan. This mirrors how during the fourth millennium BP, the
164 agricultural package of the Liaodong-Shandong area was supplemented with rice and wheat.
165 These crops were transmitted to the Korean Peninsula by the Early Bronze Age (3300-2800
166 BP) and from there to Japan after 3000 BP (Fig. 2b).
167 While population movements were not linked with monothetic archaeological cultures,
168 Neolithic farming expansions in Northeast Asia were associated with some diagnostic
169 features, such as stone tools[33] and textile technology (SI 7).[31] Domesticated animals and
170 dairying played an important role in the spread of the Neolithic in western Eurasia but, except
171 for dogs and pigs, our database shows little evidence for animal domestication in Northeast
172 Asia before the Bronze Age (SI 6). The link between agriculture and population migrations is
173 especially clear from similarities between ceramics, stone tools, and domestic and burial
174 architecture between Korea and western Japan[32].
175 Building on previous studies, we provided an overview of demographic changes
176 associated with the introduction of millet farming across the regions in our study (Extended
177 data Fig. 3). Having invested in elaborate paddy fields, wet rice farmers tended to stay in one
178 place, absorbing population growth through extra labour, while millet farmers typically
179 adopted a more expansionary settlement pattern.[33] Neolithic population densities increased

across Northeast Asia prior to a Late Neolithic population crash.[34,35] The Bronze Age then saw exponential population increases in China, Korea and Japan.

Fig. 2a Spatiotemporal distribution of sites included in the archaeological database. 2b Clustering of investigated sites according to cultural similarity in line with Bayesian analysis in Extended data Fig. 2, with indication of the spread of millet and rice in time and space. The distribution of archaeological sites in Fig. 2 is smaller than that of contemporary languages in Fig. 1 because we focus on the early dispersal of the linguistic subgroups in the Neolithic and Bronze Age and on the links between the eastward spread of farming and language dispersal.



Genetics

We report genomic analyses of 23 authenticated individuals from the Amur, Korea, Kyushu and the Ryukyus and combined them with published genomes covering the Eastern Steppe, West Liao, Amur and Yellow River regions, Liaodong, Shandong, the Primorye and Japan between 9500 and 300 BP (Fig. 3a; Extended data Fig. 4; SI 11; SI 17). We projected them onto a principal component analysis (PCA) of 149 present-day Eurasian populations and 45

East Asian populations (Extended data Fig. 5, 6, 7, 8). Fig. 3b models our key ancient populations as an admixture of five genetic components, whereby Jalainur represents Amur, Yangshao the Yellow River and Rokutsu the Jomon genome while Hongshan and Upper Xiajiadian are composed of Yellow River and Amur genomes (qpAdm admixture of various East Asian genetic components in SI 16).

Contemporary Tungusic as well as Nivkh speakers in the Amur form a tight cluster (Extended data Fig. 5). Neolithic hunter-gatherers from Baikal, Primorye and the southeastern Steppe as well as farmers from the West Liao and Amur all project within this cluster (Extended data Fig. 7). Newly-sampled Late Neolithic Angangxi farmers (SI 12) show a high proportion of Amur-like ancestry, while West Liao Neolithic millet farmers show a considerable proportion of Amur-like ancestry with a gradual shift towards the Yellow River genome over time (Extended data Fig. 7, Fig. 3b).[6] Amur-like ancestry thus likely represents the original genetic profile of Neolithic hunter-gatherers covering Baikal, Amur, Primorye, the southeastern Steppe and West Liao, continuing in the early farmers from this region.

The PCA (Extended data Fig. 7) shows a general trend for Neolithic individuals from Mongolia to harbour high Amur-like ancestry with extensive gene flow from western Eurasia increasing from the Bronze to Middle Ages.[36] While the Turkic-speaking Xiongnu,[37] Old Uyghur and Türk are extremely scattered, the Mongolic-speaking[38] Iron Age Xianbei fall closer to the Amur cluster than the Shiwei, Rouran, Khitan and Middle Mongolian Khanate from Antiquity and the Middle Ages.

As Amur-related ancestry can be traced back to speakers of Japanese and Korean, it appears to be the original genetic component common to all speakers of Transeurasian languages. By analysing the first ancient genomes from Korea (SI 12), we find that Jomon ancestry was prevalent on the Peninsula by 6000 BP (Fig. 3b; SI 13). Our PCA (Extended

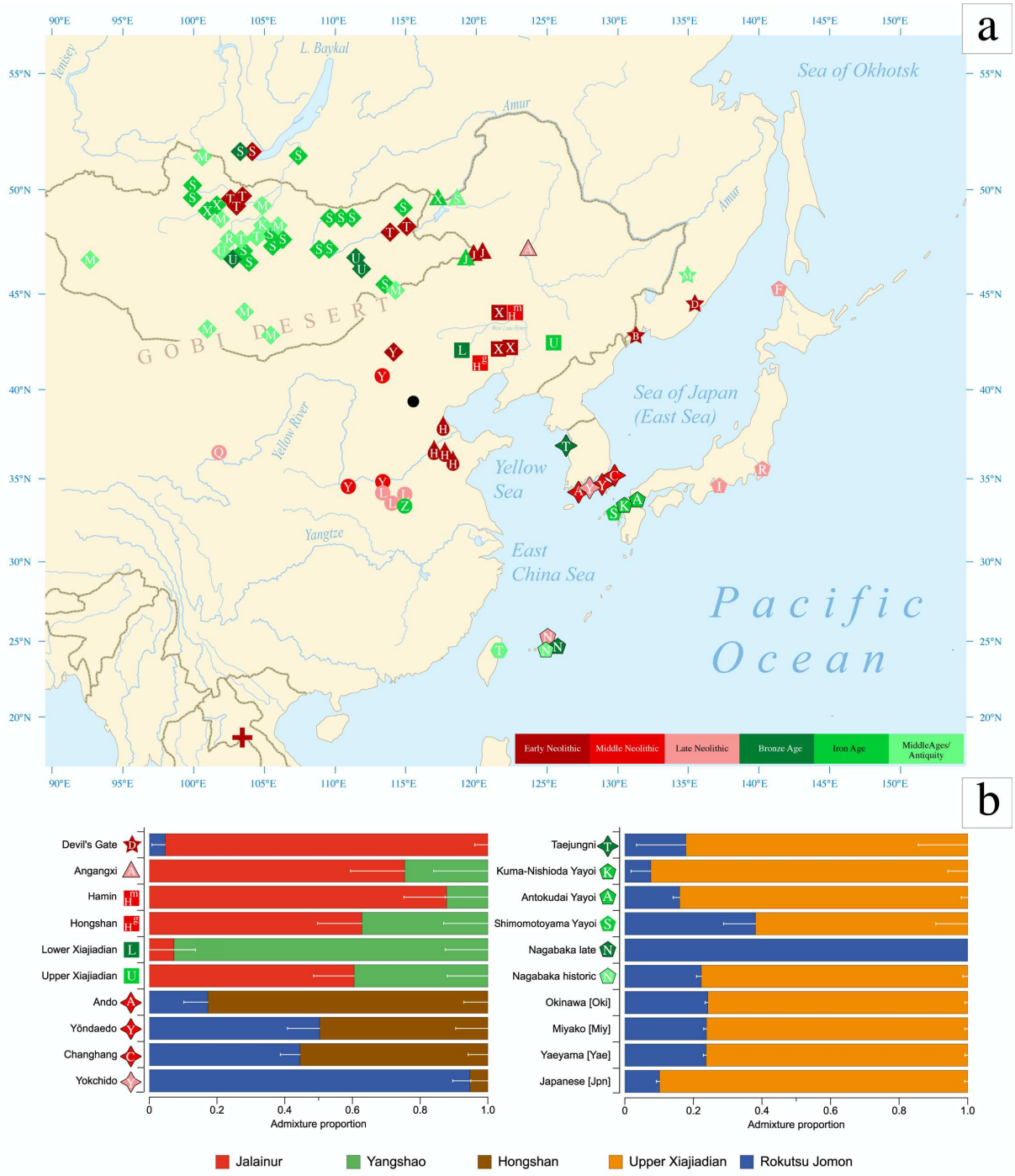
data Fig. 8) shows that all ancient Koreans and Japanese fall on a cline between Jomon and ancient mainland East Asians.

Neolithic Ando, Yŏndaedo and Changhang can be modeled as an admixture of Jomon with a high proportion of Hongshan ancestry, while Yokchido on the southern coast of Korea harbours nearly 95% Jomon ancestry. Taejungni can only be modelled as an admixture of Jomon with Upper Xiajiadian ancestry, suggesting another wave of eastward gene-flow into Korea in the Bronze Age (SI 16). We therefore associate the spread of farming to Korea with two waves of Amur and Yellow River gene-flow, modelled by Hongshan for the Neolithic introduction of millet farming and by Upper Xiajiadian for the Bronze Age addition of rice agriculture.

Analysing the genomes from Yayoi farmers (SI 12), we found that, like Taejungni, they can be modelled as indigenous Jomon ancestry admixed with Bronze Age Upper Xiajiadian ancestry. Our results support massive migration from Korea into Japan in the Bronze Age.

The Nagabaka genomes from Miyako Island (SI 12) represent the first ancient genome-wide data from the Ryukyus. Contrary to previous findings that Holocene populations reached the southern Ryukyus from Taiwan or the Philippines[39], our results unexpectedly suggest the prehistoric Nagabaka population originated in Jomon cultures to the north (Extended data Fig. 8). The genetic turn-over from Jomon- to Yayoi-like ancestry before the early modern period mirrors the late arrival of agriculture and Ryukyan languages in this region.

Fig. 3a Ancient genomes located in time and space. (For detailed legend, see Extended data Fig. 4.) Fig. 3b Admixture modelling of the ancient populations from this study and other key populations.



Discussion: Triangulation

Triangulation of linguistic, archaeological and genetic evidence shows that the origins of the Transeurasian languages can be traced back to the beginning of millet cultivation and the early Amur gene pool in Neolithic Northeast Asia. The spread of these languages involved

two major phases that mirror the dispersal of agriculture and genes (Fig. 4). The first phase represented by the primary splits in the Transeurasian family goes back to the Early-Middle Neolithic, when millet farmers associated with Amur-related genes spread from the West Liao River to contiguous regions. The second phase, represented by linguistic contacts between the five daughter branches goes back to the Late Neolithic, Bronze and Iron Ages, when millet farmers with substantial Amur ancestry gradually admixed with Yellow River, western Eurasian and Jomon populations and added rice, west Eurasian crops and pastoralism to the agricultural package.

Bringing together the spatiotemporal and subsistence patterns, we find clear links between the three disciplines (Extended data Table 1). The onset of millet cultivation in the West Liao region around the 9th millennium BP can be associated with substantial Amur-related ancestry and overlaps in time and space with the ancestral Transeurasian speech community. Lack of evidence for Yellow River influence in the ancestral language and genes is consistent with the multi-centric origins of early millet cultivation suggested in archaeobotany.[26]

The early stages of millet domestication in the 9th to 7th millennia BP are accompanied by evidence for population growth (Extended data Fig. 3), leading to the formation of environmentally or socially separated subgroups in the West Liao River region and broken connectivity between speakers of Altaic and Japano-Koreanic.

Around the mid-6th millennium BP some of these farmers started to migrate eastwards, around the Yellow Sea into Korea and via the Amur into the Primorye, bringing Koreanic and Tungusic languages to these regions and leading to the introduction of Hongshan ancestries. Our newly-analysed Korean genomes are unprecedented in that they testify to the presence of and admixture with Jomon-related ancestries outside Japan.

The Late Bronze Age saw extensive cultural exchange across the Eurasian steppe, resulting in the admixture of populations from the West Liao region and the Eastern steppe

with western Eurasian genetic lineages. Linguistically, this interaction is mirrored in the borrowing of agropastoral vocabulary by Proto-Mongolic and Proto-Turkic speakers, especially relating to wheat and barley cultivation, herding, dairying and horse exploitation.

Around 3300 BP farmers from the Liaodong-Shandong area migrated to the Korean peninsula, adding rice, barley and wheat to millet agriculture. This migration aligns with the observed Upper Xiajiadian component in our Bronze Age sample from Korea and is reflected in early borrowings between Japonic and Koreanic languages.

In the 3rd millennium BP this agricultural package was transmitted to Kyushu, triggering a transition from small- to full-scale farming, a genetic turn-over from Jomon to Yayoi ancestry and a linguistic shift to Japonic. By adding unique samples from Nagabaka in the southern Ryukyus, we traced the Farming/Language dispersal to the edge of the Transeurasian world. Demonstrating that Jomon ancestry stretched as far south as Miyako Island, our results contradict previous assumptions of a northward expansion by Austronesian populations from Taiwan. Together with the Jomon profile discovered at Yokchido in Korea, our results show that Jomon genomes and material culture did not always overlap.

While previous research on the Farming/Language Dispersal hypothesis regarded the Transeurasian zone as beyond the area of agriculture[40,41], our research shows that it remains an important model for understanding Eurasian population dispersals. Triangulation of linguistics, archaeology and genetics resolves the competition between the ‘Pastoralist’ and ‘Farming’ hypotheses and concludes that the early spread of Transeurasian speakers was driven by agriculture.

Fig 4. Integration of linguistic, agricultural and genetic expansions in Northeast Asia.

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307 **References**

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Methods

1. Linguistics

1.1. Bayesian Phylogenetics

Combining dictionary search with fieldwork, we collected a comparative dataset including 3193 datapoints representing 254 basic vocabulary concepts for 98 Transeurasian languages, including contemporary and historical varieties (SI 1). These concepts are based on a merger of the Leipzig-Jakarta 200 list[1] and the Jena 200 list (SI 2). The Turkic and Tungusic basic vocabulary included is based on a revision of recently published datasets.[2,3] Cognate coding is supported by an inventory of basic vocabulary etymologies and sound correspondences across the Transeurasian languages presented in SI 2.

We performed a Bayesian phylogenetic analysis with cognates encoded as binary data.[4] Since the data were collected such that at least one cognate was present, the data were ascertained to not contain any sites having all zeros. Ascertainment correction was applied to cater for this.[3]

We considered the following substitution models, which govern the evolutionary process of cognates along branches of a tree: continuous time Markov chain (CTMC), which assumes a constant rate of mutations, covarion, which assumes a slow and fast rate and the model switching between these two states, and the pseudo Dollo covarion model, which is based on the Dollo principle that a cognate can only appear once, but can be lost many times. A detailed description of the CTMC and covarion models[3] and of the pseudo Dollo covarion model[5] is available in the literature. For all models, we assume each meaning class has its own relative rate to capture the variation between rates of evolution of different words.

Though language evolves on average at a constant rate, we find that there can be considerable variation in rates between branches on a tree.[3,4] Such variation can be captured using the uncorrelated relaxed clock,[6] assuming rates are log-normally distributed.

A birth death model is used to describe the generative process of language creation. Since the data contain ancient languages that may be ancestral to current languages, we allow the tree to have ancestral nodes. A fossilised birth death model[7], which allows such ancestral nodes, is used as prior on the tree. Language family node ages were informed by age priors (Japonic 150BCE +/- 175, Koreanic 1150CE +/- 175, Turkic 150BCE +/- 175, Mongolian 1200CE +/- 50, Tungusic 50CE +/- 275). We found that these node age priors helped reduce uncertainty slightly in the root age distribution.

We compared the fit of different models by estimating the marginal likelihoods using nested sampling[8] (SI 18) and conclude that the pseudo Dollo covarion model with a relaxed clock has the best fit, and covarion with relaxed clock the next best fit. Both models produce compatible time estimates, though covarion estimates tend to have larger uncertainty (that is, have larger 95% HPD intervals). Time estimates of the CTMC model with relaxed clock are still compatible but even wider, and tend to have a higher mean.

All posterior estimates were performed using BEAST v2.6[9] using adaptive coupled MCMC[10]. Detailed specification of the models, priors, hyperpriors and settings used to run these models can be found in the BEAST XML files (SI 19). The results of our Bayesian analysis are visualized as a dated phylogenetic tree of the Transeurasian languages (Extended data Fig. 1).

1.2. Bayesian Phylogeography

We assumed that the dispersal of people through Eurasia can be described as a random walk, so is best captured by diffusion on a sphere.[11] In order to get an impression about the uncertainty in locating origins by such model, we performed a post-hoc analysis using the posterior tree set from the lexical analysis. We assigned point positions to the tips and randomly sampled trees from the posterior while estimating geographical parameters through MCMC. Even in this relatively restricted set-up, the uncertainty in root location does not allow us to distinguish the

different geographical origin hypotheses. The results of our analysis are represented on a map (SI 3).

1.3. Linguistic palaeontology

We compiled comparative agropastoral vocabularies for each Transeurasian subfamily, i.e., Turkic (SI 5a), Mongolic (SI 5b), Tungusic (SI 5c), Koreanic (SI 5d) and Japonic (SI 5e). We applied linguistic reconstruction, a procedure for inferring an unattested ancestral state of a language on the evidence of data that are available from a later period, to corresponding words (SI 5).

In order to distinguish between inherited and borrowed correspondence sets, we used standard criteria based on the phonology, semantics, morphology and distribution of the word involved, as specified in SI 5. Dividing our dataset into inherited *versus* borrowed subsistence vocabulary, we determined distinctive spatiotemporal and cultural patterns for each category (SI 5).

We applied linguistic palaeontology to our subsistence vocabulary, a historical comparative method that enables us to study human prehistory by correlating our linguistic reconstructions with information from archaeology about the culture of the ancient speech communities that used these words. In this way, we drew inferences about the subsistence strategies available to speakers of the different Transeurasian proto-languages in the Neolithic and Bronze Age (SI 5) and identified a plausible location for the homeland of the ancient speech communities involved (SI 4).

1.4. Diversity hotspot principle

In order to estimate the location of the ancient speech communities involved, we combined Bayesian phylogeography and linguistic palaeontology with the diversity hotspot principle.

78 The principle is based on the assumption that the homeland is closest to where one finds the
79 greatest diversity with regard to the deepest subgroups of the language family. We located
80 these areas on the map and took them as an approximation of the area where a certain proto-
81 language began to diversify (SI 4). Although this method must contend with certain
82 limitations, taken together with the other techniques for homeland location discussed here, it
83 can give us a reasonably robust estimation of the location of an ancient speech community.
84
85 *2. Archaeology*
86 *2.1. Archaeological database*
87 We scored 172 cultural traits for a total of 255 Neolithic-Bronze Age archaeological
88 sites/phases from the West Liao river basin (36), the Amur (Jilin, Heilongjiang and inland
89 Liaoning) (32), the Primorye (4), the Liaodong peninsula (37), the eastern steppes (1), the
90 Shandong peninsula (4), the Yellow River basin (2), the Korean peninsula (58) and the
91 Japanese Islands (85). Sites with several major cultural phases were scored separately. The
92 sites date from 8400-1700 BP and include the Early Neolithic to Bronze Age in northeast
93 China, the Middle Neolithic Zaisanovka culture in the Primorye, the Middle-Late Neolithic
94 Chulmun and Bronze Age Mumun cultures in Korea, and the Late Neolithic/Bronze Age
95 Final Jomon and Yayoi cultures in western Japan. Categories of cultural traits scored
96 comprised ceramics (70), stone tools (38), buildings and houses (9), plant and animal remains
97 (26), shell and bone artefacts (17), and burials (12). Definitions of scored features are found
98 in SI 6 (sheet 2) and further discussion of scoring methods can be found in SI 7. All features
99 were scored as present (1) or absent (0) following published site reports or other literature.
100 The database was used to analyse changes in the distribution of Neolithic and Bronze Age
101 artefacts over time, especially in relation to the spread of agricultural systems in Northeast
102 Asia (SI 7).

In addition, the cultural data in our archaeological database were analyzed using Bayesian phylogenetic methods. The cultural data are encoded as a binary alignment, and we applied the same substitution and clock models as for the lexical data. The pseudo Dollo model with relaxed clock fits the data best (SI 20). Since the coefficient of variation of the relaxed clock exceeded 1, which indicates a considerable amount of variation, we also ran the analysis with the standard deviation capped at 1, which only slightly affected time estimates.

The large number of sampling dates and uncertainty on number of missing cultures made it hard to apply the fossilised birth death prior, so we opted for the flexible Bayesian skyline plot instead.[12] Timing information is based on sampling dates of archaeological finds. Since there is uncertainty in dating of these findings, tip dates were uniformly sampled in these intervals during the MCMC. All analyses were performed in BEAST 2.6[8] using adaptive coupled MCMC.[9] Details on models, priors, hyperpriors and settings can be found in the BEAST XML (SI 21).

In line with previous archaeological studies[13,14,15], we constrained the clades 'Xinglongwa-Zhabaogou-Hongshan' and 'Yabuli-Primorye' to be monophyletic (SI 8). The results of our Bayesian analysis are visualised as a phylogenetic tree of archaeological cultures in Northeast Asia (Extended data Fig. 2) and interpreted in SI 8.

2.2 Archaeobotanical database

In addition to the database of archaeological features, we also compiled a list of the earliest cereal remains from each region of Northeast Asia directly dated by radiocarbon (SI 9). This list comprises 268 samples (China: 82; Primorye: 12; Korea: 31; Japan (excluding Ryukyus): 119; Ryukyu Islands: 24). Radiocarbon dates in this database were re-calibrated using OxCal 4.4. Our databases were further supplemented by published datasets for faunal remains[16,17], dolmens[18], and spindle whorls[19]. We used kernel density mapping to plot the spread of

cereals in this database over time across Northeast Asia. The results are shown in SI 7 and Extended data Fig.10.

3. Genetics

3.1. Laboratory procedures

Ancient DNA wet lab work, including the DNA extraction and library preparation was performed in a dedicated ancient DNA clean room facility at the MPI-SHH in Germany and in an ancient DNA lab at Jilin University in China following established protocols.[20] A double-stranded library was built with 8-mer index sequences at both P5 and P7 Illumina adapters. Four individuals from China characterised in Jilin were directly shotgun sequenced on the Illumina HiSeq X10 instrument in the 150-bp paired-end sequencing design to obtain an adequate coverage. 54 double-stranded libraries for 33 individuals from Korea and Japan were generated and characterised in the MPI-SHH either by shotgun sequencing or by in-solution capture at approximately 1.2 million informative nuclear SNPs. After initial screening the preservation of those libraries, a further 54 single-stranded libraries were built aiming at retrieving more endogenous DNA from the samples and again, those libraries were directly shotgun sequenced and in-solution captured at ca. 1.2 million SNPs (SI 17) and sequenced on the Illumina HiSeq 4000 platform following the manufacturer protocols.

3.2. Sequence data processing

Raw sequencing reads were processed by an automated workflow with the EAGER v1.92.55 programme.[21] Illumina adapter sequences were trimmed from the sequencing data and overlapping pairs were merged with AdapterRemoval 2.2.0.[22] We mapped the merged reads with a minimum of 30 bp to the human reference genome (hs37d5; GRCh37 with decoy sequences) using BWA v0.7.12.[23] We removed PCR duplicates by DeDup v0.12.2.[17] To minimise the impact of post-mortem DNA damage on genotyping, we masked 2 bp for non-UDG libraries and 10 bp for half-UDG libraries on both ends per read using the trimbam function on bamUtils v1.0.13.[24] The cleaned reads with both base quality (Phred-scale quality) and mapping quality (Phred-scale mapping quality) over 30 were piled up by SAMtools 1.3[19] with the mpileup function. We called pseudo-diploid genotypes using the pileupCaller program [https://github.com/stschiff/sequenceTools] against SNPs in the '1240K' panel[25,26] under the random haploid calling mode. For C/T and G/A SNPs, we used the masked BAM files, and for the rest we used the original unmasked BAM files.

3.3. Reference datasets

We compared our ancient individuals to two sets of world-wide genotype panels, one based on the Affymetrix HumanOrigins Axiom Genome-wide Human Origins 1 array ('HumanOrigins'; 593,124 autosomal SNPs)[27], the '1240k' panel.[20,28] We augmented both data sets by adding the Simons Genome Diversity Panel[29] and published ancient genomes (SI 11).

3.4. Ancient DNA authentication

We applied multiple criteria to confirm the authentication of the newly published ancient genomes from northern China, Korea and Japan. First, we characterized the post-mortem chemical modifications characteristic for ancient DNA using mapDamage v2.0.6.[30] Second, we estimated mitochondrial contamination rates for all individuals using Schmutzi v1.5.1.[31] Third, we measured the nuclear genome contamination rate in males based on X chromosome data as implemented in ANGSD v0.910.[32] Since males have only a single copy of the X chromosome, mismatches between bases, aligned to the same polymorphic position, beyond the level of sequencing error are considered as evidence of contamination.

3.5. Population structure analysis

We performed a Principal component analysis (PCA) with the smartpca v16000[33] using a set of 2,077 present-day Eurasian individuals from the 'HumanOrigins' dataset and the '1240k-Illumina' dataset with the option 'lsqproject: YES' and 'shrinkmode: YES'. We used outgroup-f_3 statistics[34,35] to obtain a measurement of genetic affinity between two populations since their divergence from an African outgroup. We calculated f_4 statistics with the '*f4mode: YES*' function in the admixtools.[31] Both f_3 and f_4 statistics were calculated using qp3Pop v435 and qpDstat v755 in the admixtools package.

3.6. Genetic sexing and uniparental haplogroup assignment

We determined the molecular sex of our ancient samples by comparing the ratio of X and Y chromosome coverages to autosomes.[36] For females, we would expect an approximately even ratio of X to autosome coverage and a Y ratio of 0. For males we would like to expect roughly half of the coverage on X and Y than autosomes.

3.7. Admixture modeling with qpAdm

We modelled the ancient individuals in this study using the qpWave/qpAdm framework (qpWave v410 and qpAdm v810) in the admixtools v5.1 package.[22] We used the following 9 populations in '1240k' datasets as outgroup ("OG"): Mbuti, Natufian, Onge, Iran_N, Villabruna, Mixe and, Ami. This set includes an African outgroup (Mbuti), early Holocene Levantine hunter-gatherers (Natufian), Andamanese islanders (Onge), early Neolithic Iranians from the Tepe Ganj Dareh site (Iran_N), late Pleistocene European hunter-gatherers (Villabruna), Central Native Americans (Mixe), and an indigenous group native to Taiwan (Ami).

4. Triangulation

The term 'triangulation' is borrowed from a navigational technique that determines a single point in space with the convergence of measurements taken from two other distinct points. In qualitative research it designates a method used to capture different dimensions of the same phenomenon by using evidence from three distinct scientific disciplines. To avoid circularity in the argumentation, data collection, analyses and results are performed or reached within the limits of each individual discipline, independently from the other two. Only in the final phase of the triangulation process are the inferences drawn by the three disciplines mapped on each other by comparing a number of variables describing the phenomenon. The purpose of triangulation is to increase the credibility and validity of the results by evaluating the extent to which the evidence from the three disciplines converges and by identifying correlations, inconsistencies, uncertainties and potential biases across the different perspectives on the investigated phenomena.

Building on previous applications of triangulation in anthropology[37], we applied the method to the dispersal of the Transeurasian languages, integrating linguistics, archaeology and genetics to contribute to a better understanding of the phenomenon. We collected different datasets and applied the variety of methods described above to draw independent inferences with regard to a number of variables such as location, chronology, migratory dynamics, continuity vs. diffusion, and subsistence patterns (Extended data Table 1).

223 Aligning the evidence offered by the three disciplines, we gained a more balanced and
224 richer understanding of Transeurasian migration than each of the three disciplines could
225 provide us with individually.
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Author contributions

The research was conceptualized by MR. Linguistic datasets were collected by AS, JD, SO, BD, RB, SR, KDA, IG, OM, JRB and MR. The linguistic database was scored by MR and analysed by MR and RB. Etymologies were established by MR. The archaeology database was scored by TL, MC, TK, GK, JU and LG, and analysed by MJH, RB, MR, MC and IB. The Nagabaka site was excavated by TK and KY under the direction of MJH with advice from MK and HI. Post-excavation analyses of materials from Nagabaka were analysed by KY, TK, NS, H Tomita, H Takamiya, JU, PR, RF and MY. YQC shared the Angangxi data, DIA the ancient Korean data, KS the Yayoi data and HI, RK, TS, HO the modern Ryukyu data. Ancient DNA data from Korea and Japan were generated by JK and the wet lab works were carried out by RB and MH. Genetic data analyses were carried out by CN with advice from Choongwon Jeong and input from HKK and FZ. The writing was done by MR, MJH and CN.

Competing interests

The authors declare no competing interests.

Data availability

All linguistics and arcahaeological datasets are available through the supplementary information. For our genetic datasets, the aligned sequences are available through the European Nucleotide Archive under accession number [to be made available on publication]. Genotype data used in analysis are available at https:// [to be made available on publication]. Any other relevant data are available from the corresponding author upon reasonable request.

Code availability

Readers can access the code underlying our Bayesian analyses of linguistic and cultural datasets through the supplementary information. The files in SI 19 relate to languages and those in SI 21 to cultures.

Figure legends

Fig. 1a. Geographical distribution of the 98 Transeurasian language varieties included in this study. Contemporary languages are represented by coloured surfaces, historical varieties by red dots. Fig. 1b. Transeurasian ancestral languages spoken during the Neolithic (red) and Bronze Age and later (green).

03_Eurasia3angle_synthesis_Fig 1ab.jpg

Fig. 2a Spatiotemporal distribution of sites included in the archaeological database. Fig. 2b Clustering of investigated sites according to cultural similarity in line with Bayesian analysis in Extended data Fig. 2 with indication of the spread of millet and rice in time and space. The distributions of archeological sites in Fig. 2 does not match that of contemporary languages in Fig. 1 because we focus on the early dispersal of the linguistic subgroups in the Neolithic and Bronze Age and on the links between the eastward spread of farming and language dispersal.

04_Eurasia3angle_synthesis_Fig 2a.jpg

Fig 3a Ancient genomes located in time and space. For detailed legend, see Extended data Fig. 5. Fig 3b Admixture modelling of the ancient populations from this study and other key populations.

05_Eurasia3angle_synthesis_Fig 3ab_genomes on map_admix plot

Fig 4. Integration of linguistic, agricultural and genetic expansions in Northeast Asia

06_Eurasia3angle_synthesis_Fig_4_overview map

Extended data legends

Extended data Fig. 1. Dated Bayesian phylogeny of the Transeurasian languages

07_Eurasia3angle_synthesis_Extended data Fig 1_language phylogeny.tree

07_Eurasia3angle_synthesis_Extended data Fig 1_language phylogeny.pdf

Extended data Fig. 2. Bayesian phylogenetic analysis of the archaeological database

08_Eurasia3angle_synthesis_Extended data Fig 2_draft cultural phylogeny.tree

08_Eurasia3angle_synthesis_Extended data Fig 2_draft cultural phylogeny.pdf

Extended data Fig. 3. Demographic changes with agriculture in Neolithic and Bronze Age Northeast Asia. The left column shows changes following the adoption of millet farming ca. 8000-4000 BP, using quantity of pottery for the West Liao[33] and radiocarbon proxy dates for Korea.[140] The right column shows long-term dynamics ca. 8000-2000 BP following the integration of millet with rice, barley and wheat in the Bronze Age and based on site numbers for NE China,[138] radiocarbon dates for Korea[140] and site numbers for Japan.[141] For references see SI 7.

09_Eurasia3angle_synthesis_Extended data Fig 3_demography

Extended data Fig. 4 Ancient genomes located in time and space, including legend
10_Eurasia3angle_synthesis_Extended data Fig 4_legend

Extended data Fig. 5 PCA displaying the genetic structure of present-day Eurasians. PC1 separates Western and Eastern Eurasian populations, PC2 Southern and Northern Eurasian populations. Transeurasian populations are colored according to subfamily (Turkic in grey, Mongolic in orange, Tungusic in yellow, Koreanic in pink, Japonic in light grey). Non-Transeurasian populations are colored according to families. Populations are labeled with three letters, for a list of abbreviations, see SI 10.
11_Eurasia3angle_synthesis_ Extended data Fig 5_PCA present-day Eurasian.

Extended data Fig. 6 PCA displaying the genetic structure of present-day East Asians. Populations are labeled with three letters, for a list of abbreviations, see SI 10.
12_Eurasia3angle_synthesis_ Extended data Fig 6_PCA present-day East Asian.

Extended data Fig. 7. Ancient genomes plotted on PCA displaying genetic structure of present-day Eurasians. For a detailed legend see Extended data Fig. 4.
13_Eurasia3angle_synthesis_ Extended data Fig 7_PCA ancient Eurasian

Extended data Fig. 8. Ancient genomes plotted on PCA displaying genetic structure of present-day East Asians. For a detailed legend see Extended data Fig. 4.
14_ Eurasia3angle_synthesis_ Extended data Fig 8_PCA_ancient East Asian

Extended data Table 1. Overview of triangulation of spatiotemporal, subsistence and demographic patterns, integrating linguistic, archaeological and genetic findings

15_Eurasia3angle_synthesis_ Extended data Fig 9_triangulation

Supplementary information legends

SI 1. Comparative dataset including 3193 datapoints representing 254 basic vocabulary concepts for 98 Transeurasian languages

16_Eurasia3angle_synthesis_SI 1_BV 254.xls

SI 2. Basic vocabulary etymologies across the Transeurasian languages, underlying semantically equivalent cognate sets scored as (1) in SI 1

17_ Eurasia3angle_synthesis_SI 2_basic etymologies.doc

SI 3. Bayesian phylogeographic analysis modelling the spatiotemporal expansion of the Transeurasian languages

18_Eurasia3angle_synthesis_SI 3_phylogeography.klm

SI 4. Integration of qualitative assessment methods and Bayesian phylogeography in identifying the ancestral homelands of Transeurasian

19_Eurasia3angle_synthesis_SI 4_homelands.docx

SI 5. Inherited and borrowed correspondence sets for agropastoral vocabulary across the Transeurasian languages.

20_Eurasia3angle_synthesis_SI 5_subsistence.docx

SI 5a. Agropastoral vocabulary shared by the Turkic languages

21_Eurasia3angle_synthesis_SI 5a_Turkic.docx

SI 5b. Agropastoral vocabulary shared by the Mongolic languages

22_Eurasia3angle_synthesis_SI 5b_Mongolic.docx

SI 5c. Agropastoral vocabulary shared by the Tungusic languages

23_Eurasia3angle_synthesis_SI 5c_Tungusic.docx

SI 5d. Agropastoral vocabulary shared by the Koreanic languages

24_Eurasia3angle_synthesis_SI 5d_Koreanic.docx

SI 5e. Agropastoral vocabulary shared by the Japonic languages

25_Eurasia3angle_synthesis_SI 5e_Japonic.docx

SI 6. Archaeological database

26_Eurasia3angle_synthesis_SI 6_E3a Matrix.xls

SI 7 Qualitative analysis of the archaeological database

27_Eurasia3angle_synthesis_SI 7_qualitative analysis

SI 8 Interpretation of our Bayesian phylogenetic analysis of the archaeological database in Extended data Fig. 2.

28_Eurasia3angle_synthesis_SI 8_Bayesian cultural interpretation

SI 9 Early crop remains with direct C14 dates from Northeast Asia. Compiled from published sources and from the radiocarbon database of the National Museum of Japanese History. Radiocarbon dates on rice from the Nabatake site (Saga) are omitted since several of the results from that site published in the early 1980s appear unreliable.

29_Eurasia3angle_synthesis_SI 9_cerealC14.xls

SI 10 List of abbreviations used for present-day Eurasian populations

30_Eurasia3angle_synthesis_SI 10_abbreviations

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35_Eurasia3angle_synthesis_SI 15_isotope

SI 16 qpAdm admixture modeling of ancient and modern populations in this study

36_Eurasia3angle_synthesis_SI 16_qpAdm

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39_Eurasia3angle_synthesis_SI 19_XML files_languages

SI 20 Comparison of fit of different models estimating the marginal likelihoods using nested sampling

40_Eurasia3angle_synthesis_SI 20

SI 21 BEAST XML files specifying the models, priors, hyperpriors and settings used to run the analyses of the archaeological database

41_Eurasia3angle_synthesis_SI 21_XML files_cultures

SI 22 Results of filtering contaminated samples included in this study, using PCA for contamination control

42_Eurasia3angle_synthesis_SI 22_filtering contamination

Supplementary Files

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- 17Eurasia3anglesynthesisSI2basicetymologies.docx
- 18Eurasia3anglesynthesisSI3phylogeography.txt
- 19Eurasia3anglesynthesisSI4homelands.pdf
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