Genomic Insights into the Demographic History of Southern Chinese

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ABSTRACT

Southern China is the birthplace of rice-cultivating agriculture, different language families, and human migrations that facilitated these cultural diffusions. The fine-scale demographic history *in situ*, however, remains unclear. To comprehensively cover the genetic diversity in East and Southeast Asia, we generated genome-wide SNP data from 211 present-day Southern Chinese and co-analyzed them with more than 1,200 ancient and modern genomes. We discover that the previously described 'Southern East Asian' or 'Yangtze River Farmer' lineage is monophyletic but not homogeneous, comprising four regionally differentiated sub-ancestries. These ancestries are respectively responsible for the transmission of Austronesian, Kra-Dai, Hmong-Mien, and Austroasiatic languages and their original homelands successively distributed from East to West in Southern China. Multiple phylogenetic analyses support that the earliest living branching among East Asian-related populations is First Americans (~27,700 BP), followed by the pre-LGM differentiation between Northern and Southern East Asians (~23,400 BP) and the pre-Neolithic split between Coastal and Inland Southern East Asians (~16,400 BP). In North China, distinct coastal and inland routes of south-to-north gene flow had established by the Holocene, and further migration and admixture formed the genetic profile of Sinitic speakers by ~4,000 BP. Four subsequent massive migrations finalized the complete genetic structure of present-day Southern Chinese. First, a southward

Sinitic migration and the admixture with Kra-Dai speakers formed the 'Sinitic Cline'. Second, a bi-directional admixture between Hmong-Mien and Kra-Dai speakers gave rise to the 'Hmong-Mien Cline' in the interior of South China between ~2,000 and ~1,000 BP. Third, a southwestward migration of Kra-Dai speakers in recent ~2,000 years impacted the genetic profile for the majority of Mainland Southeast Asians. Finally, an admixture between Tibeto-Burman incomers and indigenous Austroasiatic speakers formed the Tibeto-Burman speakers in Southeast Asia by ~2,000 BP.

INTRODUCTION

Dated to ~9,000 years before present (BP), Southern China is one of the two earliest agricultural centers in East Asia[1,2]. The First Farmers in Southern China domesticated a series of plants and animals indispensable for present-day people[3], among which the most famous one is wet rice (*Oryza japonica*)[4]. It has long been hypothesized that the farming dispersal from Southern China involves human migration and in term the language families spoken by the farmers[5]. Recent studies have shown that the First Farmers in Southeast Asia[6,7] and Pacific Islands[8-10] derived most of their ancestry from a lineage shared with modern Southern Chinese, which has further been confirmed by ancient genomes from Fujian in coastal Southern China[11] and adjacent Taiwan Island[12]. These finding supports the involvement of massive migration in the diffusion of Austronesian and Austroasiatic languages. However, our knowledge is still limited about the deep origin and early prehistory of such a 'Southern East Asian' or 'Yangtze River Farmer' lineage and its role in the genomic formation of modern Southern Chinese, especially the speakers of the other two indigenous language families in Southern East Asia, Hmong-Mien and Kra-Dai.

Here we generated new genome-wide data of 211 present-day Southern Chinese individuals, who belong to 30 geographic subgroups that have not yet been represented in genomic studies and cover the three main language families in this region, i.e., Hmong-Mien, Kra-Dai, and Sino-Tibetan. To thoroughly reconstruct the demographic history of Southern Chinese in relation to other East Asians, we co-analyzed them with ~1,200 modern and high-coverage ancient samples from East and Southeast Asia, which cover the main ethnolinguistic and archaeological diversity in East Asia that is accessible till now with a high resolution.

Our study mainly addressed on three primary questions regarding the genomic history in East Asia. (1) How many ancestries substantially contributed to the gene pool of present-day East Asians and to what extent did they participate in the diffusion of different language families? Especially, if there are any sub-structure with the Southern East Asians? (2) What is the deep history regarding the origin of these ancestries and where did they originally inhabit? (3) What migrations and admixtures did these ancestries involve in the formation of present-day Southern Chinese?

In response to questions above, we first gained an overview of genetic structure by principal component analysis (PCA)[13] (Fig. 1A and B) and model-based clustering[14] (Fig. 1C). To quantify the genetic affinity, we measured the degree of shared genetic drift[15] (Fig. 2A) and shared haplotypes[16] (Fig. 2B and C) among pairwise populations. We performed admixture graph modelling (Fig. 3A), admixture proportion estimation (Fig. 3B), and coalescent analysis based on site frequency spectrum (SFS) (Fig. 3C) to investigate the deep phylogenetic relationship and infer the geographic distribution of these ancestries. We then applied multiple methods, including the formal test of genetic homogeneity (Fig. 4), to further explore the admixtures in Southern China. Demographic history in East Asia and recent migrations and admixtures in Southern China has been summarized into map illustrations (Fig. 5). All the analyses above allow us to better decipher both the long-term prehistory and recent two millennia's documented history along with Sinicization in Southern China from a genomic perspective.

RESULTS

A. Genetic structure in East Asia highly corresponds to linguistic affiliations

PCA of all the ancient and modern East Asians in our dataset (Fig. 1A) replicates the pattern of genetic differentiation between Northern and Southern East Asians[11,12] and variations between two geographically structured clusters within Northern East Asia[12,17]. The 'Inland Yellow River Cluster' is best represented by Neolithic Farmers from Inland Yellow River Basin (Yangshao_MN and Qijia_LN[17]) and later and modern Tibetan Plateau inhabitants. In ADMIXTURE plot (Fig. 1C), the ancestry maximizing in this cluster is also ubiquitous in modern Sino-Tibetan speakers (Fig. 1C), consistent with previous linguistic studies that suggested a plausible origin of Proto-Sino-Tibetan in Yangshao Culture[18,19]. The 'Northeast Asian Cluster' is typified by the Neolithic hunter-gatherers in Amur River Basin (DevilsCave_N[18,19] and Boisman_MN[12]), Mongolian Plateau, and Cis-Baikal (Shamanka_EN and Lokomotiv_EN[19]), as well as modern populations from Amur River region (Fig. 1A), and these surrogates also harbor the highest proportion of the ancestry prevalent in modern Tungusic speakers and other Northeast Asians. We observe consistent clustering manners in pairwise outgroup-f_3 (Fig. 2A) and haplotype sharing degree measured by identity-by-descent (IBD) chunks (Fig. 2B and C).

Confirming the highly shared genetic history among the Southern East Asians, we find that Kra-Dai and Hmong-Mien populations in Southern China, Southern Han Chinese, and Austronesian Taiwanese cluster together with a high sharing degree ($f_3 > 0.320$) in outgroup-f_3 matrix (Fig. 2A). We further identify a previously unknown genetic structure within the Southern East Asians that has a strong connection with linguistic classification. That is, each of the speakers of all the four indigenous language families in Southern China and Southeast Asia has their own cluster in PCA for Southern East Asians (Fig. 1B) and their own ancestral component in ADMIXTURE plot (Fig. 1C). Austronesian-related ancestry maximizes in ancient and modern Austronesian Taiwanese with a high proportion in earlier Fujian Neolithic individuals. Austroasiatic-related ancestry maximizes in Neolithic farmers in Mekong River Basin (collectively referred as 'Mekong_N' afterwards) and is also extensively distributed in Mainland Southeast Asia. Hmong-Mien-related ancestry maximizes in the Western Hmong populations (Miao_Longlin and Miao_Xilin) newly reported in this study and is absent in all the ancient individuals, indicating that the original homeland of this ancestry has not yet been sampled in ancient genomic studies to date. Kra-Dai-related ancestry maximizes in modern Kra-Dai speakers resident in Mainland Southern China (Zhuang, Maonan, Mulam) and neighboring Hainan Island (Hlai). Especially in Austronesian- and Hmong-Mien-speaking populations, we observe a high degree of IBD sharing between the surrogate populations with other populations of the same language affiliation [number > 11.5, length > 18.5 cM for Atayal; number > 12.4, length > 32.0 cM for Miao_Longlin], which indicates strong genetic drift or founder effect in both ancestries. We use the terms 'Core Austronesians/ Kra-Dais/ Hmong-Miens/ Austroasiatics' to address modern surrogates of each of the ancestries.

We implemented point-biserial correlation to formally examine if the proportion of ancestries in ADMIXTURE is significantly associated with corresponding language families (Extended Data Table 2), which shows a strong correlation to linguistic affiliation for all the six major ancestries in East Asia ($r_{pb} > 0.500$, $p < 0.0001$). The gene-language correlation indicates that present-day speakers of the major language families in East Asia usually receive a strong genomic legacy from the speakers of corresponding proto-languages, which enables us to trace the history of these language families through the history of human populations.

B. Reconstruction of ancestral homelands in Southern China

One of the crucial historical aspects for a language family is its original homeland, or *Urheimat*. In historical linguistics, two main strategies have been applied for the reconstruction of linguistic homeland[20]. One of the strategies leverages the reconstructed vocabulary of the proto-language to inform us about the environment and lifestyle of the original speakers, which is in turn a clue for geographic origin. The other strategy assumes that the linguistic homeland tends to be located in where there is a higher linguistic diversity[21].

However, both linguistic strategies cannot work well in case of the four major language families that are indigenous in Southern East Asia and are supposed to originate from Southern China. First, all of the four language families share some words reflecting either a common origin or extensive language contact among all of them, especially the ones related to farming and domestication[22], which prevents us to infer the homeland distribution within Southern China in a higher resolution. Second, massive cultural transition happened in Southern China in recent millennia, especially Sinicization[23], may have largely decreased language diversity in this region. Given the language-associated genomic structure in Southern East Asia, here we adapted another genomics-based strategy — modelling the phylogenetic relationship among the ancestries to infer their relative geographic distribution, hence the homelands for the language families they spread.

We implemented *qpGraph*[24] to model the phylogenetic relationship of the main ancestries in East Asia, using populations in which the corresponding ancestries maximize in PCA (Fig. 1A and B) and ADMIXTURE (Fig. 1C) as surrogates. Our optimal model (Fig. 3A) shows that Northern East Asians (Mongolia_N, Boisman_MN, and Sherpa) and Southern East Asians (Hanben_IA, Hlai_Qiongzhong, Miao_Longlin, and MSEA_N) each form a monophyletic lineage, with additional admixture from an Andamanese-related deep ancestry in the common ancestor of Southern East Asians (31%). As Core Kra-Dais, Core Hmong-Miens, and the earliest Austronesian-related ancient group (Qihe_EN and Liangdao_EN) are located in Southern China, we can reasonably deduct that the common ancestor of Southern East Asian lineage and its initial diversification also took place in Southern China. Sub-topology within the Southern East Asian lineage suggests that Austronesian ancestry split with the others first, then followed by Kra-Dai ancestry, with Hmong-Mien and Austroasiatic ancestries sharing the most genetic drift with each other. Given the easternmost and westernmost geographic position respectively for the earliest Austronesian- (Qihe_EN and Liangdao_EN) and Austroasiatic-related (Mekong_N) individuals, such a topology can be explain as a result of the isolation-by-distance pattern from east to west in ancient Southern China sequentially for Austronesian, Kra-Dai, Hmong-Mien, and Austroasiatic ancestries (Fig. 5A).

To test if the pattern observed above is more extensively applicable in East Asian populations, we then used *qpAdm*[25] to parse the contribution of Northern, Coastal Southern, and Inland Southern East Asian lineages, respective represented by Mongolia_N (as they have minimal Southern East Asian ancestry in admixture graph), Fujian_LN, and Mekong_N (Fig. 3B). Core Austronesians and Core Austroasiatics respective derive most of their ancestry related to Fujian_LN (66.9%–74.3%) and Mekong_N (58.0%–75.2%), suggesting that the Neolithic genomic structure in Southern East Asians has largely preserved in these modern isolated populations. In present-day Southern China, Core Kra-Dais harbors more of their ancestry related to Fujian_LN (39.0%–53.9%) than Mekong_N (24.9%–32.3%) and we also observe a similar pattern in Southeast Han Chinese (28.9%–40.3% for Fujian_LN and 21.8%–25.2% for Mekong_N), suggesting that the Kra-Dai ancestry itself primarily derives from an Austronesian-related lineage with additional Austroasiatic-related gene flow. On the contrary, Core Hmong-Mien derives more of their ancestry related to Mekong_N (32.3%–35.3%) than Fujian_LN (23.7%–26.4%), consistent with the closest phylogenetic relationship of Austroasiatic and Hmong-Mien ancestries in admixture graph (Fig. 3A). Regardless different topology between Kra-Dai and

Austronesian ancestries suggested by *qpGraph* and *qpAdm*, both analyses indicate a consistent pattern for original geographical distribution of these four ancestries (Fig. 5A).

We used admixture-f_3 statistics[24] to examine two alternative explanations for phylogenetic relationship between Kra-Dai and Austronesian ancestries. Due to small effective population size (N_E) and strong genetic drift in many East Asian populations (Extended Table Fig. 1), we are usually unable to obtain significant negative f_3. Therefore, we focused on the lowest f_3 value given by different pairs of source populations and exhausted all the potential pairs. The results might not be statistically significant, but it can provide a consistent pattern if the same pair of source populations minimizes f_3 of a series of different target populations. For most of the Kra-Dai-speaking populations and Vietic speakers who have a genetic profile resembling their Kra-Dai neighbors (Extended Table 3C), the lowest f_3 achieves when one of the source population surrogates Austroasiatic ancestry (Mekong_N, Malaysia_LN, and Mlabri) and the other surrogates Austronesian ancestry (Fujian_LN and Austronesian Taiwanese), with the strongest negative signal in Kra-Dai and Vietic speakers in Mainland Southeast Asia (Muong, Nung, Lao). Since all of these populations live in the northern interior of Mainland Southeast Asia, a direct and recent gene flow from Austronesian speakers does not seem to be a feasible scenario. A more possible scenario is that the Kra-Dai ancestry itself, at least partially, is closely related to Austronesian ancestry and this favors the model suggested by *qpAdm*. The partial Austronesian-related origin for Kra-Dai ancestry is compatible with the 'Austro-Tai' hypothesis in historical linguistic[26-28] that suggests a common origin of Austronesian and Kra-Dai language families, and the motif Y-chromosomal haplogroup O1a-M119 that is dominant in Neolithic Fujian individuals[11] and shared by Austronesians, Kra-Dais, and Southern Han Chinese[29].

The impact of distinct Southern East Asian ancestries is not limited within Southern China and further south. In the earliest samples from Yellow River Basin, coastal individuals from Early Neolithic Shandong derive all of the southern ancestry from a Fujian_LN related lineage (32.0 ± 6.6%, Fig. 3B), consistent with their Austronesian-related ancestral component in ADMIXTURE (Fig. 1C) that largely disappears in later Northern East Asians. In contrast, inland individuals from Middle Neolithic Yangshao Culture derive all of the southern ancestry from a Mekong_N related lineage (32.2 ± 5.9%, Fig. 3B). These genomes document that the initial isolation and genomic differentiation among geographically structured populations in Southern China is no late than Early Neolithic and demographic contact between Northern and Southern China in this period is via distinct coastal and inland routes (Fig. 5A).

Instead of a direct contribution from contemporary Neolithic Fujian population, a more plausible scenario for the Austronesian-related ancestry in Shandong Neolithic individuals they received a gene flow from a currently unsampled ancient population from neighboring regions like Jiangsu or Zhejiang, who in turn harbored a Fujian_LN-related lineage (Fig. 5A). This scenario is also consistent with the strong connection between Neolithic cultures in Lower Yangtze Basin, like Hemudu Culture, and contemporary Fujian, like Tanshishan Culture, to which the Fujian_LN individuals belong[11]. Taking genomic, linguistic, and archaeological evidence together into account, Kra-Dai ancestry likely originates from the local Austronesian-related lineage in continental Southeast China approximately ranging from Zhejiang to Guangdong with additional gene flow from an Austroasiatic-related lineage (Fig. 5A), whereas the migrants from continental Southeast China to Taiwan largely preserve the original Austronesian/Austro-Tai-related genetic profile and are responsible for the massive Austronesian expansion. However, the coexistence of Kra-Dai and Austronesian ancestry once in the continent still cannot be fully excluded in light of our analysis.

With nearly absolute southern affinity to Austroasiatic-related lineage (Fig. 3B), the genetic profile of Yangshao individuals largely persists in Late Neolithic individuals from Qijia Culture (16.0 ± 8.3% for Mekong_N, 1.3 ± 10.6% for Fujian_LN) –whose expansion is supposed to parallel with the diffusion of at least some of the Tibeto-Burman languages[30]–and modern Tibeto-Burman speakers in Tibetan Plateau (18.9–24.2% for Mekong_N, 0.0% for Fujian_LN) and Tibetan-Yi Corridor like Naxi and Yi (33.7–34.1% for Mekong_N, 0.0–1.3% for Fujian_LN). In admixture-f_3 (Extended Data Table 3A), Tibeto-Burman populations in Tibetan-Yi Corridor and further south show a consistent pattern of two-way admixture by Sino-Tibetan and Austroasiatic ancestries. Multiple evidences suggest that populations with Austroasiatic ancestry likely distributed further north in Southwest China previously. Given the close relationship between Austroasiatic and Hmong-Mien ancestries, it is reasonable to deduct that the place of origin for both ancestries is in Southwest China (Fig. 5A) and both of them are possibly related to the Neolithic farming cultures in Middle Yangtze, e.g., Daxi Culture[3], which is also consistent with that modern populations with significant Hmong-Mien-related ancestry (Fig. 1C) are distributed in Guangxi, Guizhou, and Hunan of Southwest China.

C. Deep history of East Asian populations

Genetic drift-based admixture graph analysis by *qpGraph* is informative and robust for phylogenetic reconstruction with admixture events, but it cannot estimate the time of splits and admixtures since genetic drift is not proportional to time[24]. Therefore, we obtained coalescent time estimation using SFS-based framework Rarecoal[31] and whole genome sequences from Europeans, First Americans (Mixe, Piapoco, and Pima), Northern East Asians (Ulchi, Hezhen, and Oroqen), Coastal Southern East Asians (Ami, Atayal, and Igorot), and Inland Southern East Asians (Cambodian and Thai). We estimated that the divergence between East and West Eurasians is ~44,700 BP (95% confidence interval (CI) 44,600–44,800 BP, Fig. 3C), consistent with the time estimation in previous studies[19,32] and the equal genomic relationship to East and West

Eurasians for the ~45,000-year-old Ust'-Ishim individual[33].

Earlier works have discovered that the First Americans primarily derive from an East Asian-related lineage with additional admixture with West Eurasian-related Ancient North Siberians[15,19]. However, it is still unclear how the East Asian-related ancestry of First Americans relates to other East Asians. Both *qpGraph* model (Fig. 3A) and Rarecoal model (Fig. 3C) suggest that the East Asian ancestor of First Americans represents the deepest East Asian-related lineage in all the living population who split with the common ancestor of both Northern and Southern East Asian lineages ~27,700 BP (95% CI 27,400–27,900 BP, Fig. 3C). After that, the ancestor of Northern and Southern East Asians split with each other ~23,400 BP (95% CI 23,100–23,700 BP), which is prior to the Last Glacial Maximum (LGM) in East Asia (~21,000–15,000 BP)[3]. This implies that the differentiation between Northern and Southern East Asian lineages plausibly results from the isolation of geographically structured populations in different refugia during LGM. Within Southern East Asian lineage, the separation between Coastal and Inland Southern East Asian lineages took place ~16,400 BP (95% CI 16,200–16,900 BP), which is contemporary with LGM and significantly earlier than the earliest farming practice in Southern China (~9,000 BP)[3]. Such a result indicates that the Neolithic transition for different Southern East Asian ancestries might result from either independent acquisition or the spread of idea without massive population replacement.

The genomic origin of Jomon hunter-gatherers in Japanese Archipelago is mysterious due to their basal East Eurasian ancestry compared with other East Asians and their additional genetic affinity to Amur Basin populations and Austronesian Taiwanese[6,12,34]. In our admixture graph model (Fig. 3A), there are two different layers contributing to the genetic profile of Jomon hunter-gatherers. The first layer is distantly related to Andamanese hunter-gatherers, which is likely introduced by an earlier peopling of Japanese Archipelago. The second layer is a sister lineage of Southern East Asian, which explains the genetic affinity of Jomon to other coastal East Asian populations. Compared with the large proportion of Andaman-related ancestry in Jomon hunter-gatherers (56.5 ± 4.8%), the small amount of Andamanese-related ancestry in ancient (6.4–11.7%) and modern (1.0–2.1%) populations in Amur Basin also suggests that their affinity to Jomon hunter-gatherers is more feasible to be explained by an East Asian-related ancestry than an Andamanese related ancestry. Taking both *qpGraph* (Fig. 3A) and Rarecoal (Fig. 3C) into account, the formation of this sister lineage to Southern East Asian is between ~23,400 BP and ~16,400 BP, which mostly falls in the range of LGM. Therefore, a plausible geographic distribution for this lineage is in the continental coastal East Asia, which is largely below the sea level at present (Fig. 5A).

D. Migrations and admixtures shaping present-day Southern Chinese

East Asia in recent millennia has witnessed a series of massive demographic events that contribute to the formation of modern East Asians. Here we particularly focus on Southern China and characterize the most crucial migrations and admixtures revealed in light of our results (Fig. 5B).

(D.1) Formation of Han Chinese

Han Chinese comprise around one fifth of the world's population[35]. Previous studies suggest that Han Chinese is primarily formed by Yellow River Farmers (i.e., Sino-Tibetan ancestry in this study) with additional gene flow from Southern East Asian lineage[12]. However, it is still not fully known which specific ancestry mostly contribute to the southern ancestry of Han Chinese. In ADMIXTURE plot (Fig. 1C), both Northern and Southern Han Chinese have a similar genetic profile comprising both Sino-Tibetan and Kra-Dai ancestries, with an increase of Kra-Dai ancestry from North to South. The earliest individuals with such a genetic profile in Yellow River Basin are from Longshan Culture (~4,000 BP) and the genetic profile in individuals resembling the genetic profile of Northern Han Chinese is found in Dacaozi_IA and Omnogovi_IA (previously assigned as Xiongnu individuals[36]) during Han Dynasty (~4,000 BP). Formal test for pairwise genetic homogeneity conducted by *qpWave* (Fig. 4B) confirms that the genetic homogeneity between Han Dynasty individuals and any of Neolithic Shandong individuals and Inland Yellow River individuals (Yangshao_MN and Qijia_LN) is higher than the one between the latter two, consistent with a closer position for Han Dynasty individuals than Neolithic Yellow River individuals in PCA (Fig. 1A) and *qpAdm* (Fig. 3B). This indicates that the admixture between Inland and Coastal Yellow River plays an important role in the formation of Northern Han Chinese. Regarding the formation of Sinitic Cline and Southern Han Chinese, admixture-f_3 results (Extended Table 3B) suggest that the strongest signal of admixture come from the pair of surrogates for Sino-Tibetan ancestry (Qijia_LN) and Kra-Dai (Hlai) or Austronesian ancestry (Ami, Atayal, and Kankanaey). Therefore, we conclude that the Sinitic Cline is primarily formed by massive southward migration of Northern Han Chinese and subsequent admixture with indigenous Kra-Dai speakers in Southern Chinese.

(D.2) Admixture between Hmong-Mien and Kra-Dai populations

Another major genetic cline in South China is the Hmong-Mien Cline, which comprises most of the Hmong-Mien speakers as well as neighboring Kra-Dai populations in the interior of Southern China (Fig. 5B). In ADMIXTURE plot (Fig. 1C), Hmong-Mien populations from west to east show a decrease of Hmong-Mien ancestry and an increase of Kra-Dai ancestry, suggesting that the migration of Kra-Dai speakers came from the east and constantly admixed with local Hmong-Mien populations. Meanwhile, adjacent Kra-Dai speakers of Kra (Gelao) and Kam-Sui (Dong) branches also receive significant Hmong-Mien ancestry, indicating a bidirectional gene flow. Admixture time estimation performed by ALDER (Extended Data Table 4) shows that the admixture of Hmong-Mien Cline happened ~24–46 generations ago overlapping Tang Dynasty to Yuan Dynasty.

(D.3) Spread of Kra-Dai ancestry in Mainland Southeast Asia

Besides the contribution to Han Chinese and Hmong-Mien populations, Kra-Dai ancestry also has a strong impact to Mainland Southeast Asia in recent two millennia. The earliest genomic document for the arrival of Kra-Dai ancestry in Mainland Southeast Asia is Bronze Age individuals from northern Vietnam (~2,000 BP, Fig. 1C). Further extensive admixture between populations with more Kra-Dai ancestry and more Austroasiatic ancestry that arrived earlier largely explain the more obvious discrepancy between gene and language in Mainland Southeast Asians than other Southern East Asians. Especially, it is evident in PCA (Fig. 1A and B), ADMIXTURE (Fig. 1C), and outgroup-f_3 (Fig. 2A) that Austroasiatic-speaking Kinh and Muong of the Vietic branch have a more similar genetic profile with Kra-Dai speakers in South China than other Austroasiatic speakers with a more typical 'Austroasiatic' genetic profile, suggesting a language shift from incoming Kra-Dai language to local Austroasiatic language as a possible mechanism.

(D.4) Genomic origin of Tibeto-Burman-speaking Mainland Southeast Asians

The special Y-chromosomal haplogroup F2-M427 in Lahu[37] and many other Tibeto-Burman populations in Mainland Southeast Asia raise further question for their genomic origin. In ADMIXTURE plot (Fig. 1C), we find that Tibeto-Burman speakers in Mainland Southeast Asia (Lahu from China and Vietnam, Sila, HaNhi (Hani), and Cong) majorly have a genetic profile comprising Sino-Tibetan and Austroasiatic ancestries, with a consistent pattern in *qpAdm* (36.7–50.1 % for Mekong_N, 7.9–19.1% for Fujian_LN, Fig. 3B). Both results suggest that the Tibeto-Burman-speaking migrants from the north and their admixture with local Austroasiatic speakers form the genetic profile of present-day Lahu and neighboring Tibeto-Burman speakers. We also observe that such a genetic profile had occurred in the Iron Age Thailand individuals ~1,700 BP, with their genetic homogeneity with present-day Tibeto-Burman speakers in Mainland Southeast Asia confirmed by *qpWave* (Fig. 4A).

DISCUSSION

In this study, we provide a comprehensive and detailed landscape for the genomic history of East Asians, especially Southern Chinese. We retrieve the deep origin and structure for the main ancestral groups in East Asia (Fig. 5A) and we document human migrations and admixtures that form the genomic and linguistic scenario in present-day Southern China (Fig. 5B). We predict that future ancient genomes from the interior of Southern China will further improve and examine the demographic framework of Southern East Asians established in our study.

METHODS

Sampling and genotyping

We collected blood and saliva samples from 211 unrelated individuals affiliated to Miao, Zhuang, and Han ethnicities from 30 subgroups in Guangxi and Yunnan of Southern China. Further linguistic and geographic information of these subgroups was described in Extended Data Table 1. The study was approved by Ethical Committee of Youjiang Medical University for Nationalities and all the processes involved were consistent with the corresponding ethical principles. All the participants read and signed the informed content. Then, we achieved the genotyped data of these samples using the Affymetrix WeGene V1 Array, which includes 492,683 genome-wide SNPs and is referred to as '500K dataset' elsewhere in this paper. Other experimental and bioinformatic procedures for genotyping were consistent with the protocol documented in previous studies[38,39].

Dataset arrangement

We merged our 500K dataset with published present-day and ancient genomic data[6-9,11,12,17,18,24,32,33,39-56], resulting in two types of panel: (1) merged panel of 500K dataset and 1240K-capture dataset (1,233,013 SNPs, including all the ancient samples and shotgun-sequenced modern samples) with 372,929 SNPs, which is for the purpose of maximizing the number of informative SNPs; (2) merged panel of the panel above and 600K Human Origin Array dataset (597,573 SNPs, including other modern samples) with 110,931 SNPs, which is for the purpose of maximizing the number and size of populations. For Rarecoal analysis, we used whole genome sequences from Simons Genome Diversity Project (SGDP)[47].

Abbreviations

We used the following abbreviations throughout our article: LP, Late Pleistocene; M, Mesolithic; N, Neolithic; EN, Early Neolithic; MN, Middle Neolithic; LN, Late Neolithic; BA, Bronze Age; IA, Iron Age; o, outlier; HG, hunter-gatherer; MSEA, Mainland Southeast Asia; ISEA, Island Southeast Asia; AN, Austronesian; AA, Austroasiatic; HM, Hmong-Mien; KD, Kra-Dai; HO, Human Origin Array. Particularly, Mongolia_N refers to Mongolia_N_East unless otherwise specified.

Principal component analysis (PCA)

We performed PCA by *smartpca* program of EIGENSOFT[13] with parameters lsqproject: YES, shrinkmode: YES, numoutlieriter: 0, killr2: YES, r2thresh: 0.4, r2genlim: 0.1. We only used modern samples to construct PCs with ancient samples projected.

ADMIXTURE analysis

We first used PLINK[57] to prune the linkage disequilibrium by parameters --indep-pairwise 200 20 0.4. Then, we ran ADMIXTURE[14] with default parameters from K = 2 to 20. We reported the result when K = 10 as it reaches the lowest cross error (Extended Data Fig. 2).

f-statistics

We used ADMIXTOOLS[24] to compute f_3-statistics and D-statistics (Supplementary Information Table 2) with the estimation of standard error by jackknife. We used Mbuti as outgroup for Eurasian populations in outgroup-f_3.

Admixture graph modelling by *qpGraph*

We used *qpGraph* program of ADMIXTOOLS[24] to reconstruct the phylogeny with admixture by default parameters. We exhausted different feasible graph models and select the optimal model based on maximum |Z|-score and likelihood.

Admixture coefficient modelling by *qpAdm*

We used *qpAdm*[25] to compute the ancestral coefficient based on f-statistics to different outgroups. We chose the optimal model for a given target population based on the following criteria, sorted by priority. (1) The model is feasible if and only if all the ancestral coefficients fall within the range [0, 1]. (2) The full model is chosen if both full and nested models are feasible. (3) If the full model is infeasible and more than one nested models are feasible, then the nested model with the highest *p*-value is chosen. We applied 'proximal model' and 'distal model'[50] to model the ancestry contribution in different time period.

Proximal model. We used Mongolia_N_East, Mekong_N (pooled population of Vietnam_N, Laos_LN_BA.SG, and Laos_BA.WGC), and Fujian_LN as proxies for Northern East Asian, Inland Southern East Asian, and Coastal Southern East Asian ancestries. The initial outgroups that we used are: South_Africa_2000BP.SG, Ust_Ishim.DG, Yana_UP.SG, Alaska_LP, Kolyma_M, Andaman_HG, Jomon_HG, Liangdao2_EN, Malaysia_LN.SG. We also used the 'rotating' strategy[41] to further verify the nested models, in which we moved one of the proxies into the set of outgroups by turn. Since there is no high-coverage ancient sample that is sufficiently older than Mekong_N in Austroasiatic-related lineage, we expediently used Malaysia_LN.SG who closely related to Mekong_N as outgroup but we caution that it tends to underestimate *p*-values. Therefore, we also calculated relative likelihood ratios to test if a full model is better than its nested models and we find the ratios are usually higher than 100. Original results of proximal model are presented in Supplementary Information Table 1.

Distal model. We used Mongolia_N_East and Andaman_HG as proxies for East Asian and Andamanese-related ancestries. We used the following outgroups in distal model: South_Africa_2000BP.SG, Ust_Ishim.DG, Georgia_Kotias.SG, Loschbour.DG, Yana_UP.SG, Botai_EN, Russia_BA_Okunevo.SG, Russia_EHG_Karelia, Tianyuan, Papuan.DG, Mala.DG, Australian.DG, Hoabinhian.

Genetic homogeneity testing by *qpWave*

We used *qpWave*[58] to formally test if pairwise populations are homogeneous in relation to a series of outgroups. We used following outgroups for Southern East Asian populations: South_Africa_2000BP.SG, Ust_Ishim.DG, Loschbour.DG, Yana_UP.SG, Alaska_LP, Kolyma_M, Andaman_HG, Liangdao2_EN, Jomon_HG, Malaysia_LN.SG, Nepal_LN_BA_IA, DevilsCave_N, Shamanka_EN. We used following outgroups for Northern East Asian populations: South_Africa_2000BP.SG, Ust_Ishim.DG, Loschbour.DG, Yana_UP.SG, Alaska_LP, Kolyma_M, Andaman_HG, Liangdao2_EN, Jomon_HG, Malaysia_LN.SG, Nepal_LN_BA_IA, DevilsCave_N, Shamanka_EN.

Demographic modelling implemented by Rarecoal

We used Rarecoal program[31,54] to obtain a SFS-based phylogeny with time estimates using default parameters. We used mutation rate in every generation[59] of 1.25×10^{-8} and 29 years per generation[60] to scale the time.

Admixture time estimation by ALDER

We used linkage disequilibrium-based ALDER[61] to estimate admixture time of Hmong-Mien Cline using default parameters and checkmap: YES, mindis: 0.005, binsize: 0.0001.

Identity-by-descent (IBD) analysis

We first used SHAPEIT[62] to phase the modern individuals in our dataset. Then we used Refine IBD software[16] to obtain pairwise sharing of IBD segments among individuals. We normalized the results in population level by dividing it by the product of the sample size of pairwise populations.

Correlation between N_E and F_{ST} to Ust'-Ishim

We used the formula in Palamara et al.[63] to estimate N_E from shared IBD within a population. We computed F_{ST} by *smartpca*[13] with default parameters and fstonly: YES.

LGM coastline in East Asia

The coastline during LGM period in East Asia shown in Fig. 5A is adopted from Ray et al..[64]

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Figure 1. Genetic structure of East Asians. (**A to B**) PCA for (A) all the East Asians and (B) Southern East Asians. We projected ancient samples to principal components constructed by modern samples. (**C**) Unsupervised ADMIXTURE plot at K = 10, identifying six major ancestries in East Asia: orange, Northeast Asia/ Tungusic-related; red, Sino-Tibetan-related; blue, Austronesian-related; green, Kra-Dai-related; yellow, Hmong-Mien-related; purple, Austroasiatic-related.

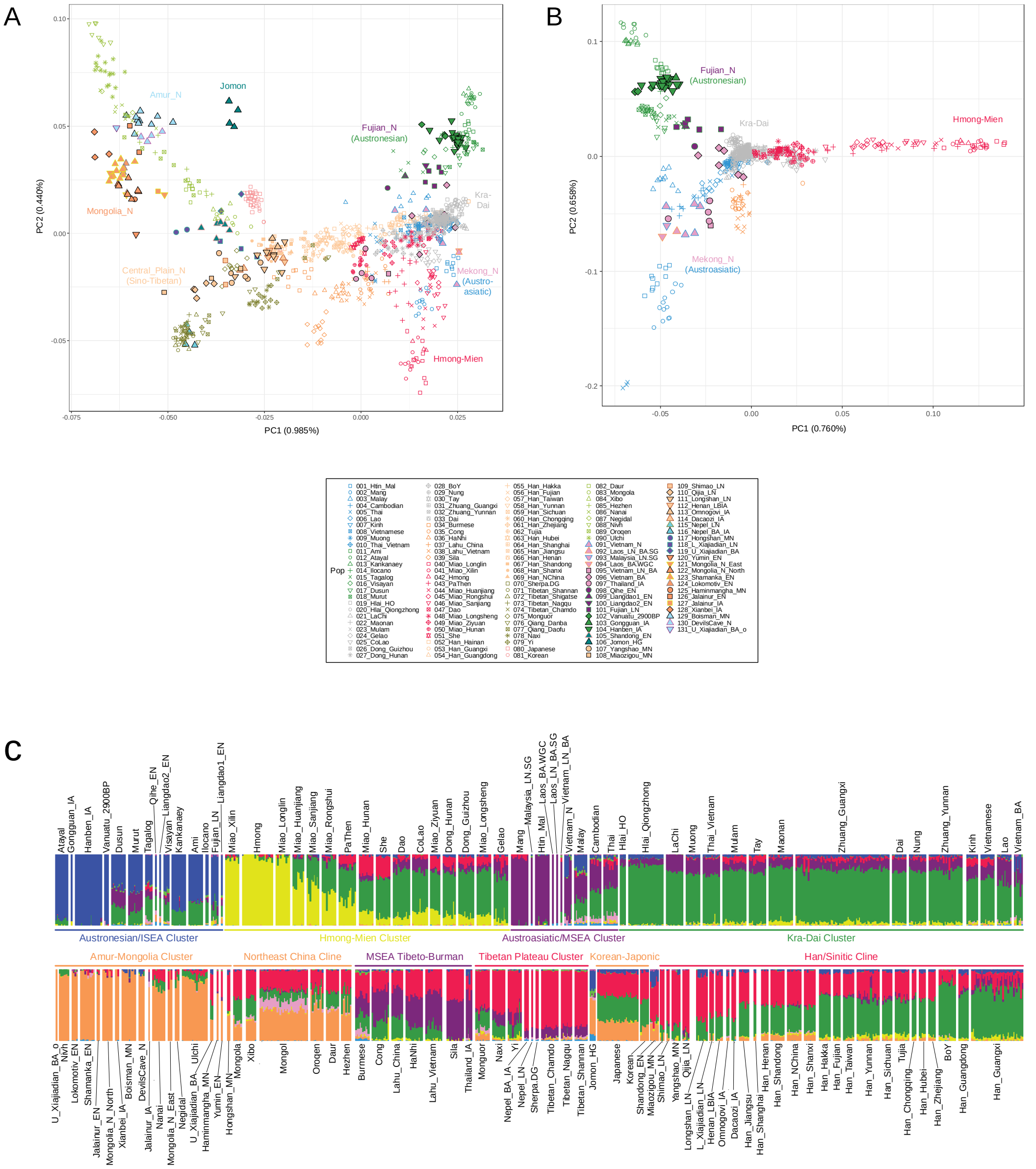
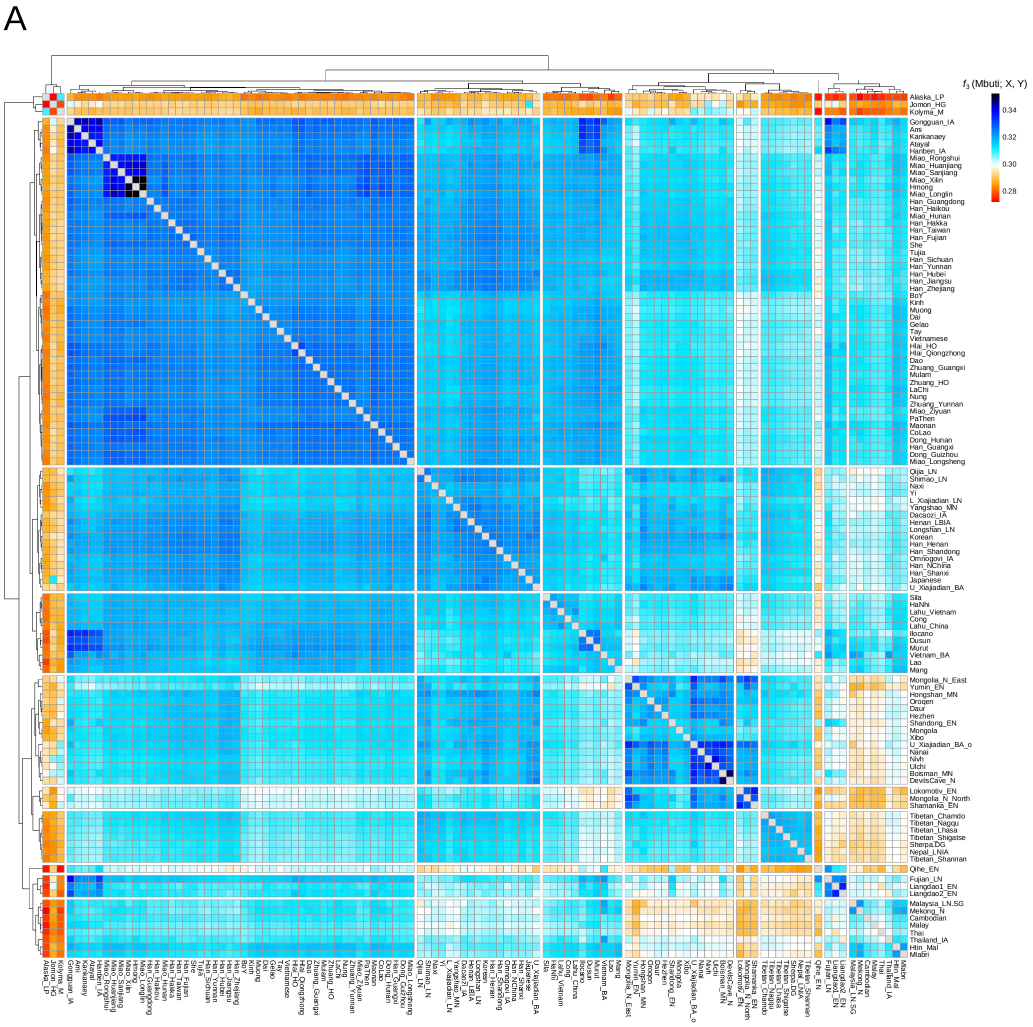
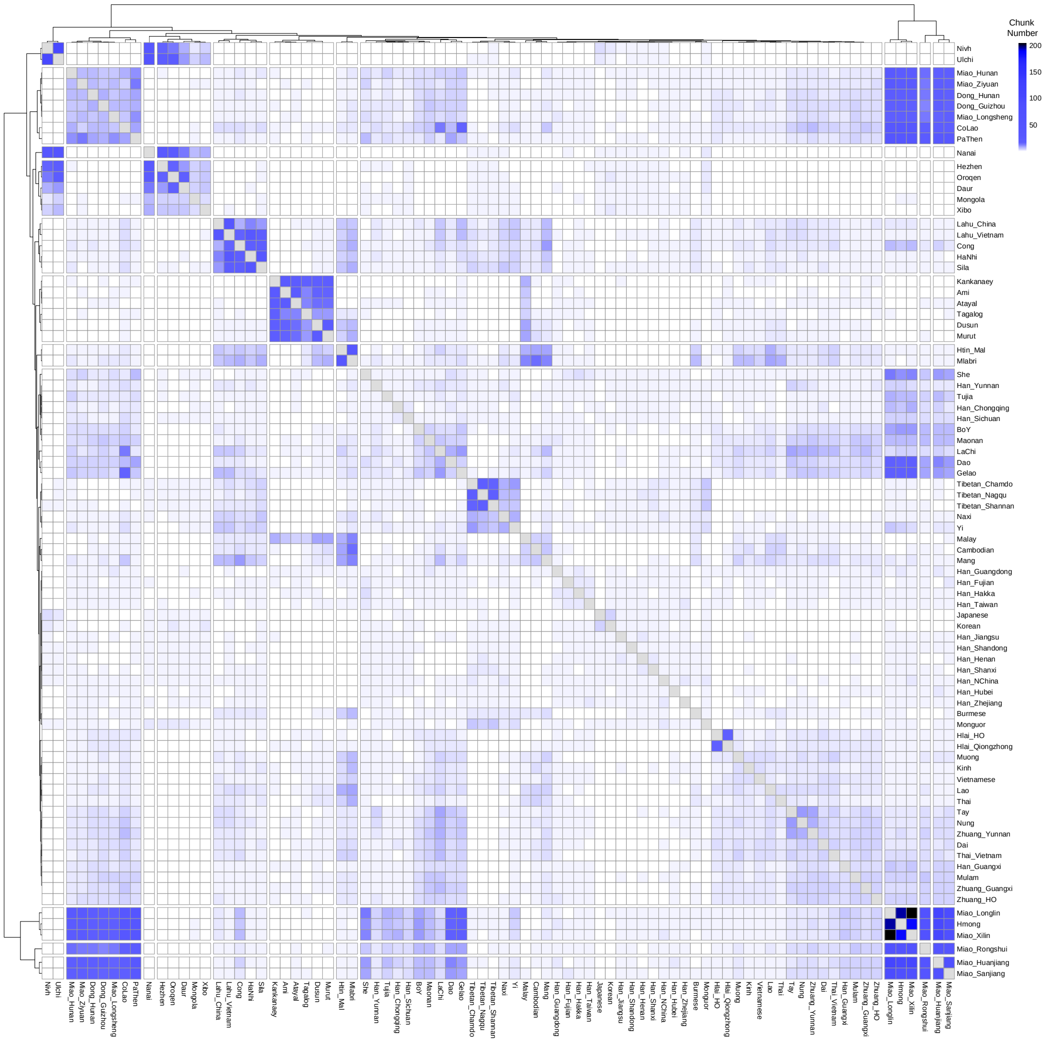


Figure 2. Quantitative measurement for pairwise genetic affinity. (**A**) Outgroup-*f_3* in the form *f_3*(Mbuti; X, Y) measuring shared genetic drift between pairwise ancient and modern East Asian populations. (**B** to **C**) Normalized haplotype sharing based on (B) the number and (C) the total length (unit: cM) of shared IBD chunks for pairwise modern East Asian populations.



B


Chunk Number
200
150
100
50
Nivh
Ulchi
Miao_Hunan
Miao_Ziyuan
Dong_Hunan
Dong_Guizhou
Miao_Longsheng
CoLao
PaThen
Nanai
Hezhen
Oroqen
Daur
Mongola
Xibo
Lahu_China
Lahu_Vietnam
Cong
HaNhi
Sila
Kankanaey
Ami
Atayal
Tagalog
Dusun
Murut
Htin_Mal
Mlabri
She
Han_Yunnan
Tujia
Han_Chongqing
Han_Sichuan
BoY
Maonan
LaChi
Dao
Gelao
Tibetan_Chamdo
Tibetan_Nagqu
Tibetan_Shannan
Naxi
Yi
Malay
Cambodian
Mang
Han_Guangdong
Han_Fujian
Han_Hakka
Han_Taiwan
Japanese
Korean
Han_Jiangsu
Han_Shandong
Han_Henan
Han_Shanxi
Han_NChina
Han_Hubei
Han_Zhejiang
Burmese
Monguor
Hlai_HO
Hlai_Qiongzhong
Muong
Kinh
Vietnamese
Lao
Thai
Tay
Nung
Zhuang_Yunnan
Dai
Thai_Vietnam
Han_Guangxi
Mulam
Zhuang_Guangxi
Zhuang_HO
Miao_Longlin
Hmong
Miao_Xilin
Miao_Rongshui
Miao_Huanjiang
Miao_Sanjiang

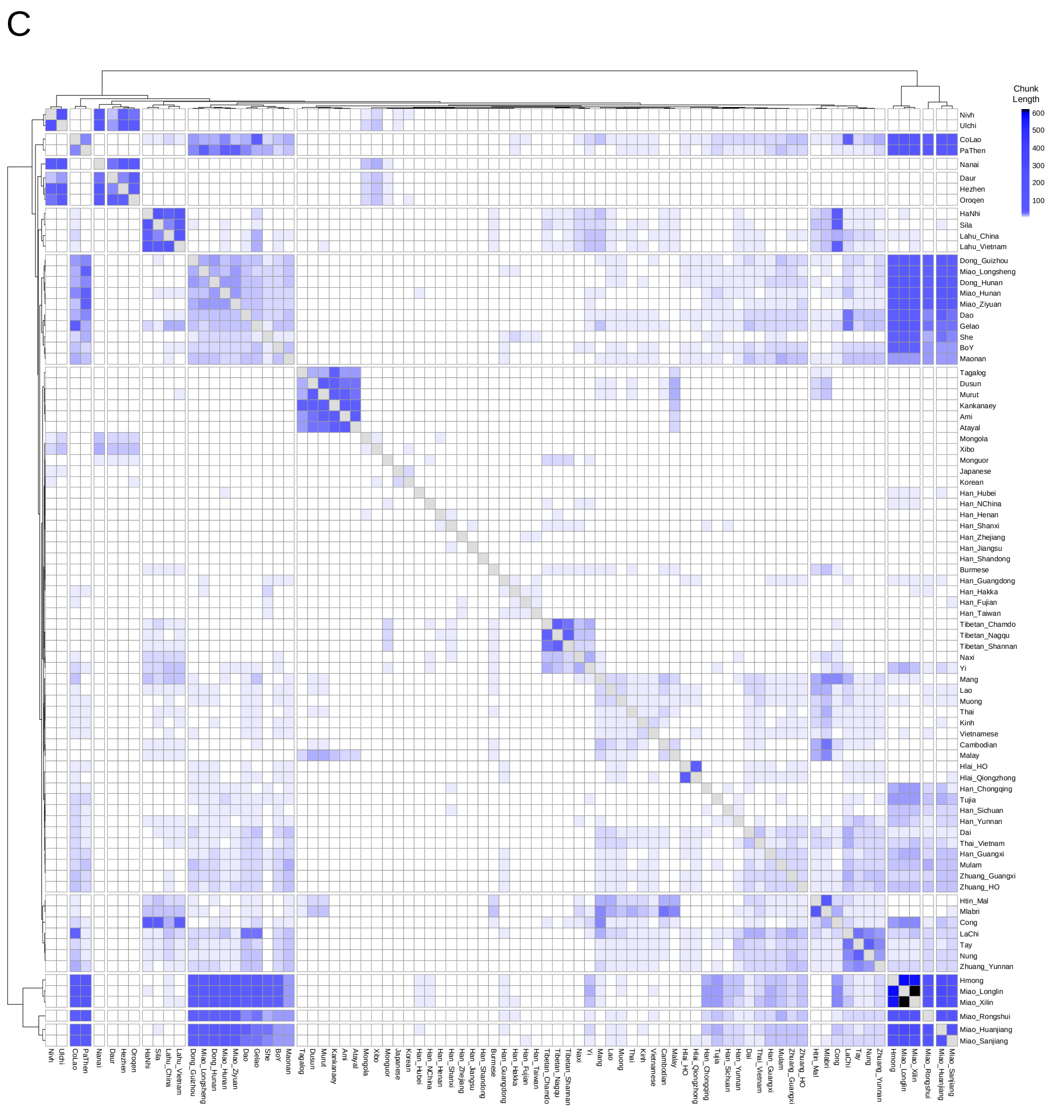
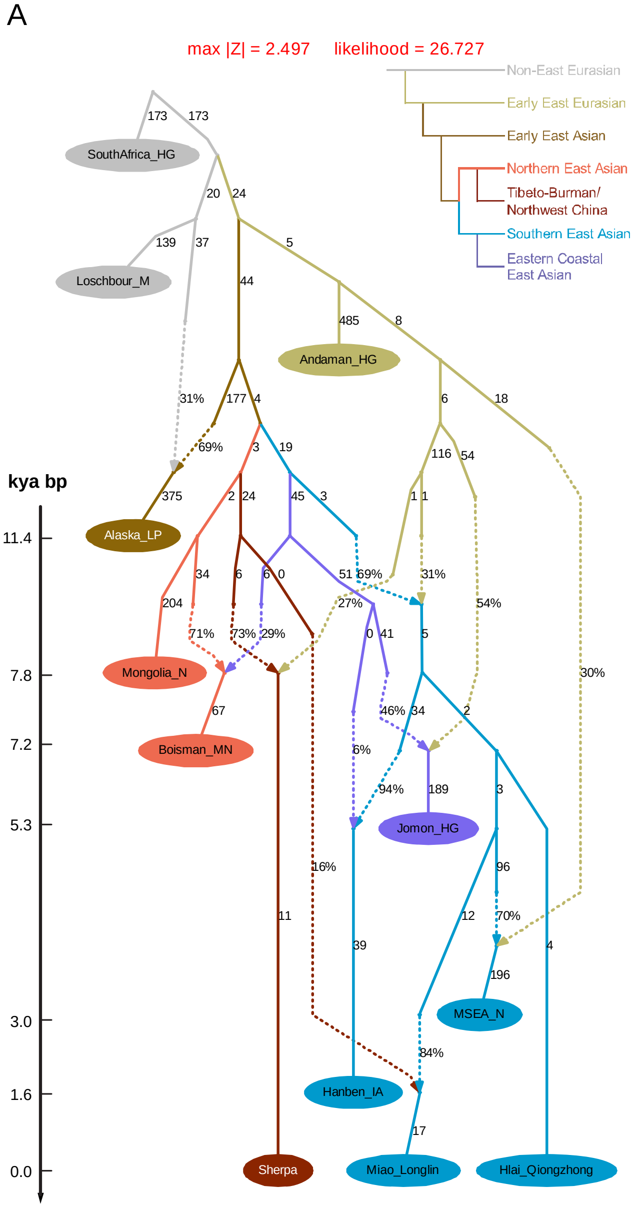
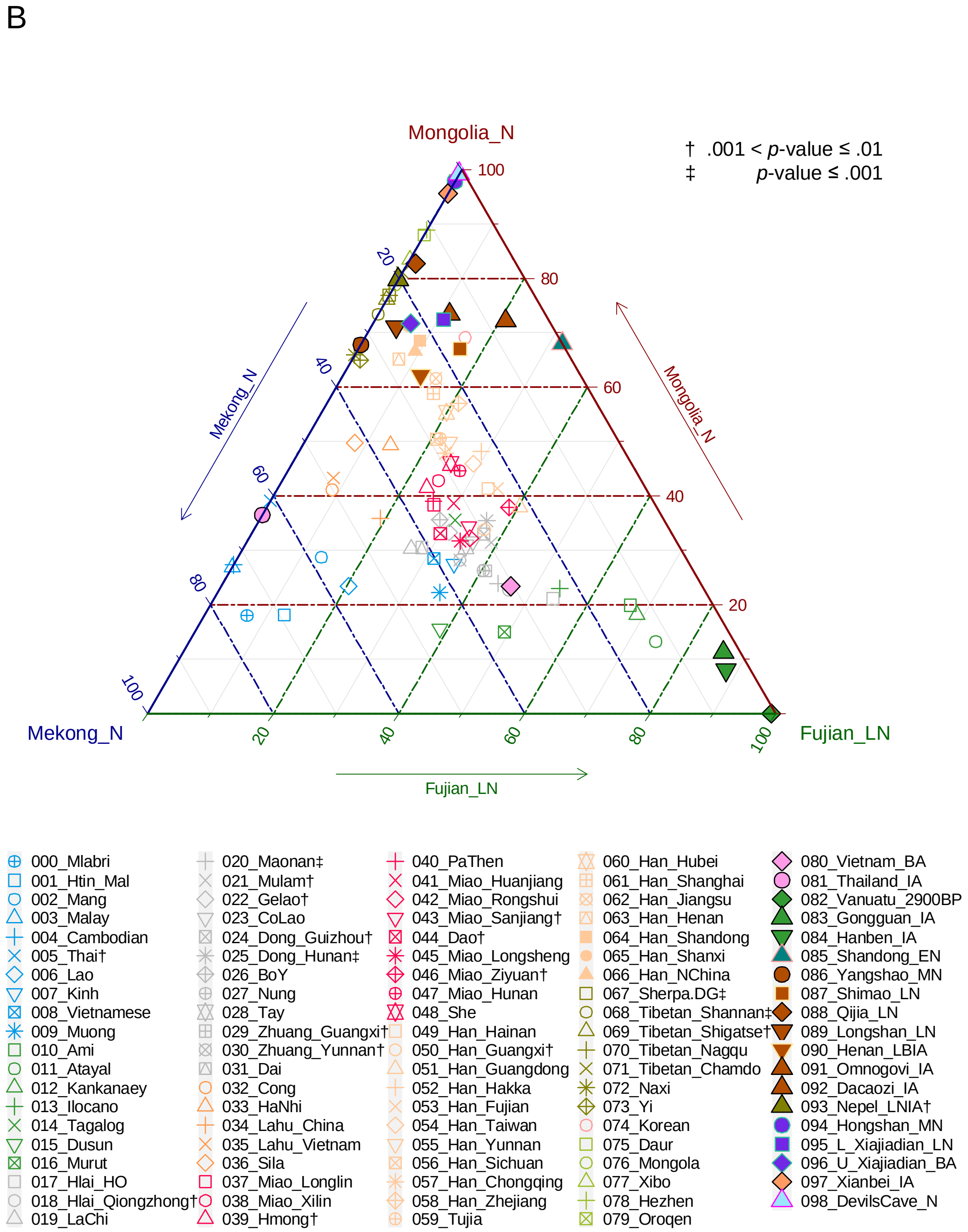

C
Chunk Length
600
500
400
300
200
100
Nivh
Ulchi
CoLao
PaThen
Nanai
Daur
Hezhen
Oroqen
HaNhi
Sila
Lahu_China
Lahu_Vietnam
Dong_Guizhou
Miao_Longsheng
Dong_Hunan
Miao_Hunan
Miao_Ziyuan
Dao
Gelao
She
BoY
Maonan
Tagalog
Dusun
Murut
Kankanaey
Ami
Atayal
Mongola
Xibo
Monguor
Japanese
Korean
Han_Hubei
Han_NChina
Han_Henan
Han_Shanxi
Han_Zhejiang
Han_Jiangsu
Han_Shandong
Burmese
Han_Guangdong
Han_Hakka
Han_Fujian
Han_Taiwan
Tibetan_Chamdo
Tibetan_Nagqu
Tibetan_Shannan
Naxi
Yi
Mang
Lao
Muong
Thai
Kinh
Vietnamese
Cambodian
Malay
Hlai_HO
Hlai_Qiongzhong
Han_Chongqing
Tujia
Han_Sichuan
Han_Yunnan
Dai
Thai_Vietnam
Han_Guangxi
Mulam
Zhuang_Guangxi
Zhuang_HO
Htin_Mal
Mlabri
Cong
LaChi
Tay
Nung
Zhuang_Yunnan
Hmong
Miao_Longlin
Miao_Xilin
Miao_Rongshui
Miao_Huanjiang
Miao_Sanjiang

Figure 3. Demographic modelling for deep history of East Asians. (A) Optimal *qpGraph* admixture model for the phylogenetic relationship among the surrogates for major ancestries in East Asia. Alaska_LP, Mongolia_N/Boisman_MN, Sherpa, Hanben_IA, Hlai_Qiongzhong, Miao_Longlin, and MSEA_N respectively surrogate First Americans, Northeast Asian, Sino-Tibetan, Austronesian, Kra-Dai, Hmong-Mien, and Austroasiatic ancestries. Drift along each edge are multiplied by 1,000. (**B**) Three-source *qpAdm* models the contribution of Northern East Asian (represented by Mongolia_N), Coastal Southern East Asian (represented by Fujian_LN), and Inland Southern East Asian (represented by Mekong_N) lineages in ancient and present-day East Asians. (**C**) Coalescent analysis using SFS of rare alleles to calibrate the time of the major splits in East Asians (implemented by Rarecoal). We used whole genome sequences from 56 individuals in this analysis. kya, thousand years ago.




B
Mongolia_N
† .001 < p-value ≤ .01
‡ p-value ≤ .001
100
80
60
40
20
Mekong_N
Mongolia_N
Mekong_N
Fujian_LN
Fujian_LN
000_Mlabri
001_Htin_Mal
002_Mang
003_Malay
004_Cambodian
005_Thai†
006_Lao
007_Kinh
008_Vietnamese
009_Muong
010_Ami
011_Atayal
012_Kankanaey
013_Ilocano
014_Tagalog
015_Dusun
016_Murut
017_Hlai_HO
018_Hlai_Qiongzhong†
019_LaChi
020_Maonan‡
021_Mulam†
022_Gelao†
023_CoLao
024_Dong_Guizhou†
025_Dong_Hunan‡
026_BoY
027_Nung
028_Tay
029_Zhuang_Guangxi†
030_Zhuang_Yunnan†
031_Dai
032_Cong
033_HaNhi
034_Lahu_China
035_Lahu_Vietnam
036_Sila
037_Miao_Longlin
038_Miao_Xilin
039_Hmong†
040_PaThen
041_Miao_Huanjiang
042_Miao_Rongshui
043_Miao_Sanjiang†
044_Dao†
045_Miao_Longsheng
046_Miao_Ziyuan†
047_Miao_Hunan
048_She
049_Han_Hainan
050_Han_Guangxi†
051_Han_Guangdong
052_Han_Hakka
053_Han_Fujian
054_Han_Taiwan
055_Han_Yunnan
056_Han_Sichuan
057_Han_Chongqing
058_Han_Zhejiang
059_Tujia
060_Han_Hubei
061_Han_Shanghai
062_Han_Jiangsu
063_Han_Henan
064_Han_Shandong
065_Han_Shanxi
066_Han_NChina
067_Sherpa.DG‡
068_Tibetan_Shannan‡
069_Tibetan_Shigatse†
070_Tibetan_Nagqu
071_Tibetan_Chamdo
072_Naxi
073_Yi
074_Korean
075_Daur
076_Mongola
077_Xibo
078_Hezhen
079_Oroqen
080_Vietnam_BA
081_Thailand_IA
082_Vanuatu_2900BP
083_Gongguan_IA
084_Hanben_IA
085_Shandong_EN
086_Yangshao_MN
087_Shimao_LN
088_Qijia_LN
089_Longshan_LN
090_Henan_LBIA
091_Omnogovi_IA
092_Dacaozi_IA
093_Nepel_LNIA†
094_Hongshan_MN
095_L_Xiajiadian_LN
096_U_Xiajiadian_BA
097_Xianbei_IA
098_DevilsCave_N

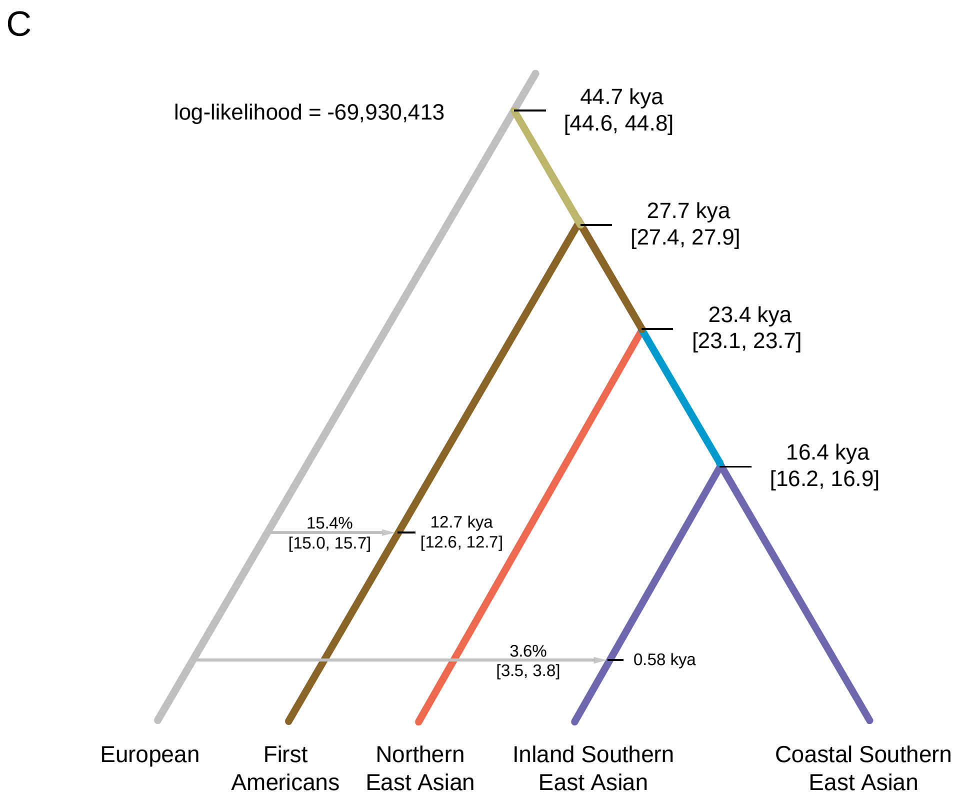
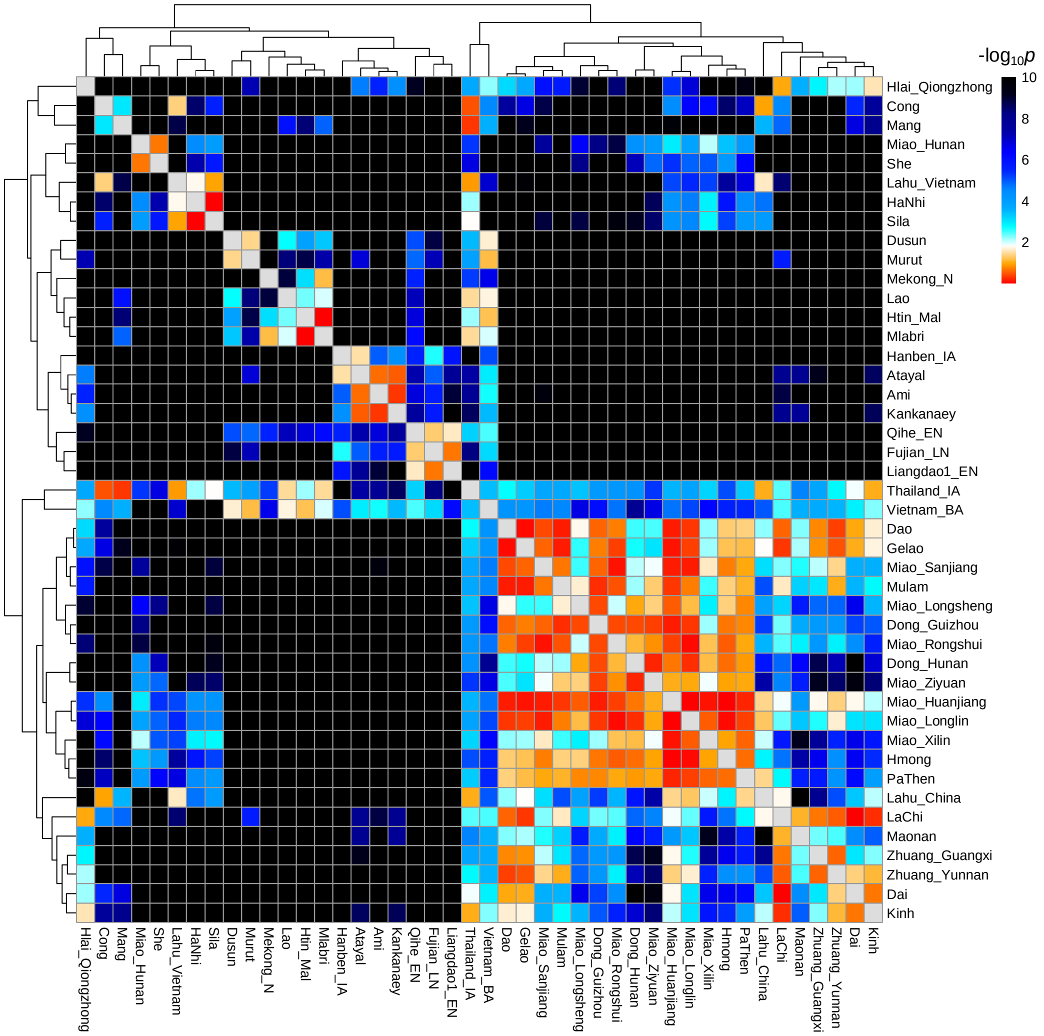

C
log-likelihood = -69,930,413
44.7 kya
[44.6, 44.8]
27.7 kya
[27.4, 27.9]
23.4 kya
[23.1, 23.7]
16.4 kya
[16.2, 16.9]
15.4%
[15.0, 15.7]
12.7 kya
[12.6, 12.7]
3.6%
[3.5, 3.8]
0.58 kya
European
First Americans
Northern East Asian
Inland Southern East Asian
Coastal Southern East Asian

Figure 4. Genetic homogeneity of pairwise populations. Heatmaps show negative logarithms for *p*-values of pairwise *qpWave* in (A) Southern East Asians and (B) Northern East Asians.

A



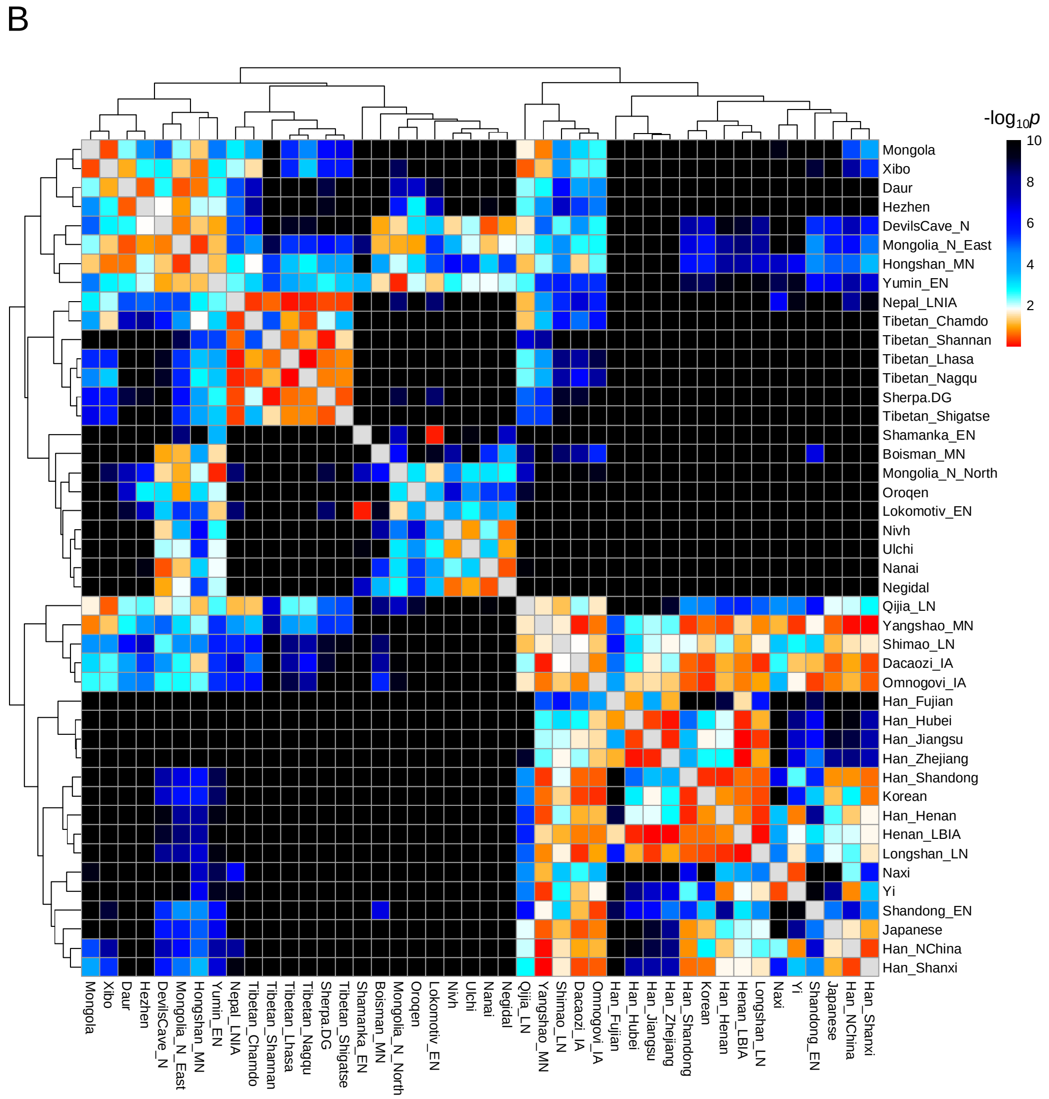
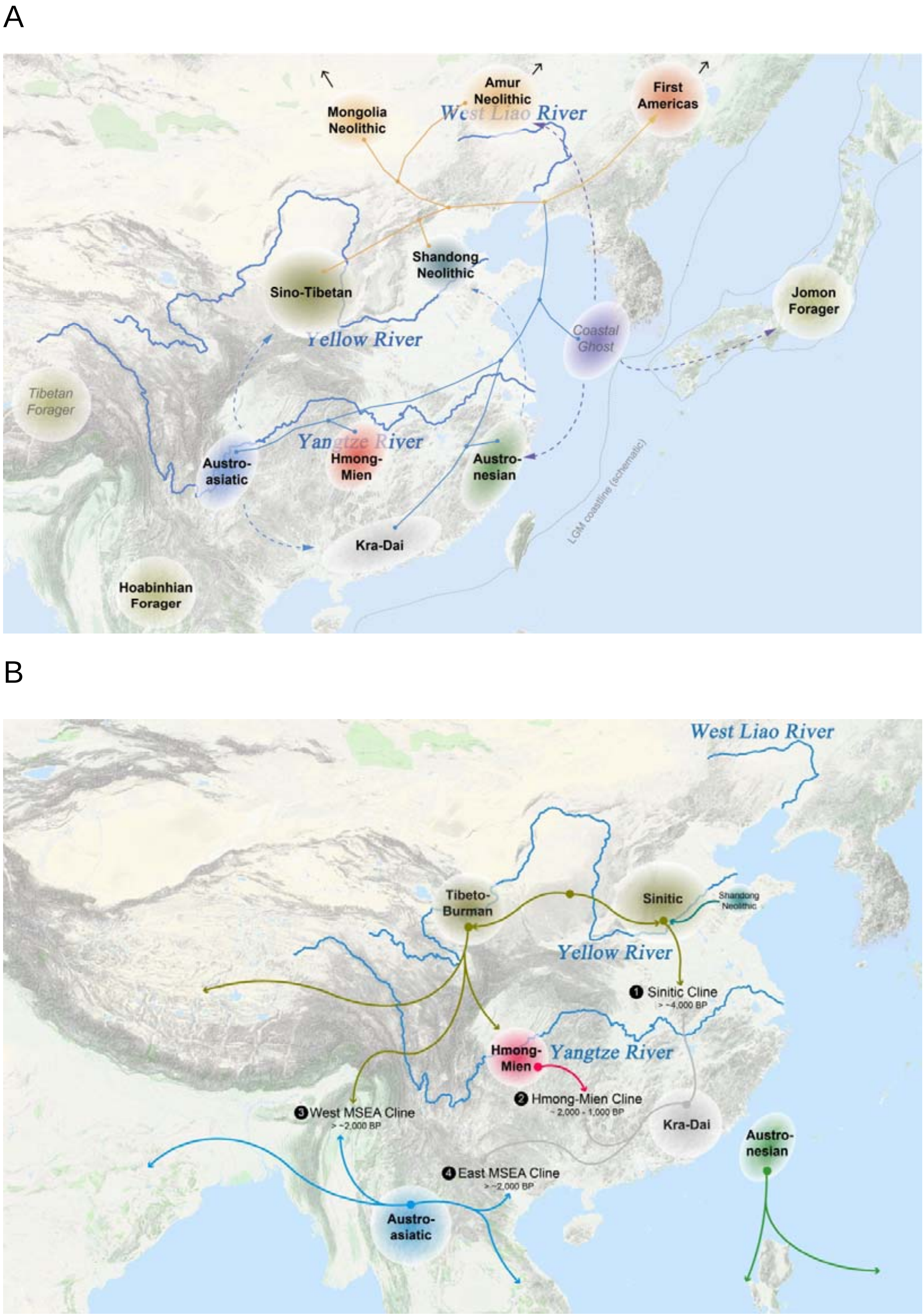
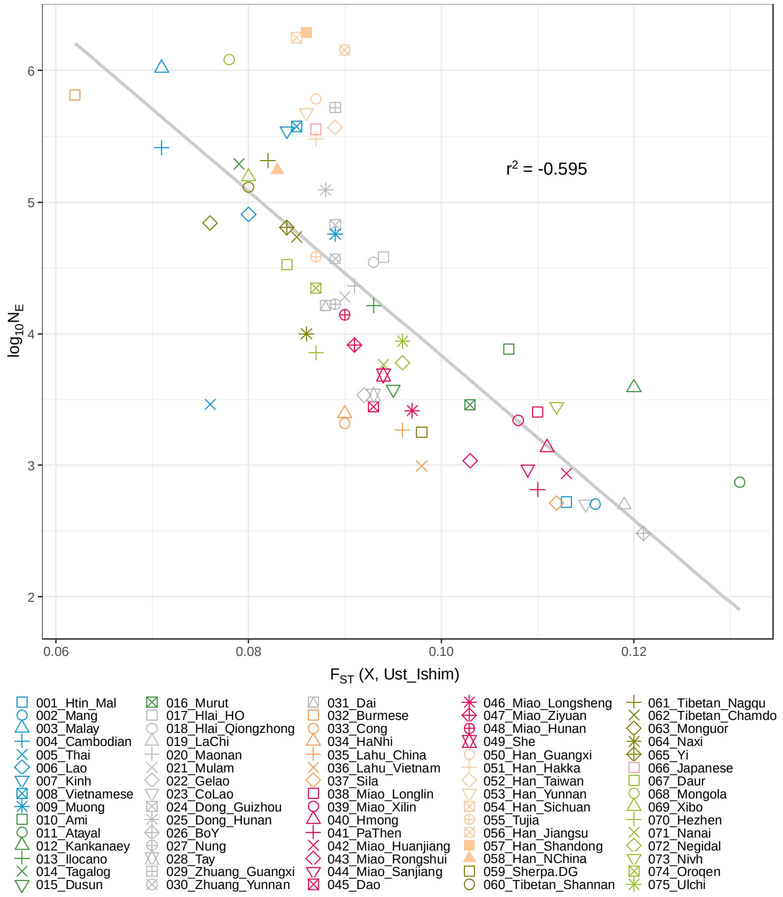

B
-log$_{10}p$
10
8
6
4
2
Mongola
Xibo
Daur
Hezhen
DevilsCave_N
Mongolia_N_East
Hongshan_MN
Yumin_EN
Nepal_LNIA
Tibetan_Chamdo
Tibetan_Shannan
Tibetan_Lhasa
Tibetan_Nagqu
Sherpa.DG
Tibetan_Shigatse
Shamanka_EN
Boisman_MN
Mongolia_N_North
Oroqen
Lokomotiv_EN
Nivh
Ulchi
Nanai
Negidal
Qijia_LN
Yangshao_MN
Shimao_LN
Dacaozi_IA
Omnogovi_IA
Han_Fujian
Han_Hubei
Han_Jiangsu
Han_Zhejiang
Han_Shandong
Korean
Han_Henan
Henan_LBIA
Longshan_LN
Naxi
Yi
Shandong_EN
Japanese
Han_NChina
Han_Shanxi

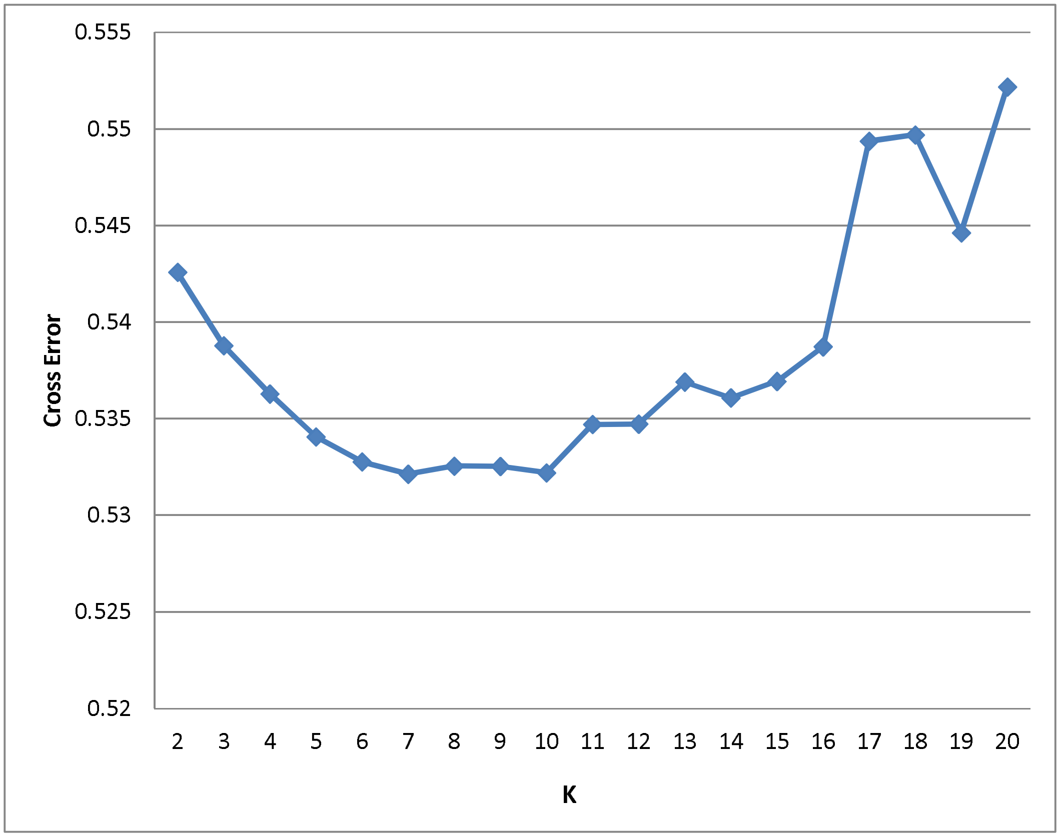
Figure 5. Illustrations for demographic history in East Asia. (**A**) The formation of geographically and linguistically structured ancestries in East Asia. (**B**) Massive migrations and admixtures forming the current genomic landscape in Southern China and neighboring regions.



Extended Data Figure 1. Correlation between effective population size (N_E) and genetic drift away from common Eurasian ancestor. Given ~45,000 years old Ust'-Ishim is genomically equally related to most of the Eurasians, we used F_{ST} away from him [F_{ST}(X, Ust'-Ishim)] to represent the genetic drift from the common Eurasian ancestor to modern East Asian populations. Negative correlation between logarithm of N_E and F_{ST}(X, Ust'-Ishim) suggests that recent genetic drift due to a small population size comprise a large proportion of the total genetic drift from common Eurasian ancestor in many modern East Asian populations.



Extended Data Figure 2. Cross error for ADMIXTURE analysis when K = 2 to 20.



Extended Data Table 1. Sample information for newly reported individuals in this study.

Population	Language Affiliation	Locality	Region	Latitude	Longitude	Grouped label	Sample size
Miao_Longlin	HM, Hmongic, Hmong	Longlin, Baise, Guangxi	China (Southwest)	24.7714	105.3456	Miao_Longlin	10
Miao_Xilin	HM, Hmongic, Hmong	Xilin, Baise, Guangxi	China (Southwest)	24.4924	105.0929	Miao_Xilin	10
Miao_Huanjiang	HM, Hmongic, Hmu, Southern Dialect	Huanjiang, Hechi, Guangxi	China (Southwest)	24.8363	108.2538	Miao_Huanjiang	8
Miao_Rongshui	HM, Hmongic, Hmu, Southern Dialect	Rongshui, Liuzhou, Guangxi	China (Southwest)	25.0748	109.2537	Miao_Rongshui	10
Miao_Sanjiang	HM, Hmongic, Hmu, Southern Dialect	Sanjiang, Liuzhou, Guangxi	China (Southwest)	25.7818	109.6064	Miao_Sanjiang	9
Miao_Ziyuan	HM, Hmongic, Hmu, Eastern Dialect	Ziyuan, Guilin, Guangxi	China (Southwest)	26.0365	110.6397	Miao_Ziyuan	10
Miao_Longsheng	HM, Hmongic, Hmu, Eastern Dialect	Longsheng, Guilin, Guangxi	China (Southwest)	25.7992	110.0081	Miao_Longsheng	10
Zhuang_Qiubei	KD, Tai, Northern Tai	Quibei, Wenshan, Yunnan	China (Southwest)	24.0428	104.1887	Zhuang_Yunnan	9
Zhuang_Guangnan	KD, Tai, Central Tai	Guangnan, Wenshan, Yunnan	China (Southwest)	24.0458	105.0535	Zhuang_Yunnan	5
Zhuang_Wenshan	KD, Tai, Central Tai	Wenshan, Wenshan, Yunnan	China (Southwest)	23.3864	104.2318	Zhuang_Yunnan	10
Zhuang_Tianlin	KD, Tai, Northern Tai	Tianlin, Baise, Guangxi	China (Southwest)	24.2946	106.2306	Zhuang_Guangxi	10
Zhuang_Tianyang	KD, Tai, Northern Tai	Tianyang, Baise, Guangxi	China (Southwest)	23.7377	106.9160	Zhuang_Guangxi	6
Zhuang_Jingxi	KD, Tai, Central Tai	Jingxi, Baise, Guangxi	China (Southwest)	23.1355	106.4171	Zhuang_Guangxi	9
Zhuang_Chongzuo	KD, Tai, Central Tai	Jiangzhou, Chongzuo, Guangxi	China (Southwest)	22.4071	107.3546	Zhuang_Guangxi	10
Zhuang_Fusui	KD, Tai, Central Tai	Fusui, Chongzuo, Guangxi	China (Southwest)	22.6350	107.9041	Zhuang_Guangxi	6
Zhuang_Wuming	KD, Tai, Central Tai	Wuming, Nanning, Guangxi	China (Southwest)	23.1560	108.2841	Zhuang_Guangxi	1
Zhuang_Hechi	KD, Tai, Northern Tai	Jinchengjiang, Hechi, Guangxi	China (Southwest)	24.6944	108.0846	Zhuang_Guangxi	9
Zhuang_Guigang	KD, Tai, Northern Tai	Gangnan, Guigang, Guangxi	China (Southwest)	23.1107	109.5978	Zhuang_Guangxi	10
Zhuang_Laibin	KD, Tai, Northern Tai	Xingbin, Laibin, Guangxi	China (Southwest)	23.7402	109.1962	Zhuang_Guangxi	6
Han_Qiubei	ST, Sinitic, SW Mandarin, Diannan	Quibei, Wenshan, Yunnan	China (Southwest)	24.0428	104.1887	Han_Yunnan	6
Han_Guangnan	ST, Sinitic, SW Mandarin, Diannan	Guangnan, Wenshan, Yunnan	China (Southwest)	24.0458	105.0535	Han_Yunnan	3
Han_Wenshan	ST, Sinitic, SW Mandarin, Diannan	Wenshan, Wenshan, Yunnan	China (Southwest)	23.3864	104.2318	Han_Yunnan	7
Han_Tianlin	ST, Sinitic, Pinghua	Tianlin, Baise, Guangxi	China (Southwest)	24.2946	106.2306	Han_Guangxi	5
Han_Tianyang	ST, Sinitic, Pinghua	Tianyang, Baise, Guangxi	China (Southwest)	23.7377	106.9160	Han_Guangxi	5
Han_Jingxi	ST, Sinitic, SW Mandarin, Guiliu	Jingxi, Baise, Guangxi	China (Southwest)	23.1355	106.4171	Han_Guangxi	5
Han_Chongzuo	ST, Sinitic, Pinghua	Jiangzhou, Chongzuo, Guangxi	China (Southwest)	22.4071	107.3546	Han_Guangxi	5
Han_Fusui	ST, Sinitic, Pinghua	Fusui, Chongzuo, Guangxi	China (Southwest)	22.6350	107.9041	Han_Guangxi	1
Han_Hechi	ST, Sinitic, SW Mandarin, Guiliu	Jinchengjiang, Hechi, Guangxi	China (Southwest)	24.6944	108.0846	Han_Guangxi	6
Han_Guigang	ST, Sinitic, Pinghua	Gangnan, Guigang, Guangxi	China (Southwest)	23.1107	109.5978	Han_Guangxi	6
Han_Laibin	ST, Sinitic, SW Mandarin, Guiliu	Xingbin, Laibin, Guangxi	China (Southwest)	23.7402	109.1962	Han_Guangxi	4

Extended Data Table 2. Correlation between the proportion of ancestries and corresponding language families. We used point-biserial correlation to quantify if an individual affiliated to a certain language family tends to have more proportion of the ancestry corresponding to this language family. We further used the *p*-value of student's t-test to quantify if the correlation is significant. r_{pb}, point-biserial correlation coefficient.

Language Families	r_{pb}	*p*-value
Hmong-Mien	0.762	2.13×10^{-31}
Kra-Dai	0.644	9.77×10^{-189}
Austroasiatic	0.536	6.73×10^{-12}
Austronesian	0.921	7.23×10^{-32}
Sino-Tibetan	0.630	4.81×10^{-83}
Tungusic/ Amuric	0.806	7.34×10^{-31}

Extended Data Table 3. Admixture-*f_3* results. **(A)** Tibeto-Burman populations. (**B**) Southeast Han Chinese. (C) Kra-Dai and Vietic populations. We report the five lowest *f_3* results for each of the populations. std.err, standard error.

A

Source_1	Source_2	Target	f_3	std.err	Z	SNPs
Mekong_N	Yumin_EN	Naxi	-0.001575	0.002227	-0.708	69321
Mlabri	Tibetan_Chamdo	Naxi	-0.001207	0.000555	-2.177	105215
Mekong_N	Sherpa.DG	Naxi	-0.001042	0.001291	-0.807	83146
Mekong_N	Tibetan_Chamdo	Naxi	-0.001036	0.00068	-1.523	87697
Mekong_N	Tibetan_Nagqu	Naxi	-0.000908	0.000777	-1.17	87061
Mlabri	Tibetan_Chamdo	Yi	-0.00375	0.000573	-6.544	105393
Malaysia_LN.SG	Yumin_EN	Yi	-0.003742	0.002493	-1.501	67896
Mekong_N	Yumin_EN	Yi	-0.003681	0.002139	-1.721	70135
Ami	Tibetan_Chamdo	Yi	-0.00366	0.000363	-10.085	106865
Malaysia_LN.SG	Tibetan_Chamdo	Yi	-0.003537	0.000795	-4.451	84607
Mekong_N	Yumin_EN	Sila	0.029056	0.002478	11.724	67679
Mekong_N	Qijia_LN	Sila	0.030261	0.001622	18.661	81896
Malaysia_LN.SG	Qijia_LN	Sila	0.03054	0.001782	17.139	78608
Mlabri	Tibetan_Chamdo	Sila	0.03056	0.000988	30.924	104727
Mekong_N	Tibetan_Chamdo	Sila	0.030608	0.001149	26.649	87209
Mekong_N	Yumin_EN	HaNhi	0.00217	0.002201	0.986	69776
Mlabri	Tibetan_Chamdo	HaNhi	0.003446	0.000648	5.317	105256
Mekong_N	Tibetan_Nagqu	HaNhi	0.003451	0.000859	4.018	87152
Mlabri	Lokomotiv_EN	HaNhi	0.003579	0.001226	2.919	89625
Mekong_N	Qijia_LN	HaNhi	0.00363	0.001297	2.799	83933
Mekong_N	Yumin_EN	Cong	0.003042	0.002203	1.381	69905
Malaysia_LN.SG	Qijia_LN	Cong	0.00389	0.001518	2.563	80814
Mekong_N	Sherpa.DG	Cong	0.004221	0.00135	3.127	83654
Mekong_N	Qijia_LN	Cong	0.004291	0.001311	3.274	84076
Malaysia_LN.SG	Yumin_EN	Cong	0.004553	0.002551	1.785	67698
Mekong_N	Yumin_EN	Lahu_China	0.009174	0.002329	3.94	67477
Malaysia_LN.SG	Yumin_EN	Lahu_China	0.010163	0.002762	3.68	65140
Malaysia_LN.SG	Qijia_LN	Lahu_China	0.010199	0.001622	6.286	78604
Malaysia_LN.SG	Tibetan_Chamdo	Lahu_China	0.010683	0.001132	9.437	84250
Mekong_N	Sherpa.DG	Lahu_China	0.010862	0.001495	7.267	81702
Mekong_N	Yumin_EN	Lahu_Vietnam	0.008825	0.00227	3.889	68785
Malaysia_LN.SG	Yumin_EN	Lahu_Vietnam	0.010852	0.002663	4.074	66561
Mekong_N	Qijia_LN	Lahu_Vietnam	0.012234	0.001375	8.895	82996
Mlabri	Yumin_EN	Lahu_Vietnam	0.012279	0.001718	7.146	84001
Malaysia_LN.SG	Qijia_LN	Lahu_Vietnam	0.012334	0.001543	7.994	79719

B

Source_1	Source_2	Target	f_3	std.err	Z	SNPs
Atayal	Qijia_LN	Han_Fujian	-0.005661	0.000819	-6.912	100135
Kankanaey	Qijia_LN	Han_Fujian	-0.004939	0.000759	-6.506	100676
Atayal	Yumin_EN	Han_Fujian	-0.004855	0.00132	-3.68	83301
Hlai_Qiongzhong	Qijia_LN	Han_Fujian	-0.004405	0.000645	-6.828	105279
Kankanaey	Yangshao_MN	Han_Fujian	-0.004354	0.000834	-5.222	100270
Atayal	Yumin_EN	Han_Guangdong	-0.005255	0.001198	-4.385	84603
Hlai_Qiongzhong	Yumin_EN	Han_Guangdong	-0.004742	0.000835	-5.677	88521
Atayal	Qijia_LN	Han_Guangdong	-0.004456	0.000746	-5.97	101411
Ami	Yumin_EN	Han_Guangdong	-0.004278	0.001073	-3.989	85412
Maonan	Yumin_EN	Han_Guangdong	-0.004173	0.000876	-4.762	87806
Atayal	Qijia_LN	Han_Taiwan	-0.004181	0.000711	-5.882	101169
Atayal	Yumin_EN	Han_Taiwan	-0.004013	0.001229	-3.266	84541
Hlai_Qiongzhong	Yumin_EN	Han_Taiwan	-0.003404	0.000833	-4.084	88057
Kankanaey	Qijia_LN	Han_Taiwan	-0.00315	0.000651	-4.836	101443
Hlai_Qiongzhong	Qijia_LN	Han_Taiwan	-0.003081	0.000511	-6.034	104904
Qijia_LN	Atayal	Han_Hakka	-0.005343	0.000696	-7.673	101131
Qijia_LN	Kankanaey	Han_Hakka	-0.004676	0.000635	-7.367	101487
Sherpa.DG	Kankanaey	Han_Hakka	-0.004664	0.000734	-6.351	100941
Tibetan_Chamdo	Ami	Han_Hakka	-0.004617	0.000436	-10.584	105655
Sherpa.DG	Ami	Han_Hakka	-0.004606	0.00068	-6.774	101421
Mongolia_N_North	Hlai_HO	Han_Guangxi	-0.004074	0.000537	-7.583	103164
Qijia_LN	Atayal	Han_Guangxi	-0.004072	0.00054	-7.54	107035
Yumin_EN	Atayal	Han_Guangxi	-0.003639	0.000981	-3.71	89909
Qijia_LN	Hlai_HO	Han_Guangxi	-0.003628	0.000494	-7.344	106925
Qijia_LN	Hlai_Qiongzhong	Han_Guangxi	-0.003512	0.00029	-12.119	107881
Atayal	Qijia_LN	Han_Zhejiang	-0.005071	0.000843	-6.015	100136
Kankanaey	Qijia_LN	Han_Zhejiang	-0.004388	0.0008	-5.486	100775
Ami	Qijia_LN	Han_Zhejiang	-0.004223	0.000729	-5.797	101373
Hlai_HO	Qijia_LN	Han_Zhejiang	-0.004132	0.000812	-5.089	99336
Hlai_HO	Boisman_MN	Han_Zhejiang	-0.003947	0.000837	-4.717	93260
Atayal	Qijia_LN	CHS.SG	-0.0021	0.000535	-3.927	107824
Kankanaey	Qijia_LN	CHS.SG	-0.0013	0.000469	-2.774	107480
Ami	Qijia_LN	CHS.SG	-0.000939	0.000421	-2.23	107882
Hlai_Qiongzhong	Qijia_LN	CHS.SG	-0.00088	0.0003	-2.936	108513
Hlai_HO	Qijia_LN	CHS.SG	-0.000867	0.000481	-1.802	107768

C

Source_1	Source_2	Target	f_3	std.err	Z	SNPs
Mlabri	Fujian_LN	Hlai_Qiongzhong	0.001787	0.0011920	1.499	69995
Mekong_N	Ami	Hlai_Qiongzhong	0.002454	0.0007040	3.485	87834
Mekong_N	Atayal	Hlai_Qiongzhong	0.003009	0.0008930	3.370	87595
Malaysia_LN.SG	Ami	Hlai_Qiongzhong	0.003022	0.0008760	3.449	84545
Mekong_N	Kankanaey	Hlai_Qiongzhong	0.003176	0.0008100	3.920	87457
Mlabri	Fujian_LN	Zhuang_Guangxi	-0.002579	0.0011180	-2.306	72220
Hlai_HO	Mongolia_N_North	Zhuang_Guangxi	-0.002157	0.0005480	-3.934	104259
Mekong_N	Ami	Zhuang_Guangxi	-0.002070	0.0006260	-3.309	90401
Hlai_HO	Kolyma_M	Zhuang_Guangxi	-0.001675	0.0008670	-1.932	108675
Mekong_N	Atayal	Zhuang_Guangxi	-0.001607	0.0008380	-1.917	90347
Mlabri	Fujian_LN	Zhuang_Yunnan	-0.002457	0.001131	-2.172	70278
Mlabri	Qihe_EN	Zhuang_Yunnan	-0.00186	0.001865	-0.998	38807
Mlabri	Kankanaey	Zhuang_Yunnan	-0.001246	0.000609	-2.045	105224
Mekong_N	Atayal	Zhuang_Yunnan	-0.001242	0.00091	-1.365	88055
Mekong_N	Ami	Zhuang_Yunnan	-0.001209	0.000707	-1.709	88247
Mlabri	Fujian_LN	CDX.SG	-0.00053	0.001087	-0.487	72015
Mlabri	Qihe_EN	CDX.SG	-0.000412	0.001793	-0.23	39820
Mlabri	Liangdao1_EN	CDX.SG	0.000201	0.001681	0.119	56649
Mekong_N	Ami	CDX.SG	0.00031	0.000664	0.466	90185
Mekong_N	Hezhen	CDX.SG	0.000581	0.000696	0.835	90781
Hlai_HO	Kolyma_M	Mulam	-0.000988	0.000961	-1.028	104445
Hlai_HO	Mongolia_N_North	Mulam	-0.000853	0.000629	-1.356	100764
Fujian_LN	Mlabri	Mulam	-0.000814	0.001178	-0.692	69313
Hlai_HO	Qijia_LN	Mulam	-0.000519	0.000571	-0.909	104153
Hlai_Qiongzhong	Qijia_LN	Mulam	-0.000489	0.000364	-1.343	106533
Mlabri	Fujian_LN	Dai	-0.001628	0.001278	-1.273	67817
Mekong_N	Atayal	Dai	-0.001387	0.000958	-1.447	85437
Mekong_N	Ami	Dai	-0.001195	0.000813	-1.47	86033
Mlabri	Liangdao1_EN	Dai	-0.001099	0.001813	-0.606	53082
Mekong_N	Kankanaey	Dai	-0.000769	0.000895	-0.858	85539
Qihe_EN	Mlabri	Maonan	-0.000708	0.001897	-0.373	38205
Fujian_LN	Mlabri	Maonan	-0.000669	0.001211	-0.553	69171
Hlai_HO	Kolyma_M	Maonan	-0.000049	0.000991	-0.05	104275
Qihe_EN	Miao_Longlin	Maonan	0.000224	0.0012	0.187	38806
Ami	Mekong_N	Maonan	0.000309	0.000745	0.414	87016
Miao_Longlin	Qihe_EN	CoLao	0.026857	0.001809	14.85	37582
Miao_Longlin	Liangdao1_EN	CoLao	0.02686	0.001497	17.938	53446
Miao_Xilin	Malaysia_LN.SG	CoLao	0.027253	0.001376	19.812	81187
Miao_Longlin	Mekong_N	CoLao	0.02745	0.001196	22.945	84419
Yumin_EN	Mekong_N	CoLao	0.027586	0.002572	10.727	66989
Mlabri	Qihe_EN	Gelao	0.000421	0.001948	0.216	37203
Mlabri	Fujian_LN	Gelao	0.00056	0.001252	0.447	67550
Mlabri	Longshan_LN	Gelao	0.001273	0.000756	1.683	102065
Mlabri	Yangshao_MN	Gelao	0.001494	0.001025	1.457	100619
Mlabri	Liangdao1_EN	Gelao	0.001592	0.001851	0.86	52851
Mlabri	Fujian_LN	LaChi	0.033654	0.00162	20.769	66235
Malaysia_LN.SG	Qijia_LN	LaChi	0.034132	0.001792	19.042	78138
Mekong_N	Ami	LaChi	0.034462	0.001275	27.033	84541
Malaysia_LN.SG	Yumin_EN	LaChi	0.034524	0.002895	11.925	64779
Mlabri	Qihe_EN	LaChi	0.034846	0.002477	14.07	36410
Malaysia_LN.SG	Yumin_EN	Kinh	-0.005497	0.002521	-2.18	66590
Mekong_N	Yumin_EN	Kinh	-0.004957	0.002151	-2.304	68862
Mlabri	Fujian_LN	Kinh	-0.00494	0.001269	-3.892	67451
Malaysia_LN.SG	Qijia_LN	Kinh	-0.004437	0.001486	-2.985	80021
Mlabri	Yangshao_MN	Kinh	-0.004388	0.001001	-4.382	100543
Mlabri	Qihe_EN	Muong	-0.003278	0.001942	-1.688	37341
Mlabri	Fujian_LN	Muong	-0.002737	0.001205	-2.273	67833
Mekong_N	Ami	Muong	-0.002661	0.000843	-3.158	85867
Mekong_N	Kankanaey	Muong	-0.00232	0.000908	-2.553	85724
Mekong_N	Atayal	Muong	-0.002275	0.000966	-2.354	85258
Mekong_N	Hezhen	KHV.SG	-0.001114	0.000653	-1.705	91653
Mekong_N	Yumin_EN	KHV.SG	-0.001059	0.002048	-0.517	75980
Malaysia_LN.SG	Qijia_LN	KHV.SG	-0.001	0.001286	-0.778	87386
Mlabri	Qihe_EN	KHV.SG	-0.000881	0.001796	-0.491	40278
Mlabri	Fujian_LN	KHV.SG	-0.000864	0.001083	-0.798	72809
Mekong_N	Ami	Nung	-0.001796	0.000768	-2.339	85969
Mekong_N	Atayal	Nung	-0.00178	0.000917	-1.941	85459
Mlabri	Fujian_LN	Nung	-0.001548	0.00118	-1.311	68167
Mekong_N	Hezhen	Nung	-0.001542	0.000792	-1.946	87392
Mlabri	Qihe_EN	Nung	-0.001188	0.001907	-0.623	37606
Mlabri	Qihe_EN	Lao	-0.006126	0.001913	-3.203	37733
Mlabri	Fujian_LN	Lao	-0.006086	0.00118	-5.158	68494
Mekong_N	Ami	Lao	-0.005638	0.000799	-7.057	86114
Mlabri	Liangdao1_EN	Lao	-0.005427	0.001802	-3.012	53597
Mekong_N	Hezhen	Lao	-0.005185	0.000809	-6.41	87452

Extended Data Table 4. Admixture time estimates for Hmong-Mien Cline inferred by ALDER.

p -value	target	reference A	reference B	Z-score	admixture time estimate
1.5E-10	Miao_Rongshui	Hmong_Core	CHB.SG	6.40	24.43 ± 3.82
1.6E-07	Miao_Sanjiang	Hmong_Core	Austronesian_Core	5.25	25.80 ± 4.92
6.8E-09	Miao_Rongshui	Hmong_Core	KHV.SG	5.80	25.92 ± 4.47
1.8E-13	Miao_Rongshui	Hmong_Core	CDX.SG	7.36	26.76 ± 3.64
4.4E-10	Miao_Sanjiang	Hmong_Core	Tibetan_Core	6.24	26.86 ± 4.30
4.8E-07	Dong_Hunan	Hmong_Core	Hlai_all	5.03	26.97 ± 5.36
5.4E-09	Miao_Rongshui	Hmong_Core	Amur_Core	5.83	27.02 ± 4.63
2.9E-09	Miao_Sanjiang	Hmong_Core	CHS.SG	5.93	27.08 ± 4.56
2.9E-09	Miao_Sanjiang	Hmong_Core	CHS.SG	5.93	27.08 ± 4.56
2.8E-06	Dong_Hunan	Hmong_Core	CHB.SG	4.69	28.36 ± 6.05
1.0E-06	Dong_Hunan	Hmong_Core	Tibetan_Core	4.89	29.32 ± 6.00
4.9E-08	Miao_Sanjiang	Hmong_Core	CDX.SG	5.46	29.33 ± 5.38
1.8E-06	Dong_Hunan	Hmong_Core	KHV.SG	4.78	29.38 ± 6.15
1.3E-07	Dong_Hunan	Hmong_Core	CHS.SG	5.28	29.91 ± 5.67
1.3E-07	Dong_Hunan	Hmong_Core	CHS.SG	5.28	29.91 ± 5.67
7.5E-18	Miao_Huanjiang	Hmong_Core	Hlai_all	8.61	31.09 ± 3.61
2.3E-12	Dong_Guizhou	Hmong_Core	KHV.SG	7.01	31.97 ± 4.56
5.7E-19	Miao_Huanjiang	Hmong_Core	KHV.SG	8.90	32.09 ± 3.61
2.5E-18	Miao_Huanjiang	Hmong_Core	CHB.SG	8.73	33.91 ± 3.88
2.1E-07	Dong_Guizhou	Hmong_Core	CDX.SG	5.19	34.58 ± 6.67
1.6E-18	Miao_Huanjiang	Hmong_Core	Zhuang_Guangxi	8.79	35.01 ± 3.98
1.3E-09	PaThen	Hmong_Core	Zhuang_Guangxi	6.07	37.30 ± 6.14
1.9E-09	Dong_Guizhou	Hmong_Core	CHB.SG	6.01	38.26 ± 6.37
1.4E-15	Dong_Guizhou	Hmong_Core	CHS.SG	7.98	38.91 ± 4.87
1.4E-15	Dong_Guizhou	Hmong_Core	CHS.SG	7.98	38.91 ± 4.87
3.0E-10	PaThen	Hmong_Core	CHS.SG	6.30	39.73 ± 6.31
3.0E-10	PaThen	Hmong_Core	CHS.SG	6.30	39.73 ± 6.31
3.8E-09	PaThen	Hmong_Core	CHB.SG	5.89	40.25 ± 6.83
1.5E-09	Dong_Guizhou	Hmong_Core	JPT.SG	6.04	40.27 ± 6.67
7.2E-19	Miao_Huanjiang	Hmong_Core	Tibetan_Core	8.87	40.86 ± 4.61
1.2E-08	Dong_Guizhou	Hmong_Core	Tibetan_Core	5.70	41.91 ± 7.09
1.7E-05	Miao_Longsheng	Hmong_Core	KHV.SG	4.30	41.91 ± 9.74
4.1E-05	Miao_Longsheng	Hmong_Core	CHS.SG	4.10	45.62 ± 11.13
4.1E-05	Miao_Longsheng	Hmong_Core	CHS.SG	4.10	45.62 ± 11.13
4.6E-05	Miao_Longsheng	Hmong_Core	CDX.SG	4.08	46.40 ± 11.38

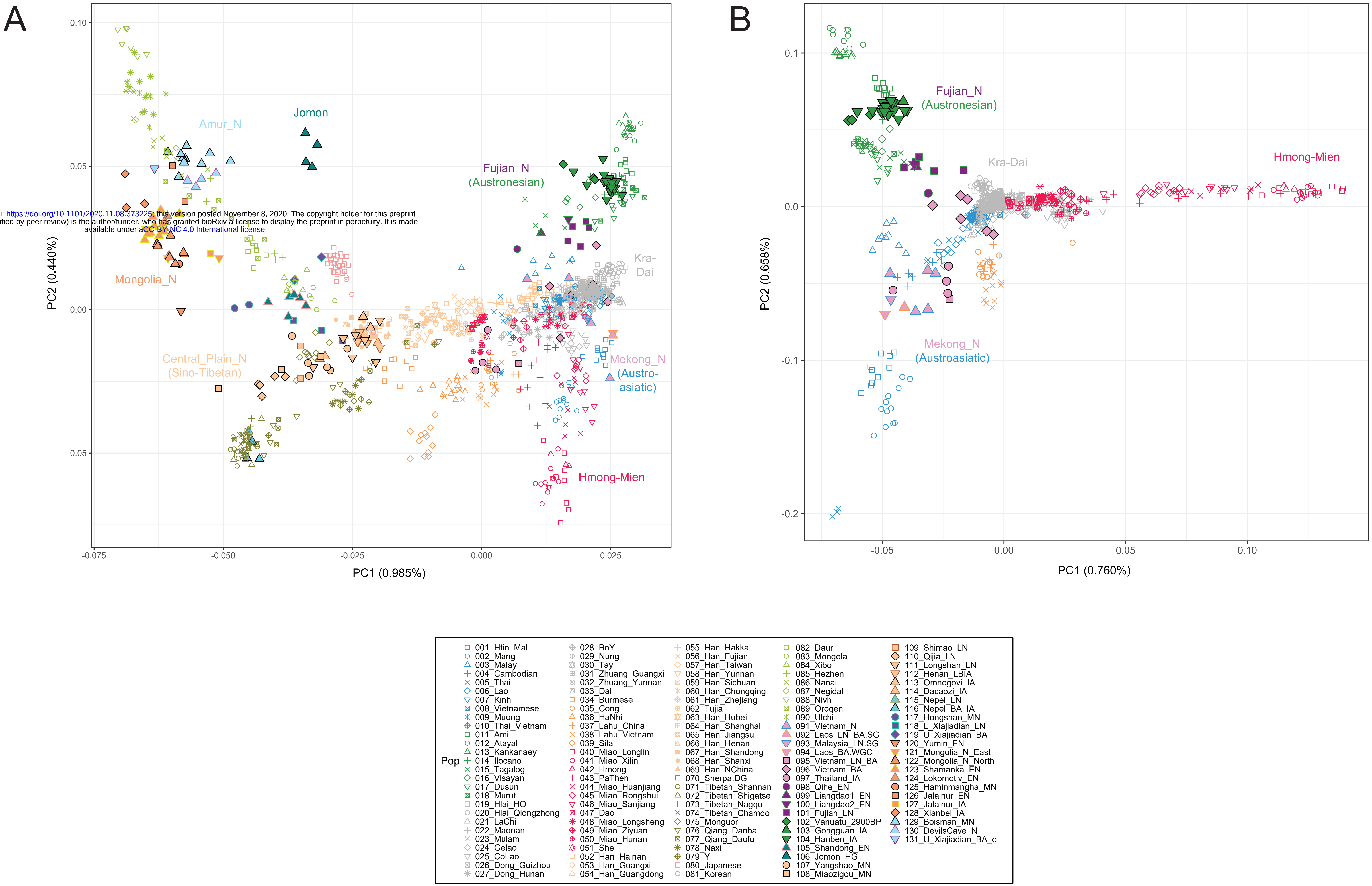
Extended Data Table 5.

Pop	P-value	Ancestry Coefficient		Standard Error	
		Mongolia_N	Andaman_HG	Mongolia_N	Andaman_HG
Haminmangha_MN	2.139E-01	0.852	0.148	0.065	0.065
Jalainur_EN	9.769E-01	0.992	0.008	0.072	0.072
Xianbei_IA	4.856E-02	0.956	0.044	0.092	0.092
Heishui_Mohe_Medieval	4.749E-01	0.707	0.293	0.073	0.073
Yankovsky_IA	2.113E-01	0.969	0.031	0.060	0.060
Boisman_MN	5.588E-01	0.936	0.064	0.040	0.040
DevilsCave_N	3.318E-01	0.883	0.117	0.042	0.042
U_Xiajiadian_BA_o	7.984E-02	1.046	-0.046	0.065	0.065
Yumin_EN	4.060E-02	0.978	0.022	0.058	0.058
Mongolia_N_North	6.086E-02	1.025	-0.025	0.043	0.043
Hongshan_MN	7.480E-01	0.869	0.131	0.044	0.044
L_Xiajiadian_LN	6.424E-01	0.837	0.163	0.045	0.045
U_Xiajiadian_BA	4.833E-01	0.900	0.100	0.057	0.057
Jomon_HG	9.088E-01	0.435	0.565	0.046	0.046
Sakhalin_HG	1.574E-01	0.552	0.448	0.116	0.116
Shandong_EN	3.289E-01	0.861	0.139	0.037	0.037
Yangshao_MN	9.339E-01	0.787	0.213	0.038	0.038
Longshan_LN	6.039E-01	0.826	0.174	0.033	0.033
Miaozigou_MN	8.369E-01	0.922	0.078	0.076	0.076
Shimao_LN	1.909E-01	0.853	0.147	0.047	0.047
Henan_LBIA	3.191E-01	0.797	0.203	0.034	0.034
Omnogovi_WestHan_IA	5.448E-01	0.786	0.214	0.042	0.042
Qijia_LN	4.798E-01	0.780	0.220	0.038	0.038
Dacaozi_IA	2.658E-01	0.820	0.180	0.044	0.044
Nepal_LN_BA_IA	9.297E-02	0.702	0.298	0.038	0.038
Laos_N	6.922E-01	0.442	0.558	0.050	0.050
Malaysia_LN.SG	3.746E-01	0.483	0.517	0.050	0.050
Vietnam_N	8.132E-01	0.426	0.574	0.105	0.105
Vietnam_LN_BA	3.047E-01	0.481	0.519	0.115	0.115
Vietnam_BA	6.560E-01	0.663	0.337	0.050	0.050
Thailand_IA	3.194E-01	0.635	0.365	0.065	0.065
Qihe_EN	5.139E-01	0.583	0.417	0.058	0.058
Liangdao1_EN	7.219E-01	0.527	0.473	0.059	0.059
Liangdao2_EN	3.856E-01	0.570	0.430	0.056	0.056
Fujian_LN	1.814E-02	0.608	0.392	0.047	0.047
Hanben_IA	8.145E-01	0.688	0.312	0.031	0.031
Gongguan_IA	5.574E-01	0.672	0.328	0.061	0.061

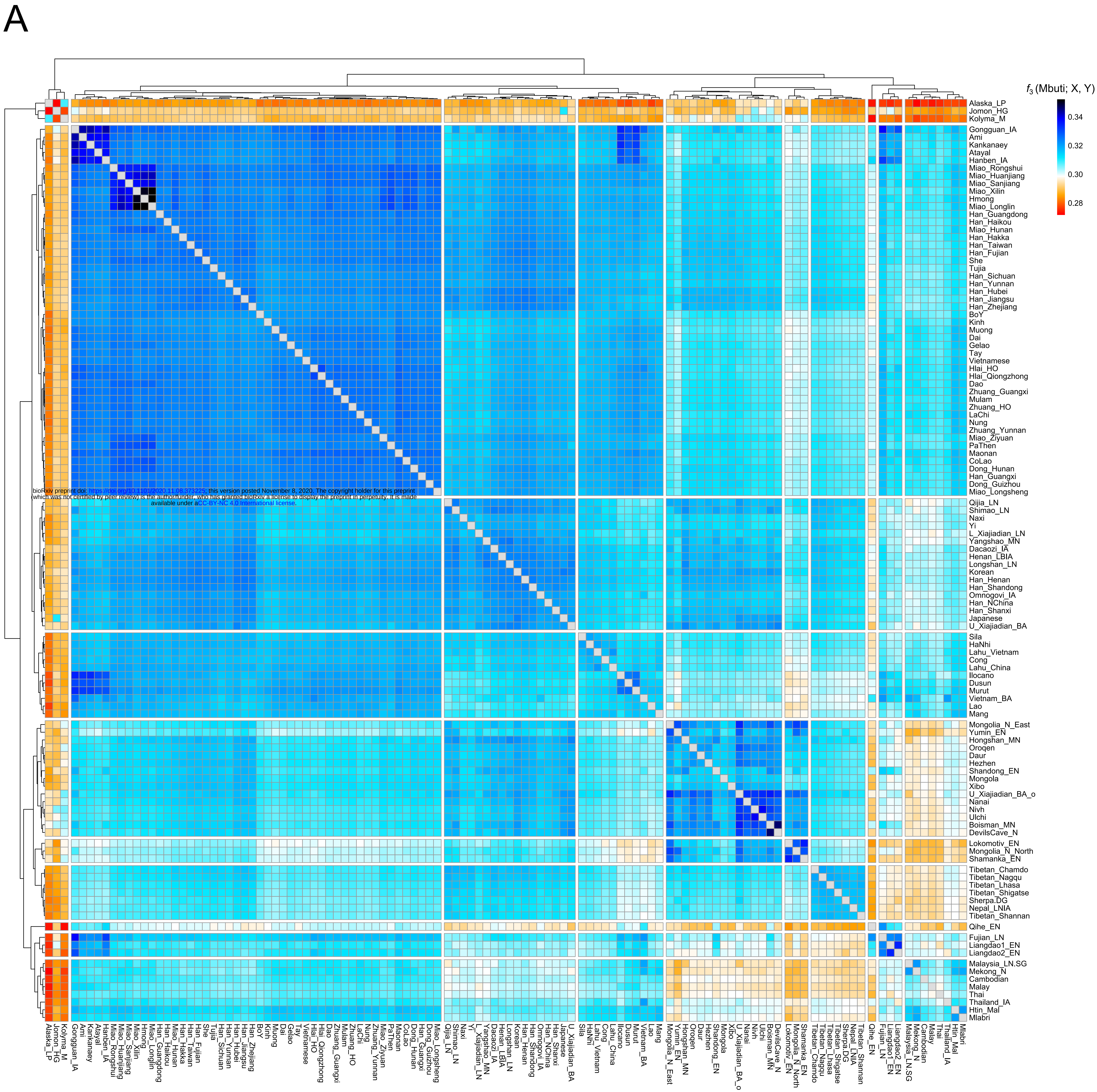
Vanuatu_2900BP_all	5.854E-01	0.638	0.362	0.061	0.061
Daur	5.628E-01	0.883	0.117	0.032	0.032
Xibo	2.916E-02	0.840	0.160	0.034	0.034
Hezhen	1.081E-01	0.905	0.095	0.033	0.033
Nanai	2.966E-01	0.966	0.034	0.034	0.034
Negidal	1.523E-01	1.017	-0.017	0.041	0.041
Nivh	1.268E-01	0.979	0.021	0.036	0.036
Oroqen	9.378E-02	0.936	0.064	0.034	0.034
Ulchi	7.103E-02	0.990	0.010	0.034	0.034
Korean	4.766E-01	0.822	0.178	0.032	0.032
Japanese	1.255E-01	0.787	0.213	0.029	0.029
JPT.SG	9.384E-02	0.795	0.205	0.030	0.030
CHB.SG	1.701E-01	0.789	0.211	0.030	0.030
CHS.SG	3.262E-01	0.746	0.254	0.029	0.029
Han_NChina	3.269E-01	0.782	0.218	0.030	0.030
Han_Shanxi	7.612E-01	0.780	0.220	0.030	0.030
Han_Shandong	3.585E-01	0.777	0.223	0.030	0.030
Han_Henan	3.620E-01	0.797	0.203	0.034	0.034
Han_Jiangsu	6.479E-01	0.790	0.210	0.031	0.031
Han_Shanghai	3.596E-01	0.771	0.229	0.035	0.035
Han_Hubei	3.524E-01	0.751	0.249	0.033	0.033
Tujia	2.355E-01	0.761	0.239	0.030	0.030
Han_Chongqing	3.799E-01	0.755	0.245	0.035	0.035
Han_Sichuan	3.907E-01	0.747	0.253	0.030	0.030
Han_Zhejiang	2.320E-01	0.757	0.243	0.032	0.032
Han_Fujian	3.615E-01	0.724	0.276	0.032	0.032
Han_Taiwan	6.705E-01	0.742	0.258	0.031	0.031
Han_Hakka	4.255E-01	0.735	0.265	0.030	0.030
Han_Yunnan	3.207E-01	0.749	0.251	0.029	0.029
Han_Guangdong	3.999E-01	0.712	0.288	0.031	0.031
Han_Guangxi	4.243E-01	0.704	0.296	0.029	0.029
Han_Haikou	4.678E-01	0.721	0.279	0.028	0.028
Monguor	4.567E-02	0.770	0.230	0.031	0.031
Yugur	1.634E-01	0.772	0.228	0.030	0.030
Qiang_Daofu	1.641E-01	0.760	0.240	0.030	0.030
Qiang_Danba	1.713E-01	0.782	0.218	0.030	0.030
Tibetan_Xinlong	2.645E-01	0.759	0.241	0.031	0.031
Tibetan_Gangcha	1.053E-01	0.774	0.226	0.030	0.030
Tibetan_Xunhua	3.318E-02	0.723	0.277	0.034	0.034
Tibetan_Chamdo	2.783E-01	0.770	0.230	0.030	0.030
Tibetan_Lhasa	3.319E-01	0.754	0.246	0.031	0.031
Tibetan_Nagqu	5.123E-01	0.759	0.241	0.030	0.030
Tibetan_Shigatse	3.908E-01	0.724	0.276	0.031	0.031
Tibetan_Shannan	3.233E-01	0.722	0.278	0.031	0.031

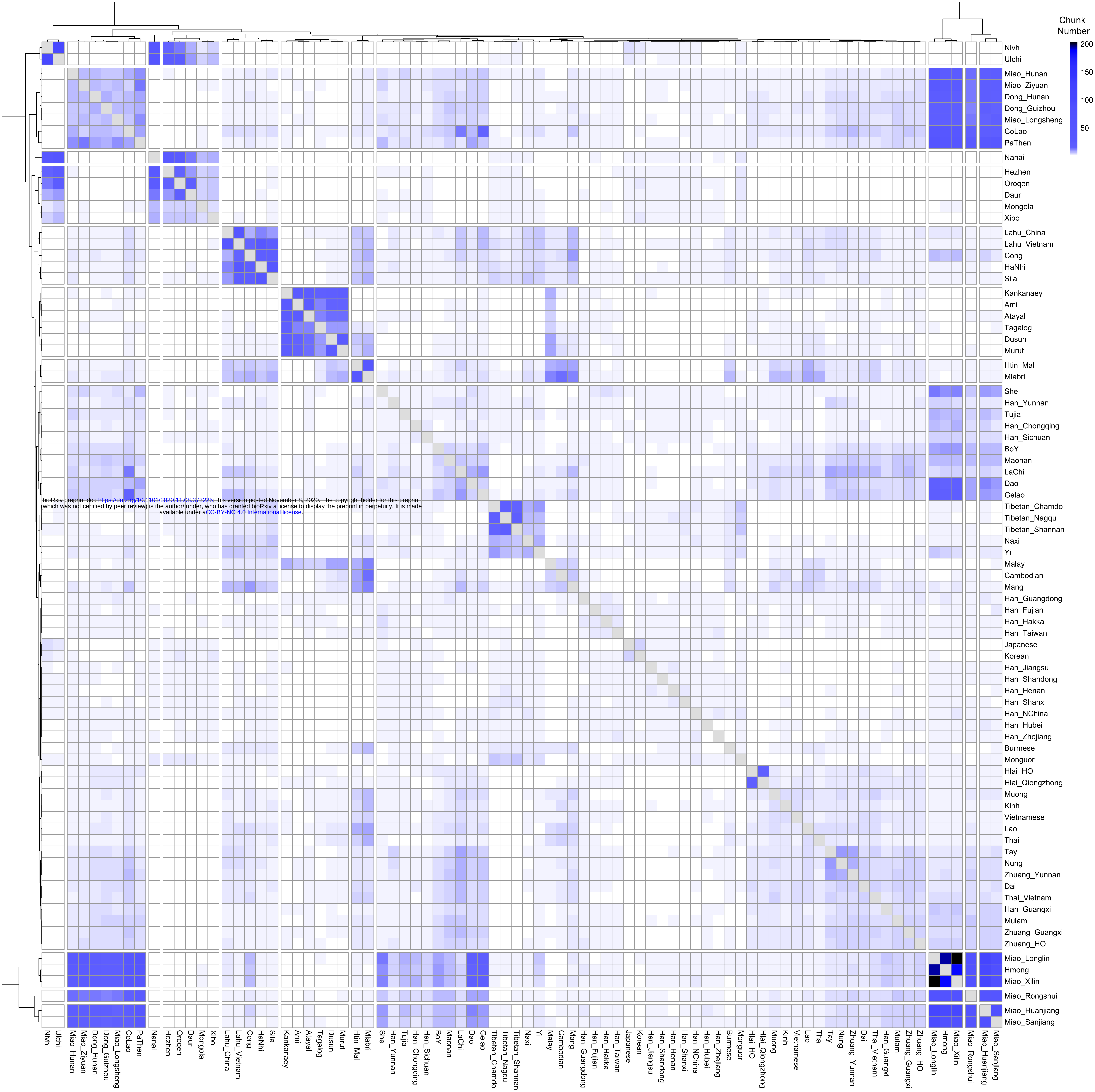
Sherpa.DG	2.050E-02	0.713	0.287	0.039	0.039
Naxi	3.315E-01	0.728	0.272	0.030	0.030
Yi	5.347E-01	0.756	0.244	0.030	0.030
Lahu_China	7.062E-01	0.652	0.348	0.029	0.029
Lahu_Vietnam	7.231E-01	0.682	0.318	0.030	0.030
Cong	6.635E-01	0.634	0.366	0.030	0.030
HaNhi	3.238E-01	0.695	0.305	0.029	0.029
Sila	5.416E-01	0.696	0.304	0.031	0.031
She	3.514E-01	0.730	0.270	0.031	0.031
Miao_Hunan	4.511E-01	0.727	0.273	0.030	0.030
Miao_Longlin	6.374E-01	0.687	0.313	0.033	0.033
Miao_Xilin	3.733E-01	0.681	0.319	0.033	0.033
Miao_Rongshui	1.874E-01	0.703	0.297	0.032	0.032
Miao_Sanjiang	2.764E-01	0.681	0.319	0.033	0.033
Miao_Huanjiang	5.102E-01	0.703	0.297	0.031	0.031
Miao_Longsheng	7.503E-01	0.699	0.301	0.031	0.031
Miao_Ziyuan	1.504E-01	0.709	0.291	0.032	0.032
Hmong	3.666E-01	0.692	0.308	0.031	0.031
PaThen	4.965E-02	0.729	0.271	0.032	0.032
Dao	3.200E-01	0.689	0.311	0.031	0.031
Gelao	2.265E-01	0.673	0.327	0.030	0.030
LaChi	3.818E-01	0.666	0.334	0.033	0.033
CoLao	3.944E-01	0.695	0.305	0.032	0.032
Maonan	3.220E-01	0.676	0.324	0.031	0.031
Mulam	1.359E-01	0.691	0.309	0.031	0.031
Dong_Guizhou	4.464E-01	0.704	0.296	0.031	0.031
Dong_Hunan	3.626E-01	0.700	0.300	0.031	0.031
Hlai_Qiongzhong	5.390E-01	0.656	0.344	0.029	0.029
Hlai_HO	2.707E-01	0.651	0.349	0.034	0.034
Zhuang_HO	4.818E-01	0.688	0.312	0.029	0.029
Zhuang_Guangxi	4.656E-01	0.689	0.311	0.028	0.028
Zhuang_Yunnan	2.399E-01	0.681	0.319	0.030	0.030
Nung	4.955E-01	0.680	0.320	0.029	0.029
Tay	3.502E-01	0.680	0.320	0.030	0.030
BoY	9.470E-02	0.685	0.315	0.033	0.033
Dai	2.867E-01	0.670	0.330	0.031	0.031
CDX.SG	4.419E-01	0.663	0.337	0.029	0.029
Muong	6.631E-01	0.671	0.329	0.030	0.030
Kinh	7.350E-01	0.663	0.337	0.030	0.030
Vietnamese	3.438E-01	0.678	0.322	0.030	0.030
KHV.SG	5.111E-01	0.664	0.336	0.028	0.028
Dusun	3.060E-01	0.586	0.414	0.031	0.031
Murut	5.699E-01	0.597	0.403	0.032	0.032
Malay	2.518E-01	0.482	0.518	0.031	0.031

Lao	8.070E-01	0.592	0.408	0.030	0.030
Thai	4.131E-02	0.538	0.462	0.032	0.032
Cambodian	1.697E-01	0.515	0.485	0.031	0.031
Mang	6.467E-01	0.615	0.385	0.030	0.030
Htin_Mal	6.216E-01	0.545	0.455	0.033	0.033
Mlabri	5.319E-01	0.498	0.502	0.039	0.039
Ami	5.141E-01	0.642	0.358	0.032	0.032
Atayal	6.564E-01	0.676	0.324	0.034	0.034
Kankanaey	7.745E-01	0.668	0.332	0.032	0.032
Tagalog	5.997E-01	0.592	0.408	0.031	0.031
Malaysia_Jehai.SG	9.572E-01	0.177	0.823	0.049	0.049
Onge.DG	7.643E-01	-0.036	1.036	0.046	0.046


A
0.10
0.05
0.00
-0.05
PC2 (0.440%)
-0.075
-0.050
-0.025
0.000
0.025
PC1 (0.985%)
Amur_N
Jomon
Fujian_N
(Austronesian)
Kra-
Dai
Mongolia_N
Central_Plain_N
(Sino-Tibetan)
Mekong_N
(Austro-
asiatic)
Hmong-Mien
B
0.1
0.0
-0.1
-0.2
PC2 (0.658%)
-0.05
0.00
0.05
0.10
PC1 (0.760%)
Fujian_N
(Austronesian)
Kra-Dai
Hmong-Mien
Mekong_N
(Austroasiatic)
Pop
001_Htin_Mal
002_Mang
003_Malay
004_Cambodian
005_Thai
006_Lao
007_Kinh
008_Vietnamese
009_Muong
010_Thai_Vietnam
011_Ami
012_Atayal
013_Kankanaey
014_Ilocano
015_Tagalog
016_Visayan
017_Dusun
018_Murut
019_Hlai_HO
020_Hlai_Qiongzhong
021_LaChi
022_Maonan
023_Mulam
024_Gelao
025_CoLao
026_Dong_Guizhou
027_Dong_Hunan
028_BoY
029_Nung
030_Tay
031_Zhuang_Guangxi
032_Zhuang_Yunnan
033_Dai
034_Burmese
035_Cong
036_HaNhi
037_Lahu_China
038_Lahu_Vietnam
039_Sila
040_Miao_Longlin
041_Miao_Xilin
042_Hmong
043_PaThen
044_Miao_Huanjiang
045_Miao_Rongshui
046_Miao_Sanjiang
047_Dao
048_Miao_Longsheng
049_Miao_Ziyuan
050_Miao_Hunan
051_She
052_Han_Hainan
053_Han_Guangxi
054_Han_Guangdong
055_Han_Hakka
056_Han_Fujian
057_Han_Taiwan
058_Han_Yunnan
059_Han_Sichuan
060_Han_Chongqing
061_Han_Zhejiang
062_Tujia
063_Han_Hubei
064_Han_Shanghai
065_Han_Jiangsu
066_Han_Henan
067_Han_Shandong
068_Han_Shanxi
069_Han_NChina
070_Sherpa.DG
071_Tibetan_Shannan
072_Tibetan_Shigatse
073_Tibetan_Nagqu
074_Tibetan_Chamdo
075_Monguor
076_Qiang_Danba
077_Qiang_Daofu
078_Naxi
079_Yi
080_Japanese
081_Korean
082_Daur
083_Mongola
084_Xibo
085_Hezhen
086_Nanai
087_Negidal
088_Nivh
089_Oroqen
090_Ulchi
091_Vietnam_N
092_Laos_LN_BA.SG
093_Malaysia_LN.SG
094_Laos_BA.WGC
095_Vietnam_LN_BA
096_Vietnam_BA
097_Thailand_IA
098_Qihe_EN
099_Liangdao1_EN
100_Liangdao2_EN
101_Fujian_LN
102_Vanuatu_2900BP
103_Gongguan_IA
104_Hanben_IA
105_Shandong_EN
106_Jomon_HG
107_Yangshao_MN
108_Miaozigou_MN
109_Shimao_LN
110_Qijia_LN
111_Longshan_LN
112_Henan_LBIA
113_Omnogovi_IA
114_Dacaozi_IA
115_Nepel_LN
116_Nepel_BA_IA
117_Hongshan_MN
118_L_Xiajiadian_LN
119_U_Xiajiadian_BA
120_Yumin_EN
121_Mongolia_N_East
122_Mongolia_N_North
123_Shamanka_EN
124_Lokomotiv_EN
125_Haminmangha_MN
126_Jalainur_EN
127_Jalainur_IA
128_Xianbei_IA
129_Boisman_MN
130_DevilsCave_N
131_U_Xiajiadian_BA_o

C
Atayal
Gongguan_IA
Hanben_IA
Vanuatu_2900BP
Dusun
Murut
Tagalog
Qihe_EN
Liangdao2_EN
Visayan
Kankanaey
Ami
Ilocano
Fujian_LN
Liangdao1_EN
Miao_Xilin
Hmong
Miao_Longlin
Miao_Huanjiang
Miao_Sanjiang
Miao_Rongshui
PaThen
Miao_Hunan
She
Dao
CoLao
Miao_Ziyuan
Dong_Hunan
Dong_Guizhou
Miao_Longsheng
Gelao
Mang
Malaysia_LN.SG
Htin_Mal
Laos_BA.WGC
Laos_LN_BA.SG
Vietnam_LN_BA
Vietnam_N
Malay
Cambodian
Thai
Hlai_HO
Hlai_Qiongzhong
LaChi
Muong
Thai_Vietnam
Mulam
Tay
Maonan
Zhuang_Guangxi
Dai
Nung
Zhuang_Yunnan
Kinh
Vietnamese
Lao
Vietnam_BA
Austronesian/ISEA Cluster
Hmong-Mien Cluster
Austroasiatic/MSEA Cluster
Kra-Dai Cluster
Amur-Mongolia Cluster
Northeast China Cline
MSEA Tibeto-Burman
Tibetan Plateau Cluster
Korean-Japonic
Han/Sinitic Cline
U_Xiajiadian_BA_o
Nivh
Lokomotiv_EN
Shamanka_EN
Jalainur_EN
Mongolia_N_North
Xianbei_IA
Boisman_MN
DevilsCave_N
Jalainur_IA
Nanai
Mongolia_N_East
Negidal
U_Xiajiadian_BA
Ulchi
Haminmangha_MN
Yumin_EN
Hongshan_MN
Mongola
Xibo
Mongol
Oroqen
Daur
Hezhen
Burmese
Cong
Lahu_China
HaNhi
Lahu_Vietnam
Sila
Thailand_IA
Monguor
Naxi
Yi
Nepel_BA_IA
Nepel_LN
Sherpa.DG
Tibetan_Chamdo
Tibetan_Nagqu
Tibetan_Shannan
Jomon_HG
Japanese
Korean
Shandong_EN
Miaozigou_MN
Shimao_LN
Yangshao_MN
Qijia_LN
Longshan_LN
L_Xiajiadian_LN
Henan_LBIA
Omnogovi_IA
Dacaozi_IA
Han_Jiangsu
Han_Shanghai
Han_Henan
Han_Shandong
Han_NChina
Han_Shanxi
Han_Hakka
Han_Fujian
Han_Taiwan
Han_Yunnan
Han_Sichuan
Tujia
Han_Chongqing
Han_Hubei
Han_Zhejiang
BoY
Han_Guangdong
Han_Guangxi


A
f_3 (Mbuti; X, Y)
0.34
0.32
0.30
0.28
Alaska_LP
Jomon_HG
Kolyma_M
Gongguan_IA
Ami
Kankanaey
Atayal
Hanben_IA
Miao_Rongshui
Miao_Huanjiang
Miao_Sanjiang
Miao_Xilin
Hmong
Miao_Longlin
Han_Guangdong
Han_Haikou
Miao_Hunan
Han_Hakka
Han_Taiwan
Han_Fujian
She
Tujia
Han_Sichuan
Han_Yunnan
Han_Hubei
Han_Jiangsu
Han_Zhejiang
BoY
Kinh
Muong
Dai
Gelao
Tay
Vietnamese
Hlai_HO
Hlai_Qiongzhong
Dao
Zhuang_Guangxi
Mulam
Zhuang_HO
LaChi
Nung
Zhuang_Yunnan
Miao_Ziyuan
PaThen
Maonan
CoLao
Dong_Hunan
Han_Guangxi
Dong_Guizhou
Miao_Longsheng
Qijia_LN
Shimao_LN
Naxi
Yi
L_Xiajiadian_LN
Yangshao_MN
Dacaozi_IA
Henan_LBIA
Longshan_LN
Korean
Han_Henan
Han_Shandong
Omnogovi_IA
Han_NChina
Han_Shanxi
Japanese
U_Xiajiadian_BA
Sila
HaNhi
Lahu_Vietnam
Cong
Lahu_China
Ilocano
Dusun
Murut
Vietnam_BA
Lao
Mang
Mongolia_N_East
Yumin_EN
Hongshan_MN
Oroqen
Daur
Hezhen
Shandong_EN
Mongola
Xibo
U_Xiajiadian_BA_o
Nanai
Nivh
Ulchi
Boisman_MN
DevilsCave_N
Lokomotiv_EN
Mongolia_N_North
Shamanka_EN
Tibetan_Chamdo
Tibetan_Nagqu
Tibetan_Lhasa
Tibetan_Shigatse
Sherpa.DG
Nepal_LNIA
Tibetan_Shannan
Qihe_EN
Fujian_LN
Liangdao1_EN
Liangdao2_EN
Malaysia_LN.SG
Mekong_N
Cambodian
Malay
Thai
Thailand_IA
Htin_Mal
Mlabri


Chunk
Number
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50
Nivh
Ulchi
Miao_Hunan
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Dong_Hunan
Dong_Guizhou
Miao_Longsheng
CoLao
PaThen
Nanai
Hezhen
Oroqen
Daur
Mongola
Xibo
Lahu_China
Lahu_Vietnam
Cong
HaNhi
Sila
Kankanaey
Ami
Atayal
Tagalog
Dusun
Murut
Htin_Mal
Mlabri
She
Han_Yunnan
Tujia
Han_Chongqing
Han_Sichuan
BoY
Maonan
LaChi
Dao
Gelao
Tibetan_Chamdo
Tibetan_Nagqu
Tibetan_Shannan
Naxi
Yi
Malay
Cambodian
Mang
Han_Guangdong
Han_Fujian
Han_Hakka
Han_Taiwan
Japanese
Korean
Han_Jiangsu
Han_Shandong
Han_Henan
Han_Shanxi
Han_NChina
Han_Hubei
Han_Zhejiang
Burmese
Monguor
Hlai_HO
Hlai_Qiongzhong
Muong
Kinh
Vietnamese
Lao
Thai
Tay
Nung
Zhuang_Yunnan
Dai
Thai_Vietnam
Han_Guangxi
Mulam
Zhuang_Guangxi
Zhuang_HO
Miao_Longlin
Hmong
Miao_Xilin
Miao_Rongshui
Miao_Huanjiang
Miao_Sanjiang
Nivh
Ulchi
Miao_Hunan
Miao_Ziyuan
Dong_Hunan
Dong_Guizhou
Miao_Longsheng
CoLao
PaThen
Nanai
Hezhen
Oroqen
Daur
Mongola
Xibo
Lahu_China
Lahu_Vietnam
Cong
HaNhi
Sila
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Ami
Atayal
Tagalog
Dusun
Murut
Htin_Mal
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Maonan
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Dao
Gelao
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Tibetan_Shannan
Naxi
Yi
Malay
Cambodian
Mang
Han_Guangdong
Han_Fujian
Han_Hakka
Han_Taiwan
Japanese
Korean
Han_Jiangsu
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Han_Henan
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Han_Zhejiang
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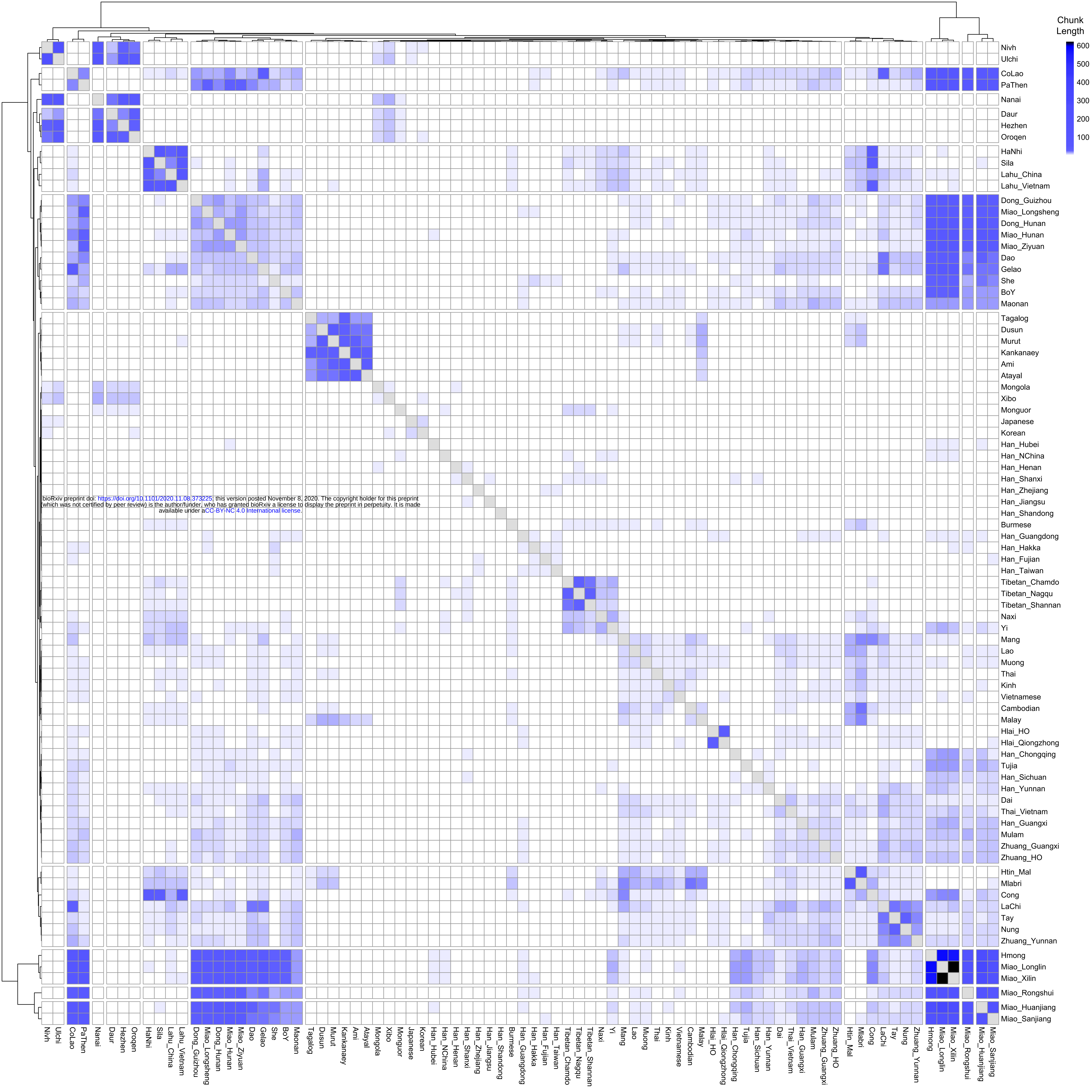
Monguor
Hlai_HO
Hlai_Qiongzhong
Muong
Kinh
Vietnamese
Lao
Thai
Tay
Nung
Zhuang_Yunnan
Dai
Thai_Vietnam
Han_Guangxi
Mulam
Zhuang_Guangxi
Zhuang_HO
Miao_Longlin
Hmong
Miao_Xilin
Miao_Rongshui
Miao_Huanjiang
Miao_Sanjiang


Chunk Length
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400
300
200
100
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Ulchi
CoLao
PaThen
Nanai
Daur
Hezhen
Oroqen
HaNhi
Sila
Lahu_China
Lahu_Vietnam
Dong_Guizhou
Miao_Longsheng
Dong_Hunan
Miao_Hunan
Miao_Ziyuan
Dao
Gelao
She
BoY
Maonan
Tagalog
Dusun
Murut
Kankanaey
Ami
Atayal
Mongola
Xibo
Monguor
Japanese
Korean
Han_Hubei
Han_NChina
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Burmese
Han_Guangdong
Han_Hakka
Han_Fujian
Han_Taiwan
Tibetan_Chamdo
Tibetan_Nagqu
Tibetan_Shannan
Naxi
Yi
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Muong
Thai
Kinh
Vietnamese
Cambodian
Malay
Hlai_HO
Hlai_Qiongzhong
Han_Chongqing
Tujia
Han_Sichuan
Han_Yunnan
Dai
Thai_Vietnam
Han_Guangxi
Mulam
Zhuang_Guangxi
Zhuang_HO
Htin_Mal
Mlabri
Cong
LaChi
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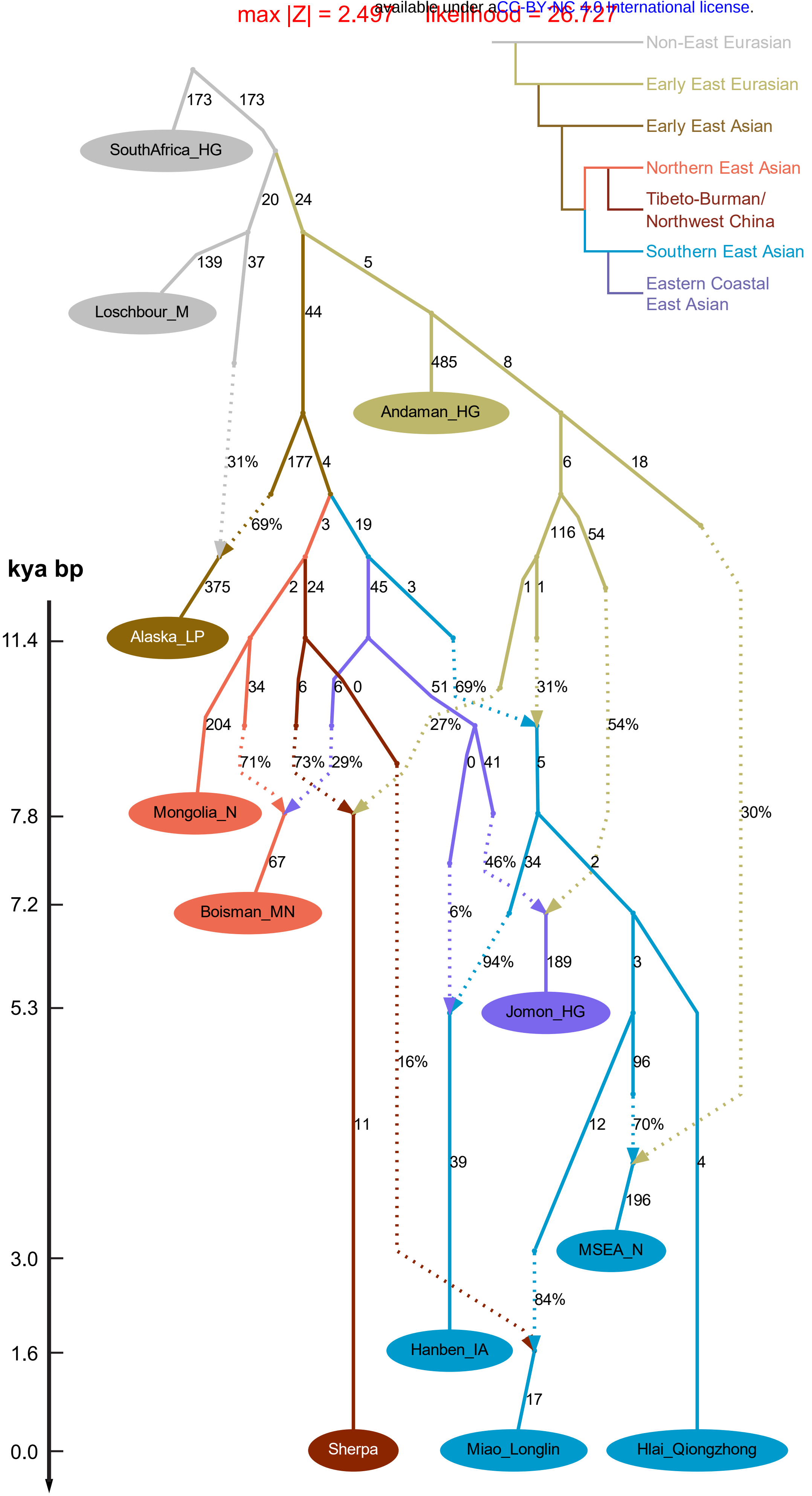
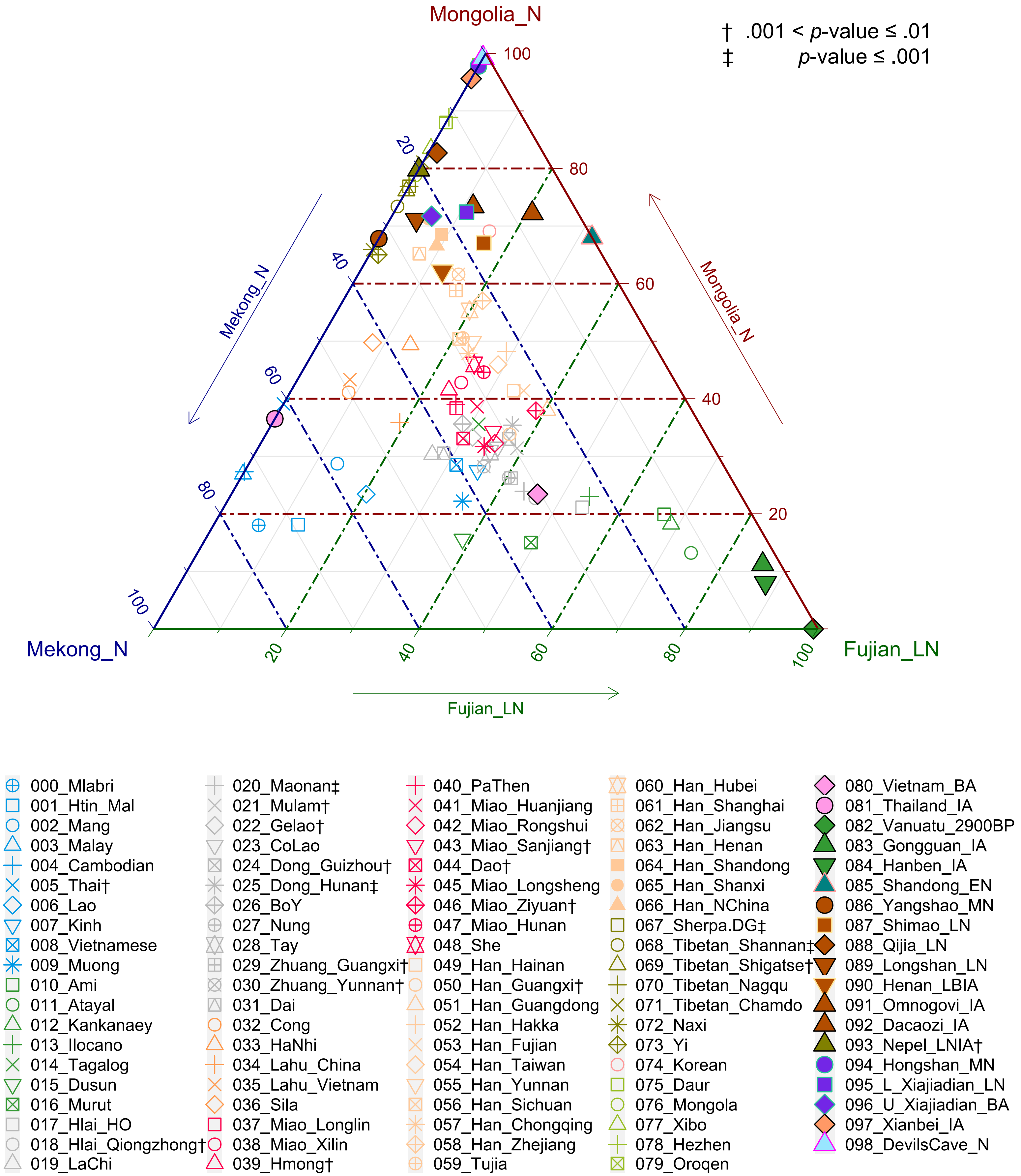
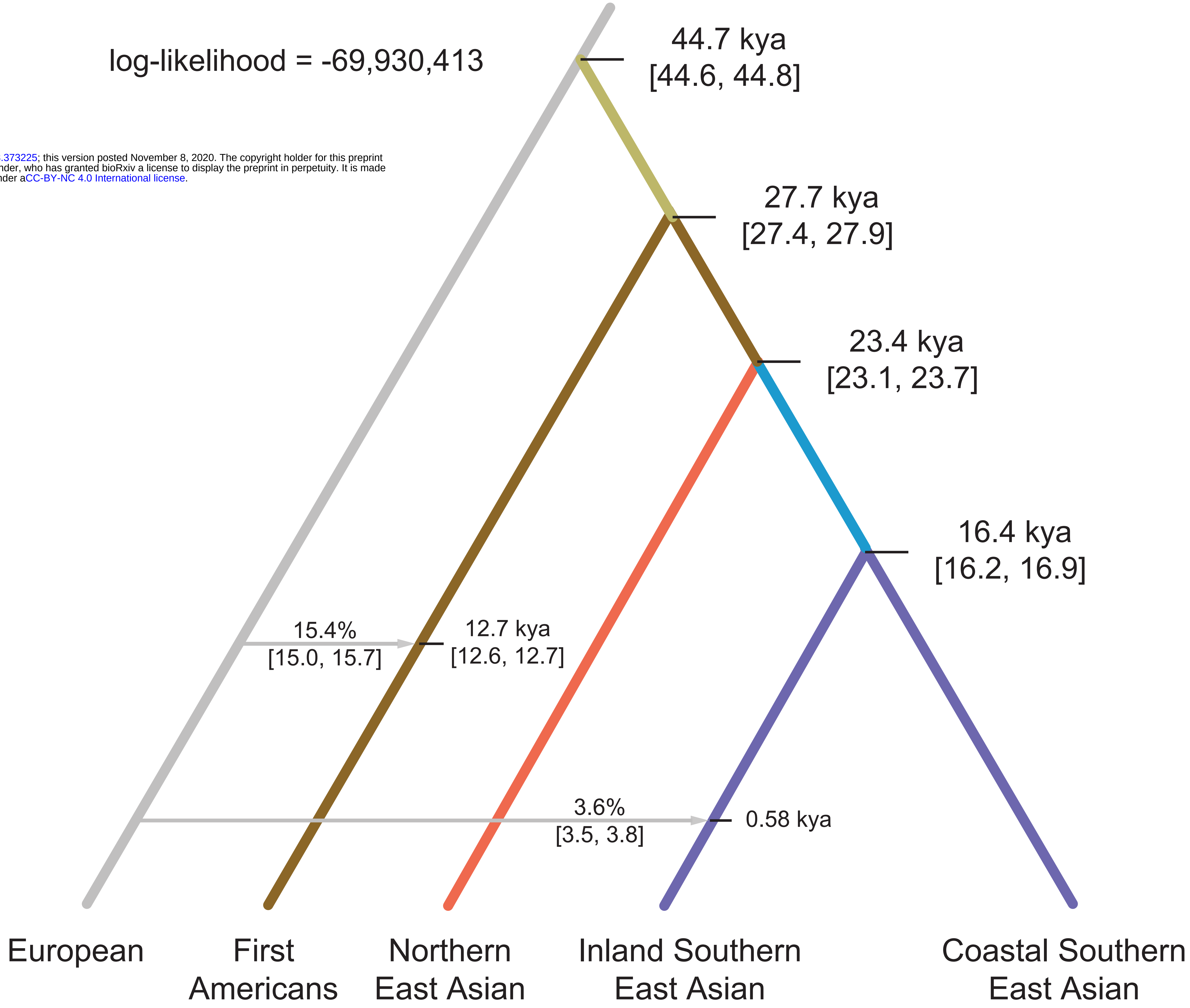
Zhuang_Yunnan
Hmong
Miao_Longlin
Miao_Xilin
Miao_Rongshui
Miao_Huanjiang
Miao_Sanjiang


max |Z| = 2.497
likelihood = 26.727
Non-East Eurasian
Early East Eurasian
Early East Asian
Northern East Asian
Tibeto-Burman/
Northwest China
Southern East Asian
Eastern Coastal
East Asian
kya bp
11.4
7.8
7.2
5.3
3.0
1.6
0.0
SouthAfrica_HG
Loschbour_M
Andaman_HG
Alaska_LP
Mongolia_N
Boisman_MN
Jomon_HG
Sherpa
Hanben_IA
MSEA_N
Miao_Longlin
Hlai_Qiongzhong
173
173
20
24
139
37
5
44
485
8
31%
177
4
6
18
69%
3
19
116
54
375
2
24
45
3
1
1
34
6
6
0
51
69%
31%
204
27%
54%
71%
73%
29%
0
41
5
67
46%
34
2
6%
94%
189
3
30%
96
16%
11
39
12
70%
4
196
84%
17


Mongolia_N
Mekong_N
Fujian_LN
† .001 < p-value ≤ .01
‡ p-value ≤ .001
100
80
60
40
20
20
40
60
80
100
20
40
60
80
100
Mekong_N
Mongolia_N
Fujian_LN
000_Mlabri
001_Htin_Mal
002_Mang
003_Malay
004_Cambodian
005_Thai†
006_Lao
007_Kinh
008_Vietnamese
009_Muong
010_Ami
011_Atayal
012_Kankanaey
013_Ilocano
014_Tagalog
015_Dusun
016_Murut
017_Hlai_HO
018_Hlai_Qiongzhong†
019_LaChi
020_Maonan‡
021_Mulam†
022_Gelao†
023_CoLao
024_Dong_Guizhou†
025_Dong_Hunan‡
026_BoY
027_Nung
028_Tay
029_Zhuang_Guangxi†
030_Zhuang_Yunnan†
031_Dai
032_Cong
033_HaNhi
034_Lahu_China
035_Lahu_Vietnam
036_Sila
037_Miao_Longlin
038_Miao_Xilin
039_Hmong†
040_PaThen
041_Miao_Huanjiang
042_Miao_Rongshui
043_Miao_Sanjiang†
044_Dao†
045_Miao_Longsheng
046_Miao_Ziyuan†
047_Miao_Hunan
048_She
049_Han_Hainan
050_Han_Guangxi†
051_Han_Guangdong
052_Han_Hakka
053_Han_Fujian
054_Han_Taiwan
055_Han_Yunnan
056_Han_Sichuan
057_Han_Chongqing
058_Han_Zhejiang
059_Tujia
060_Han_Hubei
061_Han_Shanghai
062_Han_Jiangsu
063_Han_Henan
064_Han_Shandong
065_Han_Shanxi
066_Han_NChina
067_Sherpa.DG‡
068_Tibetan_Shannan‡
069_Tibetan_Shigatse†
070_Tibetan_Nagqu
071_Tibetan_Chamdo
072_Naxi
073_Yi
074_Korean
075_Daur
076_Mongola
077_Xibo
078_Hezhen
079_Oroqen
080_Vietnam_BA
081_Thailand_IA
082_Vanuatu_2900BP
083_Gongguan_IA
084_Hanben_IA
085_Shandong_EN
086_Yangshao_MN
087_Shimao_LN
088_Qijia_LN
089_Longshan_LN
090_Henan_LBIA
091_Omnogovi_IA
092_Dacaozi_IA
093_Nepel_LNIA†
094_Hongshan_MN
095_L_Xiajiadian_LN
096_U_Xiajiadian_BA
097_Xianbei_IA
098_DevilsCave_N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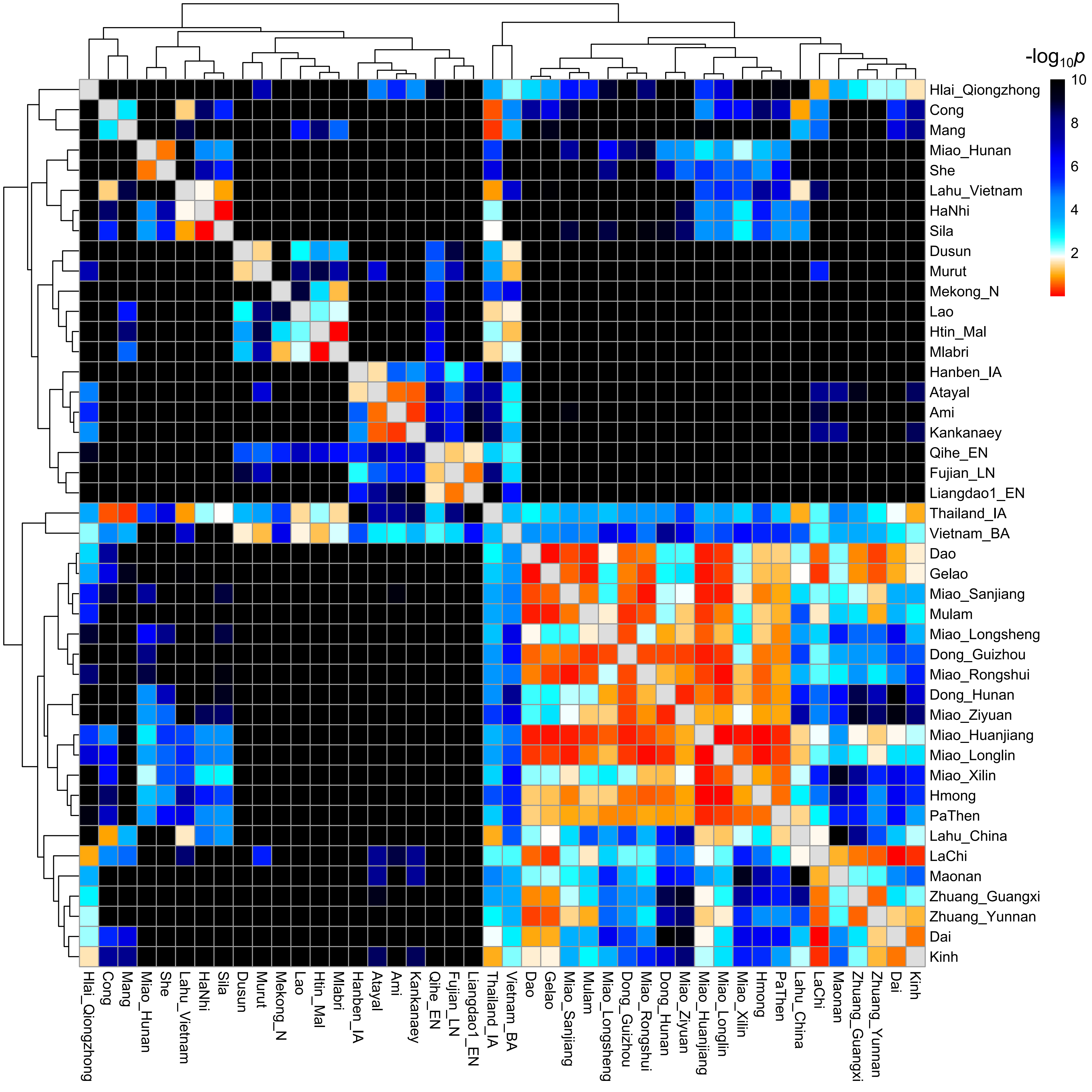
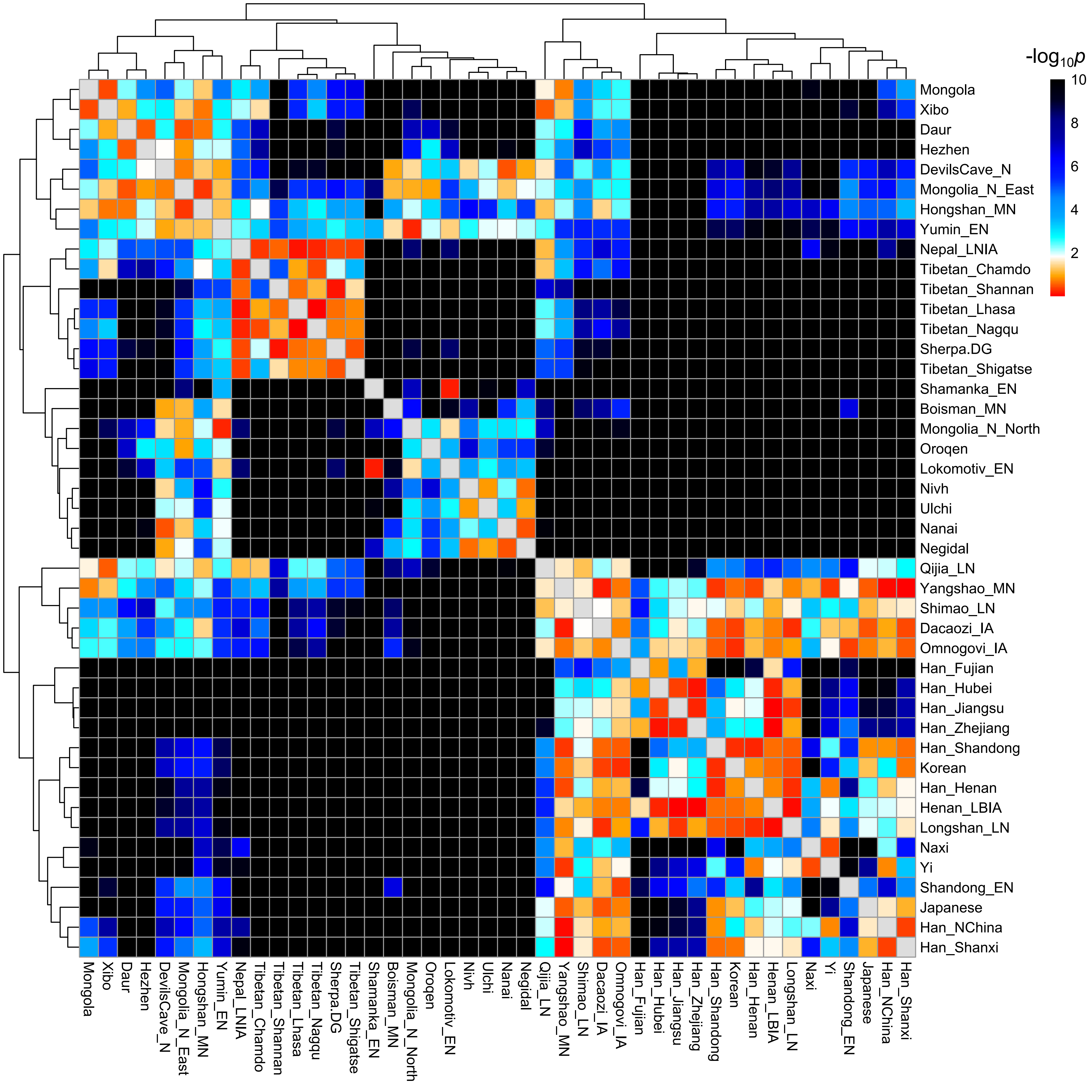
44.7 kya
[44.6, 44.8]
27.7 kya
[27.4, 27.9]
23.4 kya
[23.1, 23.7]
16.4 kya
[16.2, 16.9]
15.4%
[15.0, 15.7]
12.7 kya
[12.6, 12.7]
3.6%
[3.5, 3.8]
0.58 kya
European
First
Americans
Northern
East Asian
Inland Southern
East Asian
Coastal Southern
East Asian



-log10p
10
8
6
4
2
Hlai_Qiongzhong
Cong
Mang
Miao_Hunan
She
Lahu_Vietnam
HaNhi
Sila
Dusun
Murut
Mekong_N
Lao
Htin_Mal
Mlabri
Hanben_IA
Atayal
Ami
Kankanaey
Qihe_EN
Fujian_LN
Liangdao1_EN
Thailand_IA
Vietnam_BA
Dao
Gelao
Miao_Sanjiang
Mulam
Miao_Longsheng
Dong_Guizhou
Miao_Rongshui
Dong_Hunan
Miao_Ziyuan
Miao_Huanjiang
Miao_Longlin
Miao_Xilin
Hmong
PaThen
Lahu_China
LaChi
Maonan
Zhuang_Guangxi
Zhuang_Yunnan
Dai
Kinh


-log$_{10}p$
10
8
6
4
2
Mongola
Xibo
Daur
Hezhen
DevilsCave_N
Mongolia_N_East
Hongshan_MN
Yumin_EN
Nepal_LNIA
Tibetan_Chamdo
Tibetan_Shannan
Tibetan_Lhasa
Tibetan_Nagqu
Sherpa.DG
Tibetan_Shigatse
Shamanka_EN
Boisman_MN
Mongolia_N_North
Oroqen
Lokomotiv_EN
Nivh
Ulchi
Nanai
Negidal
Qijia_LN
Yangshao_MN
Shimao_LN
Dacaozi_IA
Omnogovi_IA
Han_Fujian
Han_Hubei
Han_Jiangsu
Han_Zhejiang
Han_Shandong
Korean
Han_Henan
Henan_LBIA
Longshan_LN
Naxi
Yi
Shandong_EN
Japanese
Han_NChina
Han_Shanxi

Mongolia Neolithic
Amur Neolithic
West Liao River
First Americas
Shandong Neolithic
Sino-Tibetan
Yellow River
Coastal Ghost
Jomon Forager
Tibetan Forager
Yangtze River
Austro-asiatic
Hmong-Mien
Austro-nesian
LGM coastline (schematic)
Kra-Dai
Hoabinhian Forager

West Liao River
Tibeto-Burman
Sinitic
Shandong Neolithic
Yellow River
1 Sinitic Cline
> ~4,000 BP
Hmong-Mien
Yangtze River
2 Hmong-Mien Cline
~ 2,000 - 1,000 BP
3 West MSEA Cline
> ~2,000 BP
Kra-Dai
Austro-nesian
4 East MSEA Cline
> ~2,000 BP
Austro-asiatic