The climatic constrains of the historical global spread of mungbean

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Abstract

While the domestication process has been investigated in many crops, the detailed route of cultivar range expansion and factors governing this process received relatively little attention. Here using mungbean (*Vigna radiata* var. *radiata*) as a test case, we investigated the genomes of more than one thousand accessions to illustrate climatic adaptation's role in dictating the unique cultivar spread routes in the face of continual human intervention. Despite the geographical proximity between South and Central Asia, mungbean cultivars first spread from South Asia to Southeast, East, and finally reached Central Asia. Combining evidence from demographic inference, climatic niche modeling, plant morphology, and records from ancient Chinese sources, we showed that the specific spread route was shaped by the unique combinations of climatic constraints and farmer practices across Asia, which imposed divergent selection favoring higher yield in the south but short-season and more drought-tolerant varieties in the north. Our results suggest that mungbean did not radiate from the domestication center as expected purely under human activity, but instead the spread route is highly constrained by climatic adaptation, echoing the idea that human commensals are more difficult to spread through the south-north axis of continents.

Main Text

Introduction

Crop domestication is a process where humans impose strong selection altering organisms for the suitability of cultivation or consumption. Examples include the loss of grain shattering in cereals, loss of fruit bitterness in squashes and melons, and reduced toxicity in tubers and roots, among many others (Larson et al., 2014; Meyer and Purugganan, 2013). In addition to the process of domestication, how the domesticated forms later expanded to a broader geographical area have also been detailed in several species, including maize (Matsuoka et al., 2002), rice (Huang et al., 2012), tomato (Razifard et al., 2020), chickpea (Varshney et al., 2021), and lettuce (Wei et al., 2021). However, it remains unclear whether these cultivars simply radiated from their center of domestication following human activities or whether the expansions have specific routes governed by other factors despite human influence. It is also unclear whether the expansion of most crops strictly follows the longitudinal axis of the continents (Diamond, 2005) or whether or why some are able to cross different climatic zones. Using the legume crop mungbean as a test case, here we illustrate how climatic adaptation results in the unique spread route and investigate the phenotypic modifications making such spread possible.

Mungbean (*Vigna radiata* (L.) Wilczek var. *radiata*), also known as green gram, is an important grain legume in Asia (Nair and Schreinemachers, 2020), providing carbohydrates, protein, folate, and iron for local diets and thereby contributing to food security (Kim et al., 2015). Among pulses, mungbean is capable of tolerating moderate drought or heat stress and has a significant role in rainfed agriculture across arid and semi-arid areas (Pratap et al., 2019), which are likely to have increased vulnerabilities to climate change. Although there have been studies about the genetic diversity of cultivated and wild mungbean (Ha et al., 2021; Kang et al., 2014; Noble et al., 2018; Sangiri et al., 2007), the evolutionary history of cultivated mungbean after domestication remains unclear. Archeological studies suggest that the domestication of mungbean occurred in India, and the increase in seed size began around 1,500 BCE to 1,000 BCE (Fuller, 2007, 2011; Fuller and Harvey, 2006). Using seed proteins (Tomooka et al., 1992) and isozymes (Dela Vina and Tomooka, 1994), previous studies proposed two expansion routes out of India, one in the south to Southeast Asia, and the other in the north along the silk road to China. While later studies used DNA markers to investigate mungbean population structure (Breria et al., 2020; Gwag et al., 2010; Islam and Blair, 2018; Noble et al., 2018; Sandhu and Singh, 2021; Sangiri et al., 2007), few have examined these hypothesized routes in detail. Therefore, despite evidence suggesting South Asia as the domestication origin, the existence of specific spread routes and the factors shaping specific routes remain unclear.

In this study, we compiled an international effort, reporting a global mungbean diversity panel of more than 1,100 accessions derived from (i) the mungbean mini-core collection of the World Vegetable Centre (WorldVeg) genebank, (ii) the Australian Diversity Panel (ADP), and (iii) the Vavilov Institute (VIR), which hosts a one-century-old collection enriched with mid-latitude Asian accessions that are underrepresented in other genebanks, some of which were old landraces collected by Nikolai I. Vavilov and his teams in the early 20th century (Burlyaeva et al., 2019). These germplasms harbor a wide range of morphological variations (Figure 1A) and constitute the most comprehensive representation of worldwide mungbean genetic variation. We used this resource to investigate the global history of mungbean after domestication to reveal a spread route highly affected by climatic constraints across Asia, eventually shaping the phenotypic characteristics for local adaptation to distinct environments.

Results

Population structure and spread of mungbean

Using DArTseq, we successfully obtained new genotype data of 290 mungbean accessions from VIR (Supplementary file 1). Together with previous data (Breria et al., 2020; Noble et al., 2018), our final set included 1,108 samples with 16 wild and 1,092 cultivars. A total of 40,897 single nucleotide polymorphisms (SNPs) were obtained. Of these, 34,469 bi-allelic SNPs, with a missing rate less than 10%, were mapped on 11 chromosomes and retained for subsequent analyses. After further linkage disequilibrium (LD) filtering ($r^2 < 0.5$), 10,831 LD-pruned SNPs were obtained.

Principal component analysis (PCA, Figure 1C) showed a triangular pattern of genetic variation among mungbean cultivars, consistent with previous studies (Breria et al., 2020; Noble et al., 2018; Sokolkova et al., 2020) and ADMIXTURE K = 3 (Figure 1B). The geographic distribution of these genetic groups is not random, as these three groups are distributed in South Asia (India and Pakistan), Southeast Asia (Cambodia, Indonesia, Philippines, Thailand, Vietnam and Taiwan), and more northernly parts of Asia (China, Korea, Japan, Russia, and Central Asia). As K increased, the cross-validation (CV) error decreased little after K = 4 (Figure 1-figure supplement 1), where the north group could be further divided (Figure 1B). Therefore, worldwide mungbean landraces could be separated into four major genetic groups corresponding to their geography: South Asian (SA), Southeast Asian (SEA), East Asian (EA), and Central Asian (CA) groups. Interestingly, the proportion of accessions from these genetic groups is highly different among genebank collections (Figure 1D). While most un-admixed accessions from Vavilov Institute (VIR) were collected from EA and CA, the Australian Diversity Panel (ADP) was enriched for the SEA group, and the World Vegetable Center (WorldVeg) contains many SA accessions. This likely reflects the different collection efforts among genebanks and demonstrates the importance of collaboration among worldwide genebanks. Therefore, unlike any other previous work in this species, this study incorporates global genetic variation among landraces of this important crop.

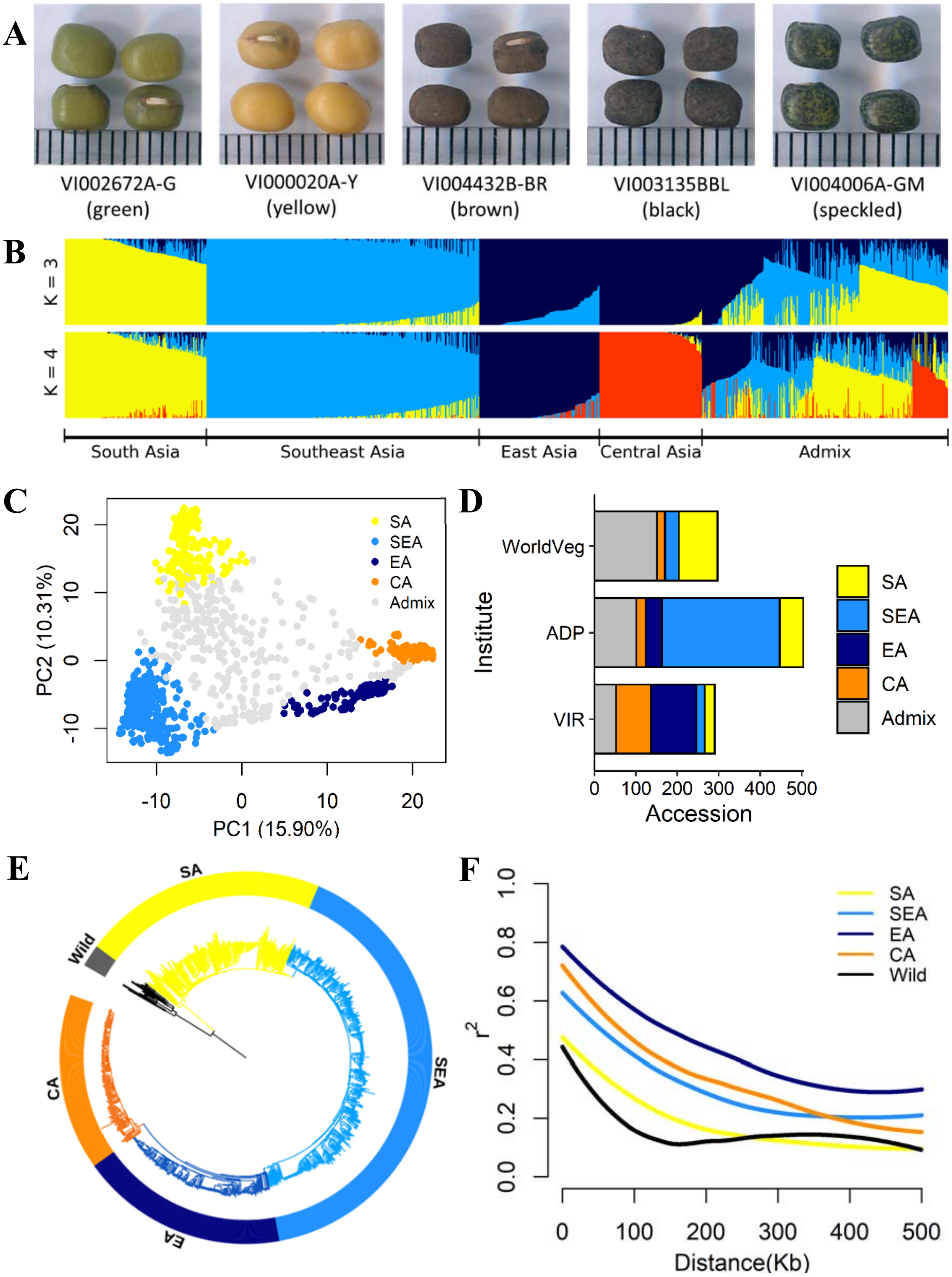

Figure 1. Diversity of mungbean in worldwide stock centers. (A) Variation in seed colour. (B) ADMIXTURE ancestry coefficients, where accessions were grouped by group assignments ($Q \geq 0.7$). (C) Principal component analysis (PCA) plot of 1,092 cultivar accessions. Accessions were coloured based on their assignment to four inferred genetic groups ($Q \geq 0.7$) while accessions with $Q < 0.7$ were coloured gray. (D) Proportion of the four inferred genetic groups from worldwide genebanks: Vavilov Institute (VIR), Australian Diversity Panel (ADP) and World Vegetable Center (WorldVeg). (E) Neighbor-joining (NJ) phylogenetic tree of 788 accessions with $Q \geq 0.7$ with wild mungbean as outgroup (black colour). (F) Linkage disequilibrium (LD) decay across the four inferred genetic groups.

Using wild progenitor *V. radiata* var. *sublobata* as the outgroup, the phylogenetic tree of the relatively pure (ADMIXTURE $Q \geq 0.7$) accessions reveals the order of landrace evolution after domestication: The SA group first diverged from wild *sublobata*, and SEA originated from a subset of SA. A small proportion of SEA later diverged as EA, a subset of which became CA (Figure 1E). The SA-SEA-EA-CA order of landrace spread after domestication (Figure 2A) is supported by the patterns of nucleotide diversity (π), which decreased from the center of origin SA (4.25×10^{-6}) to SEA (3.84×10^{-6}) and EA (3.06×10^{-6}), while the CA group has lowest diversity (1.95×10^{-6}) (Figure 2-figure supplement 1A). Pairwise F_{ST} among the four genetic groups is highest between either CA with either SA or SEA and lowest between EA and CA (Figure 2-figure supplement 1B), and outgroup *f*3 tests using wild *sublobata* as the outgroup suggest EA and CA to be the closest, followed by SEA and SA (Figure 2-figure supplement 1C and Supplementary file 2). LD also decays the fastest in wild *sublobata* and then the SA group (Figure 1F), followed by other cultivar groups. In summary, all analyses are consistent with our proposed order of landrace divergence.

Our proposed demographic history could be confounded by factors such as complex hybridization among groups. For example, SEA and CA might have independently originated from SA and later generated a hybrid population in EA (Figure 2-figure supplement 2A). Other possibilities are that either SEA or CA are the hybrid of other populations (Figure 2-figure supplement 2B, C). However, these scenarios do not fully fit the patterns we observed above. We further examined the admixture *f*3 statistics for all possible trios among the four groups to detect potential hybridizations. None of the tests gave significantly negative *f*3 values (Supplementary file 3), suggesting the lack of a strong alternative model to our proposed SA-SEA-EA-CA spread.

Based on the whole-genome phylogeny (Figure 1E), we used fastsimcoal2 to model the divergence time among these groups, allowing population size change and gene flow at all time points (Figure 2B). According to this model, after initial domestication, the SEA group diverged from SA at about 8.3 thousand years ago (kya) with 50% parametric bootstrap range between 6.3 and 10.2 kya. Not until more than five thousand years later (2.7 kya, 50% range 1.7-3.8 kya) did EA diverge from SEA and moved north. Within a few thousand years, EA migrated west and gave rise to CA relatively recently (0.2 kya, 50% range 0.1-0.4 kya).

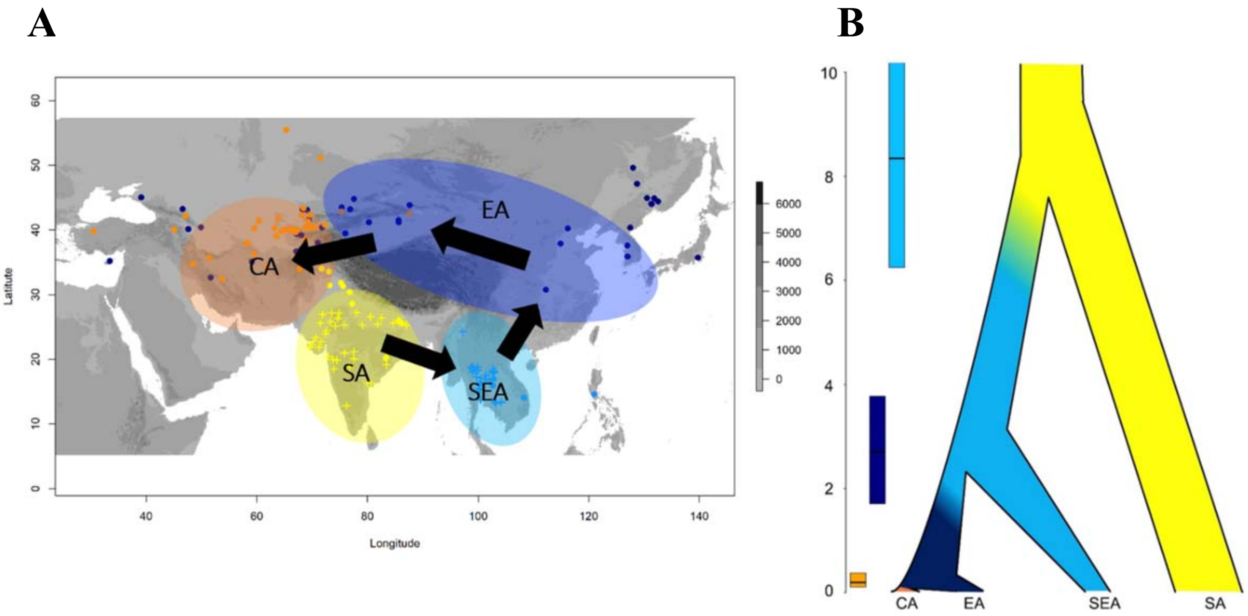

Figure 2. Demographic history of the four inferred genetic groups. (A) Proposed spread of mungbean from its centre of origin. The map was shaded as gray colour representing altitude (meters above sea level). Coloured circles on the map indicate the geographic distribution of each genetic group. Arrows indicates the possible expansion route. (B) Schematic model of the demographic scenario inferred by fastsimcoal2. Colored bars on the left label the 50% range of inferred divergence time of each group.

While populations that were established in a region for an extended time could accumulate genetic differentiation generating patterns of isolation by distance, rapid-spreading populations in newly colonized regions could not (Lee et al., 2017; The 1001 Genomes Consortium, 2016). Using this idea, Mantel's test revealed a significantly positive correlation between genetic and geographic distances for the SA genetic group (r = 0.463, P = 0.015), followed by SEA (r = 0.250, although not as significant, P = 0.066). No such association was found for EA (r = 0.032, P = 0.141) or CA (r = 0.053, P = 0.257). In addition, the southern groups (SA and SEA) together (r = 0.804, P = 0.001) have a much stronger pattern of isolation by distance than the northern groups (EA and CA, r = 0.325, P = 0.001) (Figure 2-figure supplement 3). These results are again consistent with our proposed order of SA-SEA-EA-CA spread as well as the divergence time estimates (Figure 2): While the southern groups (SA and SEA) existed since about 9 kya, the northern groups (EA and CA) are much younger.

Environmental differentiation of the inferred genetic groups

We further examined the possible causes governing the specific spread route of mungbean cultivars. Being a crop that has lost the ability of pod shattering, the spread of mungbean was governed by commerce or seed exchange, which is prevalent between South and Central Asia throughout history (see Discussion). Given that geographic barrier might not be the most important factor and these cultivars do not have the stepwise and distance-dependent dispersal patterns as in wild plants, instead of standard models of isolation by distance or resistance, we investigated whether climatic adaptation, that is, the inability of mungbean to establish in a geographic region after human-mediated long-range expansion, could be the cause.

Multivariate analysis of variance (MANOVA) of eight bioclimatic variables (after removing highly-correlated ones; Supplementary file 4) indicated strong differentiation in the environmental niche space of the four genetic groups (Supplementary file 5 and 6). PCA of climatic factors clearly reflects geographic structure, where the axis explaining most variation (PC1, 42%) separates north and south groups and is associated with both temperature- and precipitation-related factors (Figure 3A and Supplementary file 7). Consistent with their geographic distribution, overlaps between EA and CA and between SA and SEA was observed. Given the wide longitudinal distribution of EA, in some later analyses we separated EA into the eastern (northeast NE) and western (northwest NW) groups. Environmental niche modeling revealed distinct suitable regions of these five groups except for CA and NW, whose geographical ranges largely overlap (Figure 3B). Consistent with PCA, pairwise Schoener's D values are smallest between the northern and southern groups while largest between the eastern and western subsets within north and south (Figure 3B). Projecting their current niches to paleoclimates at the mid-Holocene (about 6 kya) when Central Asia was likely wetter (Chen et al., 2008; Zhang et al., 2016), we found similar results that the SA group could not inhabit Central Asia (Figure 3-figure supplement 1). This suggests the SA-SEA-EA-CA spread of mungbean after domestication is contingent on environmental similarity.

While both temperature and precipitation variables differ strongly between north and south, one should note that these year-round temperature variables do not correctly reflect conditions in the growing seasons. In the north, mungbean are mostly grown in summer where the temperature is close to the south (Figure 3-figure supplement 2A-C). On the other hand, precipitation differs drastically between north and south, especially for the CA group, where the summer growing season is the driest of the year (Figure 3-figure supplement 2D). By estimating the regression slope of precipitation on geographical distance, we obtained a gradient of precipitation change per unit geographic distance between pairs of genetic groups (Figure 3C). Despite the SA-SEA transect having the steepest gradient (slope = 0.21), the spread from SA to SEA has been accompanied by an increase of precipitation and did not impose drought stress. The second highest slope (0.18), however, is associated with strong precipitation decrease if the SA group were to disperse to Central Asia. This likely explains why no direct historic spread is observed from SA to CA. Finally, our SA-SEA-EA-CA spread model posits that EA first diverged from SEA and occupied northeastern Asia followed by a westward expansion. Consistent with this model, the genetic variation of the EA group gradually declines from east to west (Figure 3D), accompanied by the gentlest decline of precipitation per unit geographic distance across Asia (Figure 3D).

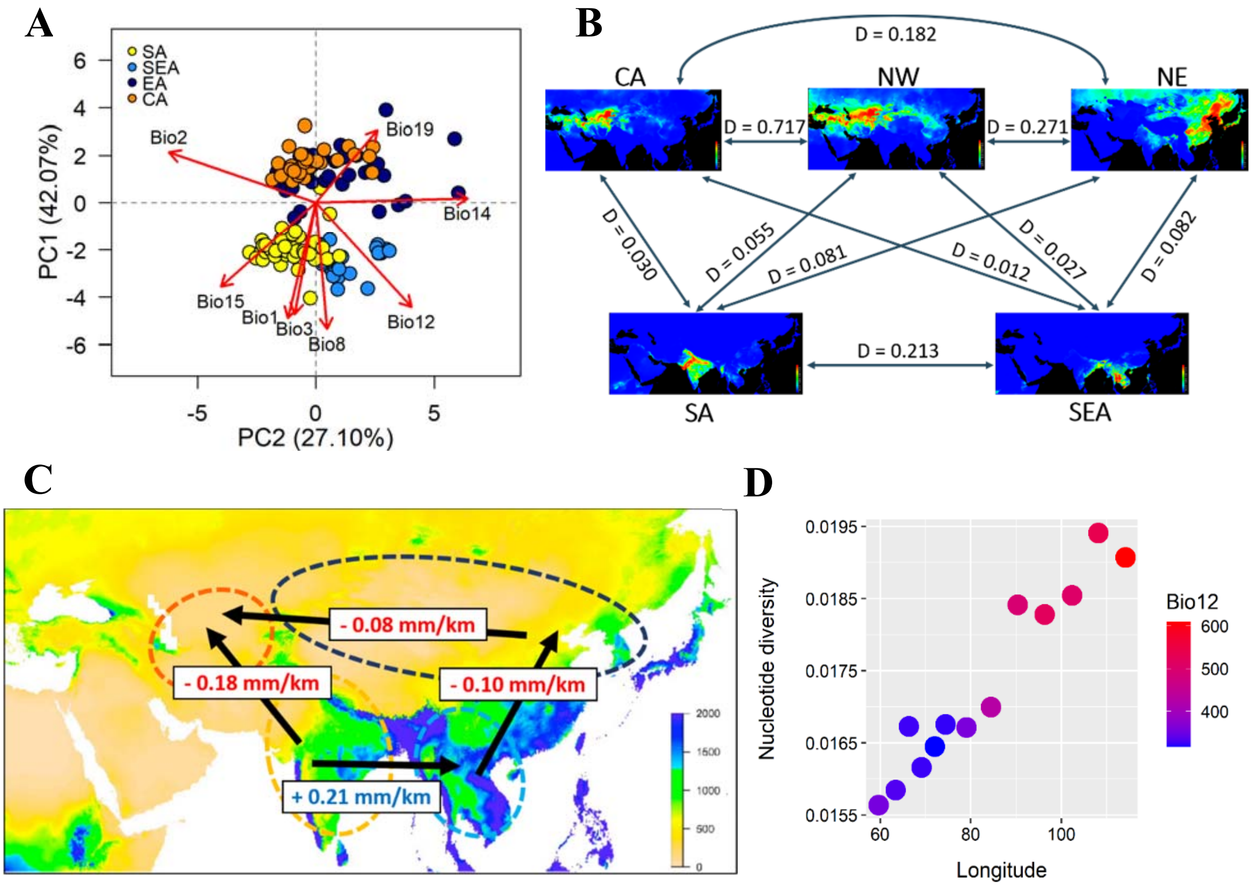

Figure 3. Environmental variation among genetic groups of mungbean. (A) Principal component analysis (PCA) of the eight bioclimatic variables. (B) Predicted distribution at current climate. Red colour indicates high suitability and blue indicates low suitability. Values between pairs represent niche overlap measured using Schoener's D. (C) Environmental gradient across potential directions of expansion. The value on each arrow indicates change of annual precipitation per kilometer. Background map is colored according to annual precipitation (Bio12, in mm). (D) Relationship between Bio12 and nucleotide diversity (π) of East Asia genetic group across the east-west axis of Asia. Dot colors represent annual precipitation of each population.

Trait variation among genetic groups

If environmental differences, especially water availability, constrain the spread route of mungbean, the current landraces occupying distinct environments should have locally adaptive traits for these environments. Indeed, PCA of four trait categories show substantial differences among genetic groups (phenology, reproductive output, and size in field trials as well as plant weight in lab hydroponic systems, Figure 4A). In the field, CA appears to have the shortest time to flowering, lowest yield in terms of seed size and pod number, and smallest leaf size (Figure 4B and Supplementary file 8). On the other hand, SEA landraces maximize seed size, while SA landraces specialize in developing the largest number of pods (Figure 4B). These results suggest that CA has a shorter crop duration, smaller plant size, and less yield, consistent with drought escape phenotypes.

In terms of seedling response to drought stress, the Q_{ST} values of most traits (root, shoot, and whole plant dry weights under control and drought treatments) are higher than the tails of SNP F_{ST}, suggesting trait evolution driven by divergent selection (Figure 4C). Significant treatment, genetic group, and treatment by group interaction effects were observed except in a few occasions (Table 1). Consistent with field observation, SEA has largest seedling dry weight (Figure 4D). While simulated drought significantly reduced shoot dry weight for all groups, the effect on SEA is especially pronounced (treatment-by-group interaction effect, $F_{2,575}$=23.55 $P <$ 0.001, Table 1 and Figure 4D), consistent with its native habitats with abundant water supply (Figure 3-figure supplement 2D and Supplementary file 9). All groups react to drought in the same way by increasing root:shoot ratio (Figure 4D), suggesting such plastic change may be a strategy to reduce transpiration. Despite the lack of treatment-by-group interaction ($F_{2,575} = 1.39$, $P > 0.05$), CA consistently exhibits significantly higher root:shoot ratio, a phenotype that is potentially adaptive to its native environment of lower water supply (Figure 3-figure supplement 2D and Supplementary file 9).

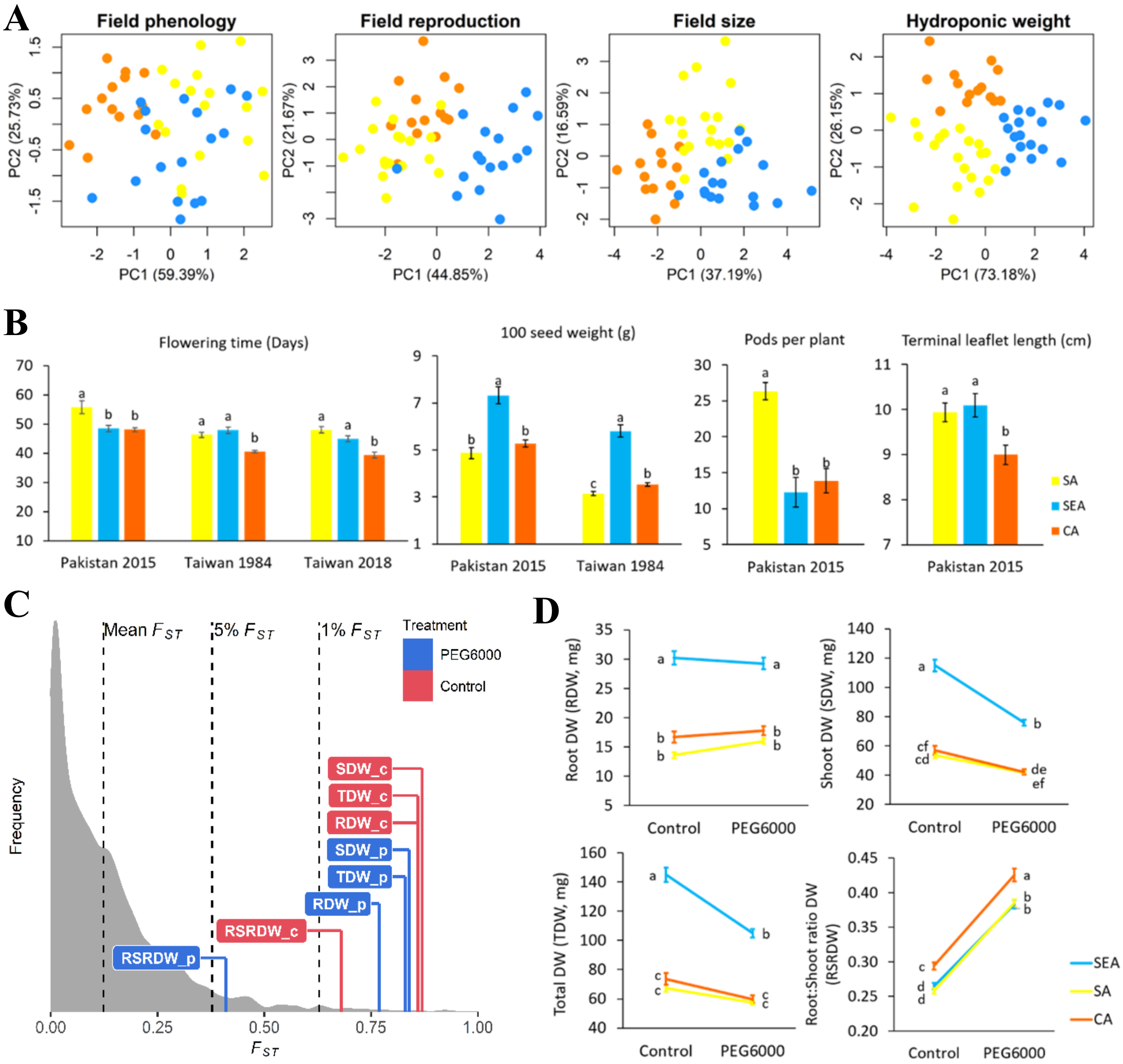

Figure 4. Quantitative trait differentiation among genetic groups. (A) Principal component analysis (PCA) of four trait categories. (B) Trait variability from common gardens in field experiments. (C) Comparison of Q_{ST}-F_{ST} for four drought-related traits under two environments. F_{ST} values (mean, 5% and 1%) were indicated by black dashed lines. The Q_{ST} for each trait was colored according to treatment. Abbreviations: RDW: root dry weight; SDW: shoot dry weight; TDW: total dry weight; RSRDW: root:shoot ratio dry weight; c: control; p: PEG6000. (D) Effect of PEG6000 (-0.6 MPa) on root dry weight (RDW), shoot dry weight (SDW), total dry weight (TDW) and root:shoot ratio dry weight (RSRDW) among genetic groups. Data were expressed as the mean ± standard error. In (B) and (D), lower-case letters denote significant difference under Tukey's HSD.

Table 1. Analysis of variance (ANOVA) *F* values for the dry weight (mg) of mungbean seedlings across three different genetic groups

Source of variation	df	RDW	SDW	TDW	RSRDW
Treatment	1	$2.65^{n.s.}$	133.26***	72.26***	978.76***
Genetic group	2	60.63***	79.62***	76.54***	13.27***
Treatment x Genetic group	2	3.29*	23.55***	17.79***	$1.39^{n.s.}$

(df: degrees of freedom; RDW: root dry weight; SDW: shoot dry weight; TDW: total dry weight; RSRDW: root:shoot ratio dry weight. Significance level * $P < 0.05$, *** $P < 0.001$, n.s. non-significant)

Support from ancient Chinese sources

Mungbean has been occasionally mentioned in ancient Chinese sources. Here we report the records associated with our proposed mungbean spread route and the underlying mechanisms. The “Classic of Poetry” (Shijing 詩經) contains poems dating between the 11th to 7th centuries BCE near the lower and middle reaches of the Yellow River. While crops (especially soy bean, 菽), vegetables, and many other plants have been mentioned, mungbean was not recorded. This is consistent with our results that mungbean had not reached the northern parts of East Asia at that time (the EA group diverged from the SEA group at around 2.6 kya), although we recognize the absence of evidence does not equal the evidence of absence. The first written record of mungbean in China is in an agricultural encyclopedia Qimin Yaoshu (齊民要術, 544 AD, Chinese text and translation in Supplementary note), whose spatiotemporal background (~1.5 kya near the lower reaches of Yellow River) is again consistent with our estimated origin of the EA group.

Regarding the phenotypic characteristics, Xiangshan Yelu (湘山野錄, 1068-1077 AD) records that mungbean from South Asia (likely also includes the Southeast Asian genetic groups if accessions near eastern Indian and Bangladesh were included) at that time had higher yield and larger grains than native cultivars in northern China (Chinese text and translation in Supplementary note). This is consistent with our results that northern accessions have lower yield as a consequence of their rapid life cycle.

Regarding the rapid life cycle of northern accessions, Tiangong Kaiwu (天工開物, 1637 AD) mentioned mungbean must be sown during July and August (Chinese text and translation in Supplementary note). This is consistent with the short-day requirement for this crop to flower: Being sown earlier, “mungbean stems would spread for meters with few pods set”, because long days inhibit flowering. Being sown later, “the plants would flower and set pods at any time, also with low yield”, as short days facilitate flowering. The record suggests that daylength requirement restricts the sowing period of mungbean in the north. Together with the dry summer (Figure 3-figure supplement 2D) and soon-arriving autumn frost, there might be strong selection favoring accessions with rapid life cycle. Therefore, the unique distribution of climatic zones in Asia resulted in not only the specific spread route but also the evolution of novel phenotypic characteristics in mungbean.

Discussion

Using mungbean as a test case, we combined population genomics, environmental niche modeling, empirical field and laboratory investigation, and ancient Chinese text analyses to demonstrate the importance of climatic adaptation in dictating the unique spread route of crops even after domestication.

The climate-driven spread route of mungbean cultivars

Combining divergence time estimates (Figure 2B) and niche modeling (Figure 3), our results suggest that after mungbean was domesticated in South Asia, the large environmental difference, mostly likely precipitation, strongly restricted its northwards spread to Central Asia. Supported by archaeobotanical remains from the Thai-Malay Peninsula date to ca. 400-100 BCE (Castillo, 2019; Castillo et al., 2016), mungbean first spread to Southeast Asia where the environment is more benign during the Holocene Climate Optimum, but it took about six thousand years until mungbean further spread to northeast Asia due to the environmental difference, consistent with historical records from China. In rice, the climate cooling that started at about 4.2 kya is associated with the divergence of the temperate *japonica* from tropical *japonica* (Gutaker et al., 2020). The 50% confidence range of our SEA-EA divergence (1.7-3.8 kya) happened after that, and we noticed this is the period when cooling was slightly attenuated (Marcott et al., 2013), suggesting climate change might also be associated with the northward expansion of mungbean. After that, the EA group spread across the northern part of Asia within a few thousand years. Our proposed route suggests mungbean reached Central Asia at the latest, consistent with its absence from archeological sites in Central Asia (Kazakhstan, Uzbekistan, and Turkmenistan) during the Bronze and Iron Ages (Miller, 1999; Spengler et al., 2017) and the medieval period (800-1100 AD) (Spengler et al., 2018). Consistently, the history of Central Asia suggests mungbean likely appeared in this region from the late 18th to the early 19th century (Annanepesov and Bababekov, 2003).

The effect of human activities and distinct regional usages of mungbean

In this study, we suggest that geographic barriers (such as the Hindu Kush mountains) may not be an essential factor restricting mungbean spread from SA to CA. Mungbean cultivars have lost the natural ability of pod shattering to disperse seeds, and they mostly traveled through landscapes by human-mediated seed exchange or commerce. As early as about 4 kya, the Bactria–Margiana Archaeological Complex (BMAC) civilization north of the Hindu Kush had extensive contact with the Indus Valley. Despite this, temperate crops were mostly found in archeological sites there (Jeong et al., 2019). The travels between Central and South Asia had also been made by the Aryans, Alexander the Great, and later frequently through the silk road, and empires such as Kushan and Mughal had their territories covering both sides of Hindu Kush, suggesting it was not a barrier for human. In the Chinese language, crop names starting with the character 胡 (Hu, meaning northwestern tribes) refer to those introduced from Central Asia. While mungbean (綠豆, meaning green bean) does not bear such a name, several presumably India-originated crops do, such as pepper (胡椒), cucumber (胡瓜), and sesame (胡麻), suggesting it is still possible for India-originated crops to spread to East Asia through Central Asia.

Despite the profound impact of human-mediated dispersal on the spread of these and many other crops (Herniter et al., 2020; Kistler et al., 2018), in mungbean we suggest adaptation to distinct climatic regimes to be an important factor in the establishment after dispersal. Compared with other crops, mungbean might not be a highly valued crop under extensive care during cultivation. Indeed, the earliest record of mungbean in China (Qimin Yaoshu 齊民要術, 544 AD) emphasizes its use as green manure. In Central Asia, mungbean is a minor crop (Rani et al., 2018) grown with little input, only in the short duration between successive planting of main crops and using residual soil moisture with little irrigation. We suggest that the lack of extensive input subjects mungbean to more substantial local climatic challenges than highly valued high-input crops that receive intensive management, including irrigation. Therefore, the combination of climatic constraints and cultural usage, instead of physical barriers, may have shaped the historical spread route of mungbean despite extensive human activities across the Hindu Kush.

In addition to the constraint of soil moisture, other factors may have contributed to the selection for short-season accessions in the north. In the short summer seasons of much of Central Asia, short crop cycling is a requirement. In Uzbekistan, mungbean is often sown in early July after the winter wheat season and harvested before mid-October to avoid delays in the next round of winter wheat and escape frost damage. Therefore, fast-maturing accessions are essential for this production system (Rani et al., 2018). Similar rotation systems using mungbean to restore soil fertility during the short summer season after the harvest of the main crop were also mentioned in ancient Chinese sources (Chen, 1980). Mungbean is a short-day species from the south, and day length likely limits the window when mungbean could be grown in the north: Chinese texts during the 17th century (Tiangong Kaiwu 天工開物, 1637 AD) specifically mentioned the suitable duration to sow mungbean to control the flowering behavior for maximum yield (Supplementary note). Therefore, unlike in the south where yield appears to be an important selection target, the unique combination of day length, agricultural practices, soil water availability, and frost damage in the north requires the selection for short-season accessions, likely limiting the direct adoption of southern cultivars in the north.

Conclusion

Our study demonstrates that mungbean's range expansion after domestication is associated with climatic conditions, which shaped the genetic diversity and contributed to adaptive differentiation among genetic groups. The climatic differences likely also resulted in farmers' differential emphasis on using it mainly as a grain or green manure crop, further intensifying the phenotypic diversification among regional cultivars. Therefore, this collection and the investigation of global landraces adapted to diverse environments is an invaluable genetic resource for the genetic improvement of mungbean. Our results further echo the notion in popular science (Diamond, 2005) and previous research (Lee et al., 2017) that human commensals are more prone to east-west longitudinal spread rather than north-south latitudinal expansion due to environmental constraints.

Materials and Methods

Plant materials and SNP genotyping

A total of 290 cultivated mungbean (*V. radiata* var. *radiata*) accessions were provided by the Vavilov Institute (VIR). Most of the landraces collected during 1910-1960 are considered the oldest mungbean collection from VIR (Burlyaeva et al., 2019). The complete list of material can be found in Supplementary file 1. Genomic DNA was extracted from a single plant per accession using QIAGEN Plant Mini DNA kit according to the manufacturer's instruction with minor modification. DNA samples were sent to Diversity Arrays Technology Pty Ltd, Canberra, Australia for diversity array technology sequence (DArTseq) genotyping.

DArTseq data of 521 accessions from the Australian Diversity Panel (ADP) (Noble et al., 2018) and 297 accessions from the World Vegetable Center (WorldVeg) mini-core (Breria et al., 2020) were also included in this study. In total, our dataset contains more than one thousand accessions (1092) and covers worldwide diversity of mungbean representing a wide range of variation in seed colour (Figure 1A). Sixteen wild mungbean (*V. radiata* var. *sublobata*) accessions were included as an outgroup.

The major goal of this study is to investigate the patterns of population expansion and the underlying ecological causes instead of detailed haplotype analyses of specific genomic regions. For this goal, genomewide SNPs provide similar information as whole-genome sequencing, as have been shown in other species. Compared to other genotyping-by-sequencing technologies, DArTseq has the additional advantage of less missing data among loci or individuals, providing more robust estimation of population structure.

SNP calling

Trimmomatic version 0.38 (Bolger et al., 2014) was used to remove adapters based on the manufacturer's adapter sequences. Reads for each accession were trimmed for low-quality bases with quality scores of Q ≤ 10 using SolexaQA version 3.1.7.1 (Cox et al., 2010) and mapped to the mungbean reference genome (Vradiata_ver6, Kang et al., 2014) using the Burrows-Wheeler Aligner (BWA) version 0.7.15 (Li and Durbin, 2009). Reads were then sorted and indexed using samtools version 1.4.1 (Li et al., 2009). SNPs were called using Genome Analysis Toolkit (GATK) version 3.7-0-gcfedb67 (McKenna et al., 2010). SNPs with more than two alleles and 10% missing data were removed using VCFtools version 0.1.13 (Danecek et al., 2011). To reduce SNP redundancy caused by linkage disequilibrium (LD), SNPs were pruned based on a 50-SNP window with a step of 5 SNPs and r^2 threshold of 0.5 in PLINK (Purcell et al., 2007).

Population genetics and differentiation analyses

Population structure was investigated using ADMIXTURE (Alexander et al., 2009) with the number of clusters (K) ranging from 1 to 10. The analyses were run ten times for each K value, and cross-validation (CV) error was used to obtain the most probable K value for population structure analysis. ADMIXTURE plots were generated using "Pophelper" in R (Francis, 2017).

Genetic groups of accessions were assigned based on ancestry coefficient Q ≥ 0.7, otherwise the accession was considered admixed. The population structure was also examined with principal component analysis (PCA). The neighbor-joining phylogenetic tree was calculated using TASSEL (Trait Analysis by aSSociation, Evolution and Linkage) software version 5.2.60 (Bradbury et al., 2007) and visualized using FigTree version 1.4.4 (http://tree.bio.ed.ac.uk/software/figtree/). For each genetic group, nucleotide diversity (π) was estimated with 300 kb sliding windows and a step size of 10 kb using VCFtools version 0.1.13 (Danecek et al., 2011) and genetic differentiation (F_{ST}) between groups was calculated accordingly. The calculation was based on SNP markers with minor allele frequency, MAF ≥ 0.05. LD decay for each genetic group was estimated using PopLDdecay (Zhang et al., 2019). The curves were fitted by a LOESS function and an LD decay plot was drawn using R.

To examine the role of geographic distance in shaping spatial genetic differentiation, Mantel tests with 1,000 permutations were performed separately for the four genetic groups using "ade4" in R. Pairwise genetic distance between accessions was estimated using "StAMPP" in R while the great circle geographic distance was determined using "fields" in R.

*f*3 statistics was computed using ADMIXTOOLS version 7.0 (Patterson et al., 2012), as implemented in the "admixtools" in R. The statistic compares allele frequencies in two potential source populations (A, B) and a target population C. A negative value of *f*3 indicates that the C is admixed of A and B. The Z-score < -3 was considered to be statistically significant. The estimated *f*3 statistics was further used to construct the topology of an admixture graph.

Based on the shape of the phylogenetic tree, we used fastsimcoal2 (Excofffier et al., 2021; Excoffier and Foll, 2011), which does not rely on whole-genome sequencing, to estimate the split time among genetic groups. Fifty accessions were randomly picked from each genetic group. Population size was allowed to change, and gene flow was allowed among populations. This analysis used all sites (67K sites) covered by the DArT tags (including monomorphic sites), and the mutation rate was set to $1\text{x}10^{-8}$, assuming one generation per year. The model was run independently 100 times, each with 100,000 simulations. After obtaining the run with the highest likelihood, we performed parametric bootstrapping 100 times to obtain the confidence interval of each parameter as described in the fastsimcoal2 manual.

Ecological niche modelling (ENM)

Climate data for conditions between 1960-1990 were downloaded from the WORLDCLIM 1.4 database (Hijmans et al., 2005), which included monthly minimum, maximum, mean temperature, precipitation, and 19 bioclimatic variables. All climatic variables of accession collection sites were extracted. To reduce redundancy and minimize high correlations, pairwise Pearson correlations between the 19 bioclimatic variables were calculated using ENMTools version 1.4.4 (Warren et al., 2010), excluding one of the two variables that has a correlation above 0.8 (Supplementary file 4). As a result, eight bioclimatic variables were used for all further analyses including Bio1 (annual mean temperature), Bio2 (mean diurnal range), Bio3 (isotermality), Bio8 (mean temperature of wettest quarter), Bio12 (annual precipitation), Bio14 (precipitation of driest month), Bio15 (precipitation seasonality) and Bio16 (precipitation of coldest month). PCA and multivariate analysis of variance (MANOVA) were conducted to examine whether there was significant habitat difference among genetic groups. Ecological niche modelling (ENM) was performed using MAXENT version 3.3.1 (Phillips et al., 2006) to predict the geographic distribution of suitable habitats for cultivated mungbean.

To understand whether the habitats of genetic groups are differentiated, 248 sampling sites (82 for East Asia, 45 for Southeast Asia, 49 for South Asia and 72 for Central Asia genetic groups), in combination with additional presence records obtained from the Global Biodiversity Information Facility (GBIF, https://www.gbif.org/), were used for the analysis. The ENM analysis was run with random seed, a convergence threshold of 5,000 and 10-fold cross-validation. As a measure of the habitat overlaps of the four genetic groups, pairwise of Schoener's D was calculated using ENMTools. The value ranges from 0 (no niche overlap) to 1 (niche complete overlap).

Drought phenotyping

A total of 52 accessions with ancestry coefficients $Q \geq 0.7$ from three genetic groups (Southeast Asia, South Asia and Central Asia) were selected for experiments of seedling-stage drought response. The experiment was laid out in a completely randomized design with three replicates of each accession under two treatments (control/drought). The experiment was conducted in two independent batches, and the whole experiment included 624 plants (52 accessions x 2 treatments x 3 plants per treatment x 2 batches).

Mungbean seeds were surface-sterilized with 10% bleach for 10 mins and rinsed with distilled water for three times. Seeds were further treated with 70% ethanol for 5 mins and washed three times in distilled water. Sterilized seeds were placed on wet filter paper in petri dishes for germination. The experiment was conducted in a 740FLED-2D plant growth chamber (HiPoint, Taiwan) at temperature of 25 ± 1^{o}C and 12 hours of photoperiod (light ratios of red: green: blue 3: 1: 1) with light intensity 350 μmol $m^{-2}s^{-1}$ and relative humidity at 60 ± 5%. After three days of germination, the seedling was transplanted to a hydroponic system with half-strength Hoagland nutrient solution (Phytotechnologies Laboratories, USA). The nutrient solution was changed on alternate days and the pH of the solution was adjusted to 6.0 with 1M KOH or 1M HCl.

Plants were grown in the nutrient solution for six days and exposed to treatments of drought or control (in the same nutrient solution). The drought stress simulated osmotic potential (-0.6 MPa) by adding PEG6000 (polyethylene glycol, Sigma-Aldrich, Germany) to the nutrient solution according to Michel and Kaufmann (1973).

After five days of PEG6000 treatment, samples were evaluated for shoot dry weight (SDW) and root dry weight (RDW), measured on digital balance after oven-drying at 70^{o}C for 48 hours. All traits were analysed by mixed-model analysis of variance (ANOVA) with the treatment (control/drought) and genetic group as fixed effects. The models included accessions as a random effect nested within genetic groups and a random effect of batches. Tukey’s test was conducted to compare genetic groups. All statistics were performed using JMP v3.0.0 (SAS Institute, 2016).

Q_{ST}-F_{ST} comparisons

For each trait, quantitative trait divergence (Q_{ST}) was calculated separately with respect to each treatment. Variance components were estimated using a model with genetic groups, accessions nested within genetic groups and batches as random factors. Since mungbean is a predominantly self-pollinated species, Q_{ST} was calculated based on Neji et al. (2015) as $\sigma^2_p / (\sigma^2_p + \sigma^2_w)$, where σ^2_p and σ^2_w represent the variance among and within genetic groups, respectively. The F_{ST} was calculated only using accessions in the phenotyping experiment.

Field evaluation

Among the 52 accessions used for laboratory experiments, phenotyping of 49 accessions was conducted at WorldVeg, Taiwan in 1984 and 2018 and at Crop Sciences Institute, National Agricultural Research Centre, Pakistan in 2015. The traits related to phenology (days to 50% flowering), reproduction (100 seed weight, pod length, pods per plant, 1000 seed weight, seeds yield per plant, and seeds per pod), and plant size (petiole length, plant height, plant height at flowering, plant height at maturity, primary leaf length, primary leaf width, terminal leaflet length, and terminal leaflet width) were included. Trait values were inverse normal transformed. The ANOVA was performed to test for inferred genetic groups differences for each trait using R software (version 4.1.0).

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Data Availability

Sequences generated in this study are available under NCBI BioProject PRJN809503. Accession names, GPS coordinates, and NCBI accession numbers of the Vavilov Institute accessions are available under Supplementary file 1. Plant trait data are available at Dryad https://doi.org/10.5061/dryad.d7wm37q3h. Sequences and accession information of the World Vegetable Centre mini-core and the Australian Diversity Panel collections were obtained from Breria et al. (2020) and Noble et al. (2018).

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Supplementary note. Text analysis and translation of ancient Chinese texts regarding mungbean

Qimin Yaoshu (齊民要術, about 544 AD)

Qimin Yaoshu, compiled by Sixie Jia (賈思勰), is one of the earliest and most complete agricultural sources in China, detailing agricultural techniques near the lower reaches of Yellow River at that era. This is the earliest record of mungbean in China, demonstrating mungbean has reached northern China at that time and is consistent with our estimates of population divergence time. The popularity of mungbean is demonstrated by it being mentioned multiple times under different contexts, most notably as a green manure:

「若糞不可得者，五六月中，穊種菉豆，至七月、八月，犁掩殺之。如以糞糞田，則良美與糞不殊，又省功力。」

Translation: “Should feces be unavailable, during May and June one could grow mungbean. Until July or August, one could plow mungbean plants into the soil. This is equivalent to using feces to manure the land. This is as good as using feces and saves efforts.”

Notice that the months used in ancient China are slightly different from the Gregorian calendar.

Xiangshan Yelu (湘山野錄, 1068-1077 AD)

Xiangshan Yelu was written by a monk, Wen-Ying (文瑩), recording anecdotes during that era. Its records about the Emperor Zhenzong of Song (宋真宗, 968-1022 AD) detailed the phenotypes of Indian mungbean at that time:

「真宗深念稼穡，聞占城稻耐旱、西天綠豆子多而粒大，各遣使以珍貨求其種。占城得種二十石，至今在處播之。西天中印土得菉豆種二石，不知今之菉豆是否？」

Translation: “Zhenzong of Song deeply concerned about agriculture. He heard Champa rice being drought tolerant and mungbean from India produce numerous and large seeds. Diplomats were sent to exchange the seeds with treasure. Twenty dans of Champa rice were obtained and propagated everywhere. Two dans of mungbean were obtained from India, but it is unclear whether the mungbean today descended from these.”

"Dan" (石) is a unit of volume in ancient China and is called "Koku" in Japanese. The exact amount varied with time.

The texts provide us with two pieces of important information. First, mungbean from South Asia (likely also includes the Southeast Asian genetic groups if accessions near eastern India and Bangladesh were included) at that time had higher yield and larger seeds than native cultivars in northern China, consistent with our results on trait divergence. Second, compared to the clear success of Champa rice in China, it was unclear whether those southern accessions had prospered in northern China, likely suggesting an unsuccessful introduction of southern high-yield and large-seeded accessions to the north.

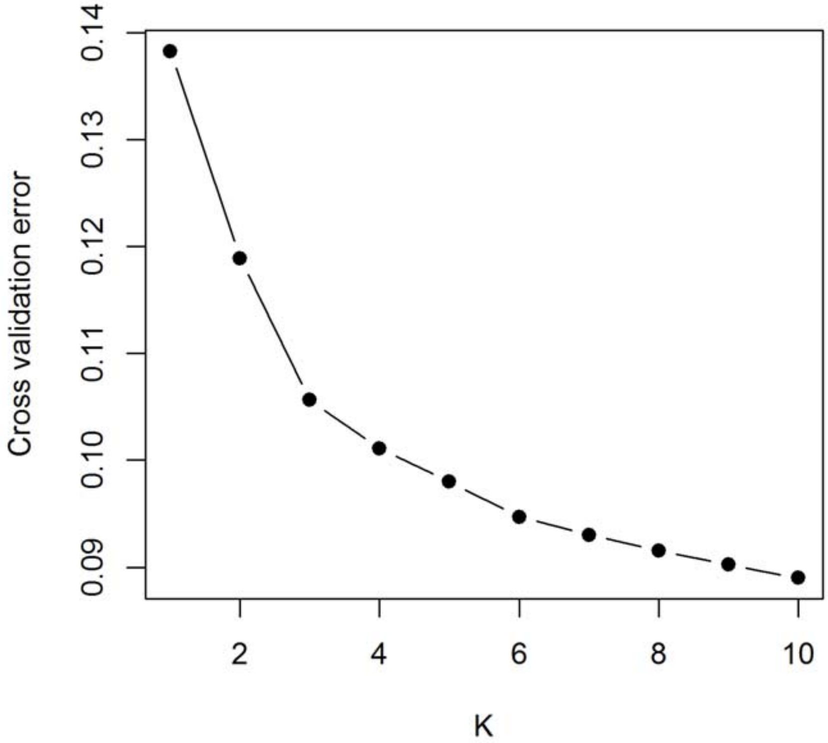
Tiangong Kaiwu (天工開物, 1637 AD)

Tiangong Kaiwu is a famous Chinese encyclopedia compiled by Song Yingxing (宋應星). While it mostly covers technologies at that time, a section about agricultural practices covers mungbean:

「綠豆必小暑方種，未及小暑而種，則其苗蔓延數尺，結莢甚稀。若過期至於處暑，則隨時開花結莢，顆粒亦少。」

Translation: "Mungbean must be sown at or after Xiaoshu (Gregorian 7-8 July). Being sown before Xiaoshu, mungbean stems would spread for meters with few pods set. Being sown as late as Chushu (Gregorian 23-24 August), the plants would flower and set pods at any time, also with low yield."

As a short-day plant, being sown too early when the days are too long, mungbean would have mostly vegetative growth. Being sown too late when the days are too short, flowering would be induced too quickly before sufficient vegetative development. In addition to our results that short-season accessions were favored in the north due to the requirement for drought escape, this source provides us with another support that mungbean could only be sown in a narrow time window due to daylength requirement. Given the autumn frost damage in the north, not being able to be sown earlier restricts the growing season length in the north, limiting the adoption of southern long-season accessions.



795 **Figure 1-figure supplement 1.** Cross-validation (CV) errors of ADMIXTURE. Means of CV errors were
796 calculated based on K values ranging 1 to 10 with 10 independent runs.

797

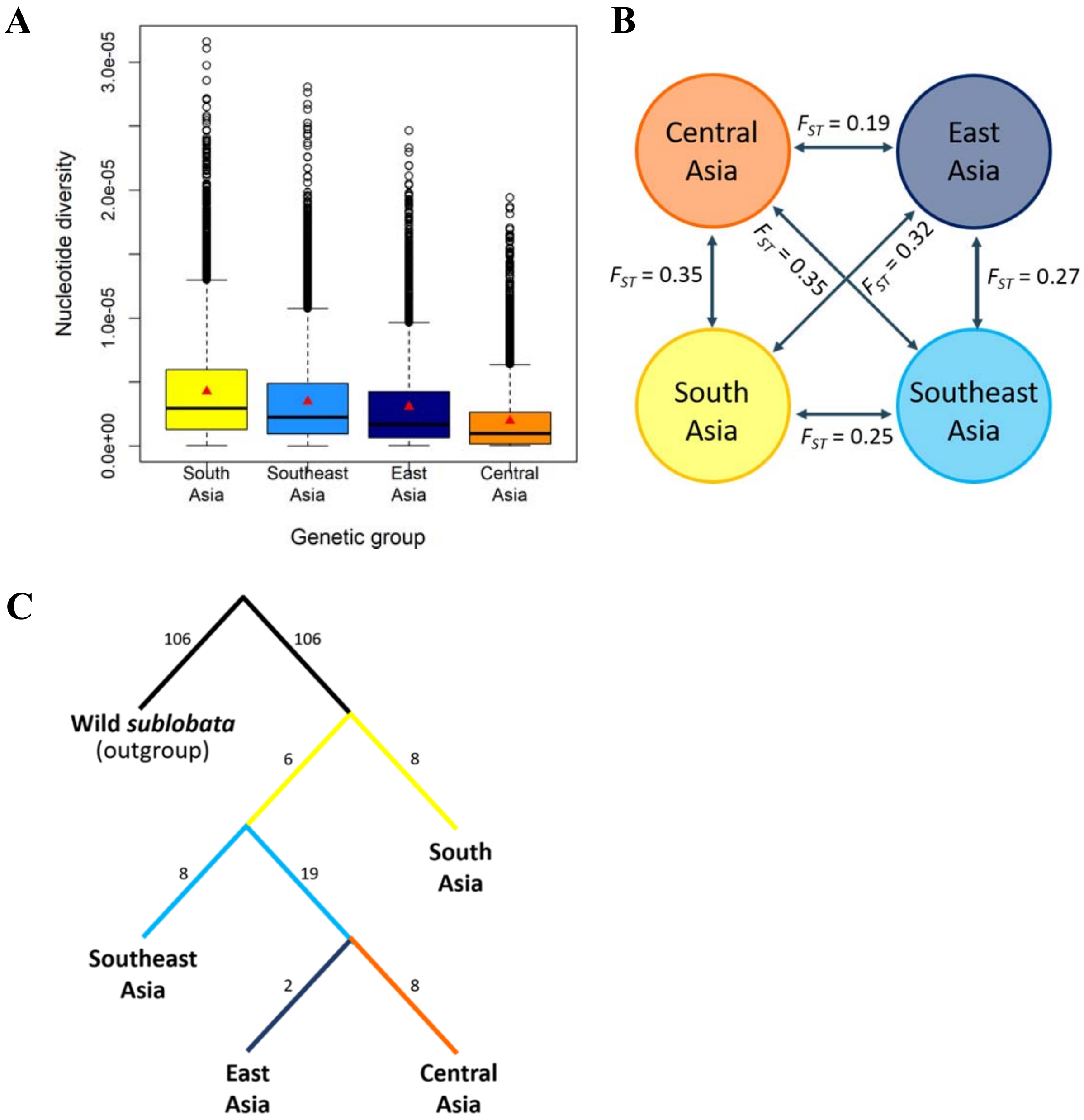


Figure 2-figure supplement 1. Diversity patterns within and between inferred genetic groups. (A) Nucleotide diversity and (B) Pairwise genetic differentiation (F_{ST}) across the four genetic groups. (C) Best fitting admixture graphs showing no admixture events between four genetic groups with wild mungbean as outgroup.

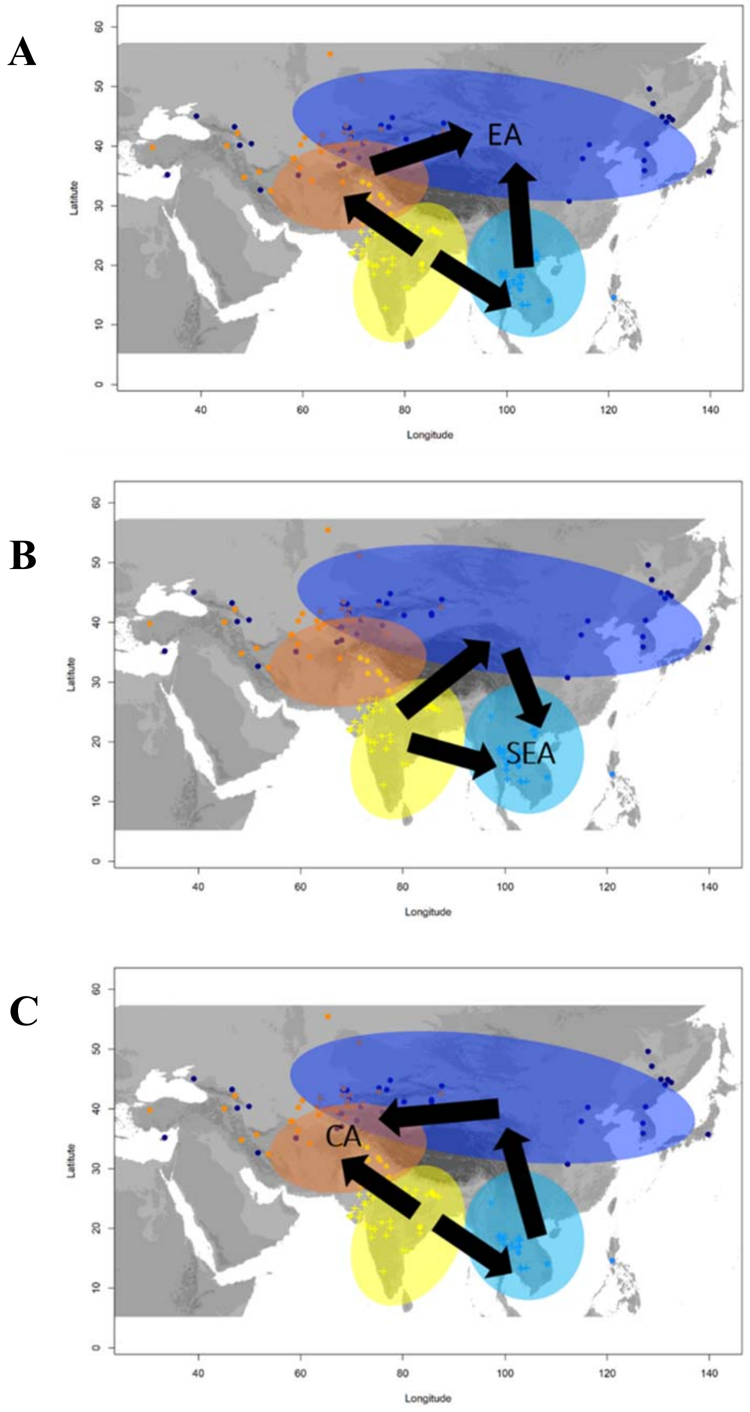
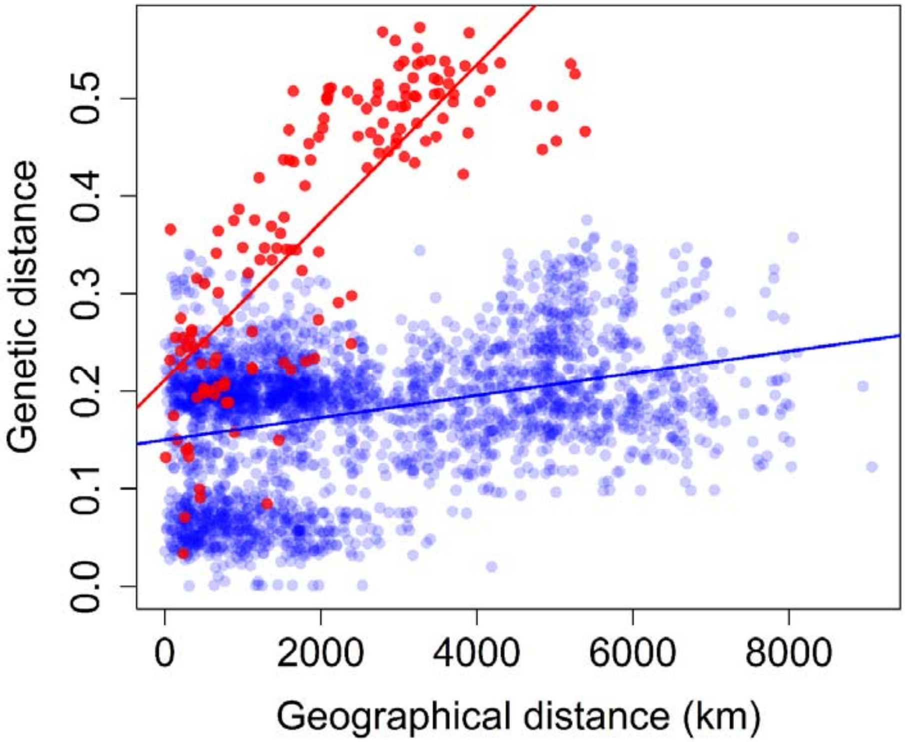


Figure 2-figure supplement 2. Schematic representation to investigate presence of admixture in a target population from two source populations using admixture *f*3-statistics. (A) *f*3(EA; SEA, CA), (B) *f*3(SEA; SA, EA) and (C) *f*3(CA; EA, SA). Coloured circles indicate the geographic area occupied by distinct genetic groups. Arrows indicates the possible direction of expansion and admixture among populations.



809 **Figure 2-figure supplement 3.** Isolation by distance plot of genetic distance versus geographic
810 distance within Southern group in red circles (Mantel test: $r = 0.804$, $P < 0.001$) and Northern
811 group in blue circles (Mantel test: $r = 0.325$, $P < 0.001$).

812

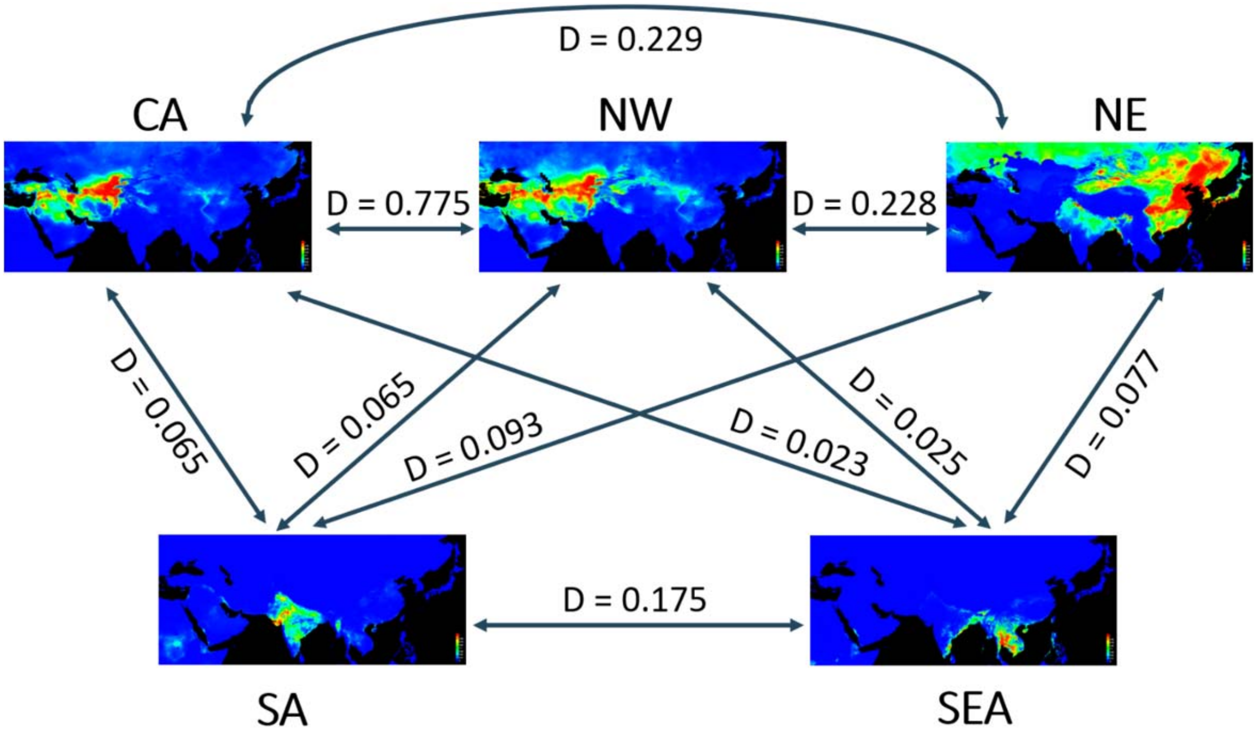
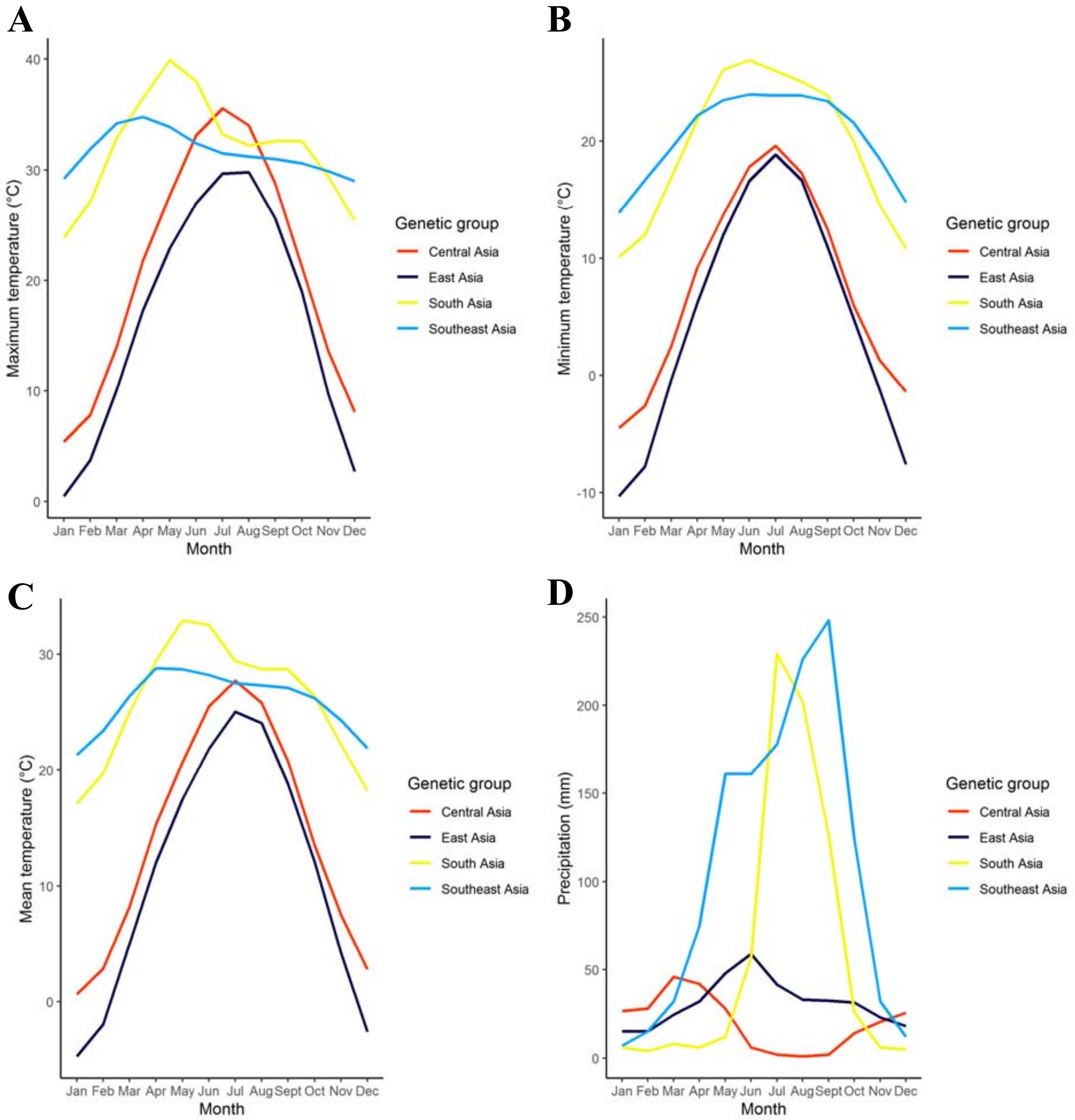


Figure 3-figure supplement 1. Predicted distributions of five groups at Mid-Holocene (about 6 kya) based on Community Climate Simulation Model 4 (CCSM4). Red colour indicates high suitability and blue indicates low suitability. Values between groups represent niche overlap measured using Schoener’s D.



818 **Figure 3-figure supplement 2.** Monthly temperature and precipitation variations among the four genetic groups. Monthly (A) maximum temperature, (B) minimum temperature, (C) mean temperature and (D) precipitation were computed based on median value among all accessions of a group. Genetic group were coloured the same as in Fig. 1.

Supplementary file 1. Mungbean accessions from Vavilov Institute (VIR) collection

Sample name	Country	Latitude	Longitude	NCBI SRA accession	NCBI Biosample accession
1.B	USA	NA	NA	SRR18125483	SAMN26179197
100.A	Cyprus	35.1856	33.3823	SRR18125482	SAMN26179198
101.A	Morocco	33.9716	-6.8498	SRR18125266	SAMN26179199
102.A	Israel	32.4971	35.4973	SRR18125200	SAMN26179200
103.A	Indonesia	-6.5971	106.806	SRR18125367	SAMN26179201
104.B	Russia	44.9003	131.8351	SRR18125356	SAMN26179202
105.A	Chile	-36.8305	-73.1167	SRR18125345	SAMN26179203
106.A	India	22.5587	88.2911	SRR18125298	SAMN26179204
107.A	India	22.5726	88.3639	SRR18125287	SAMN26179205
108.A	India	25.9821	85.6486	SRR18125276	SAMN26179206
109.A	Italy	41.9028	12.4964	SRR18125481	SAMN26179207
10A	China	47.1216	128.7382	SRR18125398	SAMN26179208
110.B	Portugal	38.7223	-9.1393	SRR18125387	SAMN26179209
111.A	Portugal	38.7223	-9.1393	SRR18125376	SAMN26179210
112.A	Russia	45.0347	39.0978	SRR18125329	SAMN26179211
113.A	Tajikistan	40.2675	69.6453	SRR18125318	SAMN26179212
114.B	India	31.5204	74.3587	SRR18125307	SAMN26179213
115.B	India	31.5204	74.3587	SRR18125476	SAMN26179214
116.A	Russia	49.6152	127.9945	SRR18125465	SAMN26179215
116.B	Russia	49.6152	127.9945	SRR18125454	SAMN26179216
117.B	Russia	44.0281	131.3273	SRR18125264	SAMN26179217
118.A	Russia	44.0118	131.3835	SRR18125253	SAMN26179218
119.A	Russia	44.39	132.558	SRR18125242	SAMN26179219
11A	China	47.1216	128.7382	SRR18125231	SAMN26179220
120.A	Argentina	-32.8895	-68.8458	SRR18125434	SAMN26179221
122.A	Japan	31.5969	130.5571	SRR18125423	SAMN26179222
123.B	Kyrgyzstan	55.4649	65.3054	SRR18125412	SAMN26179223
124.B	Ethiopia	12.9545	36.1573	SRR18125223	SAMN26179224
125.A	China	42.5246	87.5396	SRR18125212	SAMN26179225
126.A	China	42.5246	87.5396	SRR18125201	SAMN26179226
127.A	China	42.5246	87.5396	SRR18125199	SAMN26179227
128.A	Democratic Republic of the Congo	1.9293	30.0492	SRR18125198	SAMN26179228
128.B	Democratic Republic of the Congo	1.9293	30.0492	SRR18125197	SAMN26179229
129.A	Korea	37.5665	126.978	SRR18125196	SAMN26179230

12A	China	47.1216	128.7382	SRR18125195	SAMN26179231
13.A	Iran	32.4279	53.688	SRR18125194	SAMN26179232
130.A	Korea	37.5665	126.978	SRR18125371	SAMN26179233
131.A	Korea	37.5665	126.978	SRR18125370	SAMN26179234
132.B	Korea	40.3399	127.5101	SRR18125369	SAMN26179235
133.A	Korea	40.3399	127.5101	SRR18125368	SAMN26179236
134.A	Korea	40.3399	127.5101	SRR18125366	SAMN26179237
135.A	Korea	40.3399	127.5101	SRR18125365	SAMN26179238
136.A	Korea	40.3399	127.5101	SRR18125364	SAMN26179239
137.A	China	42.5246	87.5396	SRR18125363	SAMN26179240
138.A	China	39.4677	75.9938	SRR18125362	SAMN26179241
139.A	Uzbekistan	41.2995	69.2401	SRR18125361	SAMN26179242
14.B	Uzbekistan	39.7681	64.4556	SRR18125360	SAMN26179243
140.B	China	42.5246	87.5396	SRR18125359	SAMN26179244
141.A	China	43.8256	87.6168	SRR18125358	SAMN26179245
142.B	China	42.5246	87.5396	SRR18125357	SAMN26179246
144.A	Ukraine	48.4647	35.0462	SRR18125355	SAMN26179247
145.A	Brazil	-22.9329	-47.0738	SRR18125354	SAMN26179248
146.B	Kazakhstan	43.222	76.8512	SRR18125353	SAMN26179249
147.A	Turkey	39.7646	30.4559	SRR18125352	SAMN26179250
148.B	Turkey	39.7646	30.4559	SRR18125351	SAMN26179251
149.A	Ukraine	48.0386	30.9497	SRR18125350	SAMN26179252
151.A	Tajikistan	38.5598	68.787	SRR18125349	SAMN26179253
154.A	Brazil	-14.235	-51.9253	SRR18125348	SAMN26179254
155.A	United Kingdom	52.3555	-1.1743	SRR18125347	SAMN26179255
156.A	India	25.9821	85.6486	SRR18125346	SAMN26179256
157.A	India	25.9821	85.6486	SRR18125344	SAMN26179257
158.A	India	25.9821	85.6486	SRR18125343	SAMN26179258
159.B	India	25.9821	85.6486	SRR18125342	SAMN26179259
16.A	Uzbekistan	39.7681	64.4556	SRR18125341	SAMN26179260
160.A	Uzbekistan	40.8154	72.2837	SRR18125340	SAMN26179261
161.A	Uzbekistan	40.8154	72.2837	SRR18125339	SAMN26179262
162.A	South Africa	-26.7145	27.097	SRR18125338	SAMN26179263
163.A	South Africa	-26.7145	27.097	SRR18125337	SAMN26179264
164.A	South Africa	-26.7145	27.097	SRR18125336	SAMN26179265
165.B	USA	39.9526	-75.1652	SRR18125299	SAMN26179266
166.A	USA	39.9526	-75.1652	SRR18125297	SAMN26179267
167.B	Kyrgyzstan	42.8224	75.3179	SRR18125296	SAMN26179268
168.A	Kyrgyzstan	42.8224	75.3179	SRR18125295	SAMN26179269
17.B	Uzbekistan	39.7681	64.4556	SRR18125294	SAMN26179270
170.A	Russia	43.2562	46.5893	SRR18125293	SAMN26179271

171.A	Russia	43.2562	46.5893	SRR18125292	SAMN26179272
172.B	Iran	32.4279	53.688	SRR18125291	SAMN26179273
173.A	Iran	32.4279	53.688	SRR18125290	SAMN26179274
174.A	Korea	40.3399	127.5101	SRR18125289	SAMN26179275
175.A	Uzbekistan	40.2504	63.2032	SRR18125288	SAMN26179276
175.B	Uzbekistan	40.2504	63.2032	SRR18125286	SAMN26179277
176.A	Uzbekistan	40.2504	63.2032	SRR18125285	SAMN26179278
177.A	Uzbekistan	40.2504	63.2032	SRR18125284	SAMN26179279
178.A	Uzbekistan	40.2504	63.2032	SRR18125283	SAMN26179280
179.A	Uzbekistan	39.9208	66.4271	SRR18125282	SAMN26179281
18.B	Uzbekistan	39.7681	64.4556	SRR18125281	SAMN26179282
180.A	Uzbekistan	39.9208	66.4271	SRR18125280	SAMN26179283
181.A	Uzbekistan	39.9208	66.4271	SRR18125279	SAMN26179284
182.B	Uzbekistan	39.9208	66.4271	SRR18125278	SAMN26179285
183.A	Uzbekistan	40.3734	71.7978	SRR18125277	SAMN26179286
184.A	China	41.482754	85.626702	SRR18125275	SAMN26179287
187.A	China	38.10222	76.993816	SRR18125274	SAMN26179288
188.B	China	41.1675	80.2634	SRR18125273	SAMN26179289
189.A	China	41.1675	80.2634	SRR18125272	SAMN26179290
19.B	Iran	32.4279	53.688	SRR18125271	SAMN26179291
190.A	China	42.9513	89.1898	SRR18125270	SAMN26179292
191.A	China	41.175324	85.660861	SRR18125269	SAMN26179293
192.A	India	31.8183	75.2071	SRR18125268	SAMN26179294
193.A	India	31.326	75.5762	SRR18125267	SAMN26179295
193.B	India	31.326	75.5762	SRR18125265	SAMN26179296
194.A	India	30.3752	76.7821	SRR18125480	SAMN26179297
195.A	India	28.7041	77.1025	SRR18125407	SAMN26179298
195.B	India	28.7041	77.1025	SRR18125406	SAMN26179299
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199.A	Senegal	14.4974	-14.4524	SRR18125404	SAMN26179301
1A	USA	NA	NA	SRR18125403	SAMN26179302
201.B	Pakistan	31.5204	74.3587	SRR18125402	SAMN26179303
202.B	Canada	43.6502	-79.9036	SRR18125401	SAMN26179304
203.A	Ethiopia	9.3126	42.1227	SRR18125400	SAMN26179305
204.B	Indonesia	-6.5971	106.806	SRR18125399	SAMN26179306
205.A	Indonesia	-6.5971	106.806	SRR18125397	SAMN26179307
205.B	Indonesia	-6.5971	106.806	SRR18125396	SAMN26179308
206.A	Hungary	47.1625	19.5033	SRR18125395	SAMN26179309
207.A	Viet Nam	14.0583	108.2772	SRR18125394	SAMN26179310
21.B	Kazakhstan	51.1605	71.4704	SRR18125393	SAMN26179311
210.A	Afghanistan	36.6926	67.118	SRR18125392	SAMN26179312

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215.A	Guinea	8.5383	-9.4728	SRR18125390	SAMN26179314
216.A	Uzbekistan	39.972132	65.558096	SRR18125389	SAMN26179315
217.B	Uzbekistan	40.162885	66.227209	SRR18125388	SAMN26179316
218.A	Uzbekistan	40.013465	64.943243	SRR18125386	SAMN26179317
219.A	Turkmenistan	40.243331	59.540314	SRR18125385	SAMN26179318
22.B	Kazakhstan	42.3417	69.5901	SRR18125384	SAMN26179319
220.A	Turkmenistan	40.243331	59.540314	SRR18125383	SAMN26179320
223.A	Uzbekistan	40.483568	70.546311	SRR18125382	SAMN26179321
224.A	Iran	32.6539	51.666	SRR18125381	SAMN26179322
225.A	Pakistan	30.3753	69.3451	SRR18125380	SAMN26179323
226.B	Pakistan	30.3753	69.3451	SRR18125379	SAMN26179324
227.A	Pakistan	30.3753	69.3451	SRR18125378	SAMN26179325
228.B	Turkmenistan	39.0041	63.5688	SRR18125377	SAMN26179326
229.A	Pakistan	31.4504	73.135	SRR18125375	SAMN26179327
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232.A	Iran	34.3277	47.0778	SRR18125334	SAMN26179332
233.A	Iran	32.4279	53.688	SRR18125333	SAMN26179333
234.A	India	28.6139	77.209	SRR18125332	SAMN26179334
235.A	Pakistan	33.5651	73.0169	SRR18125331	SAMN26179335
235.B	Pakistan	33.5651	73.0169	SRR18125330	SAMN26179336
236.A	Pakistan	34.0155	71.6888	SRR18125328	SAMN26179337
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238.A	Egypt	26.8206	30.8025	SRR18125326	SAMN26179339
239.A	Kazakhstan	44.7689	77.5573	SRR18125325	SAMN26179340
24.A	Uzbekistan	41.4065	60.3685	SRR18125324	SAMN26179341
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244.A	Uzbekistan	41.773406	63.780613	SRR18125319	SAMN26179346
245.A	Kazakhstan	43.47491	75.335144	SRR18125317	SAMN26179347
246.A	Algeria	35.6971	-0.6308	SRR18125316	SAMN26179348
247.A	Tanzania	-5.0425	32.8197	SRR18125315	SAMN26179349
249.A	Australia	-32.9283	151.7817	SRR18125314	SAMN26179350
25.A	Uzbekistan	41.4065	60.3685	SRR18125313	SAMN26179351
250.B	Russia	NA	NA	SRR18125312	SAMN26179352
251.B	USA	NA	NA	SRR18125311	SAMN26179353

252.A	Afghanistan	34.7602	69.8121	SRR18125310	SAMN26179354
253.A	Afghanistan	34.7602	69.8121	SRR18125309	SAMN26179355
254.A	Yemen	15.5527	48.5164	SRR18125308	SAMN26179356
254.B	Yemen	15.5527	48.5164	SRR18125306	SAMN26179357
255.A	Afghanistan	36.6926	67.118	SRR18125305	SAMN26179358
256.A	Afghanistan	36.6926	67.118	SRR18125304	SAMN26179359
257.B	Afghanistan	36.6926	67.118	SRR18125303	SAMN26179360
258.B	Afghanistan	33.9391	67.71	SRR18125302	SAMN26179361
259.B	Colombia	4.5709	-74.2973	SRR18125301	SAMN26179362
26.B	Uzbekistan	41.4065	60.3685	SRR18125300	SAMN26179363
260.A	Philippines	14.5995	120.9842	SRR18125479	SAMN26179364
261.B	Kenya	-1.2921	36.8219	SRR18125478	SAMN26179365
262.A	Kenya	-1.2921	36.8219	SRR18125477	SAMN26179366
263.A	Kenya	-1.2921	36.8219	SRR18125475	SAMN26179367
264.A	Kenya	-1.2921	36.8219	SRR18125474	SAMN26179368
265.B	Kenya	-1.2921	36.8219	SRR18125473	SAMN26179369
266.A	Kenya	-1.2921	36.8219	SRR18125472	SAMN26179370
267.A	Kenya	-1.2921	36.8219	SRR18125471	SAMN26179371
268.A	Kenya	-1.2921	36.8219	SRR18125470	SAMN26179372
269.B	Kenya	-1.2921	36.8219	SRR18125469	SAMN26179373
27.A	Uzbekistan	39.7681	64.4556	SRR18125468	SAMN26179374
270.A	Kenya	-1.2921	36.8219	SRR18125467	SAMN26179375
271.A	South Korea	35.8987	127.0392	SRR18125466	SAMN26179376
272.A	Australia	NA	NA	SRR18125464	SAMN26179377
273.A	Kenya	-1.2921	36.8219	SRR18125463	SAMN26179378
274.A	Kenya	-1.2921	36.8219	SRR18125462	SAMN26179379
275.A	Kenya	-1.2921	36.8219	SRR18125461	SAMN26179380
276.A	Kenya	-1.2921	36.8219	SRR18125460	SAMN26179381
277.B	Kazakhstan	43.1521	68.2581	SRR18125459	SAMN26179382
278.B	Kazakhstan	43.0631	69.0851	SRR18125458	SAMN26179383
279.A	Kazakhstan	41.5295	69.4133	SRR18125457	SAMN26179384
28.A	Russia	42.1432	47.095	SRR18125456	SAMN26179385
280.B	Kazakhstan	41.5295	69.4133	SRR18125455	SAMN26179386
281.B	South Korea	35.8987	127.0392	SRR18125453	SAMN26179387
282.B	South Korea	35.8987	127.0392	SRR18125452	SAMN26179388
283.B	South Korea	35.8987	127.0392	SRR18125451	SAMN26179389
284.A	Tajikistan	38.0116	71.003	SRR18125450	SAMN26179390
285.A	Tajikistan	37.074793	67.957222	SRR18125449	SAMN26179391
286.A	Tajikistan	37.028926	68.004059	SRR18125448	SAMN26179392
287.A	Tajikistan	39.179338	68.012339	SRR18125447	SAMN26179393
288.A	Philippines	14.5995	120.9842	SRR18125446	SAMN26179394

289.B	Philippines	14.5995	120.9842	SRR18125445	SAMN26179395
290.A	China	40.2374	116.2305	SRR18125444	SAMN26179396
290.B	China	40.2374	116.2305	SRR18125263	SAMN26179397
291.A	China	40.2374	116.2305	SRR18125262	SAMN26179398
292.A	China	30.7378	112.2384	SRR18125261	SAMN26179399
293.A	China	30.7378	112.2384	SRR18125260	SAMN26179400
294.A	China	40.2374	116.2305	SRR18125259	SAMN26179401
295.B	China	37.8957	114.9042	SRR18125258	SAMN26179402
296.A	China	37.8957	114.9042	SRR18125257	SAMN26179403
297.A	China	47.1216	128.7382	SRR18125256	SAMN26179404
298.B	China	47.1216	128.7382	SRR18125255	SAMN26179405
299.A	China	40.2374	116.2305	SRR18125254	SAMN26179406
2A	China	47.1216	128.7382	SRR18125252	SAMN26179407
3.B	China	47.1216	128.7382	SRR18125251	SAMN26179408
30.A	Russia	42.1432	47.095	SRR18125250	SAMN26179409
300.A	China	47.1216	128.7382	SRR18125249	SAMN26179410
31.A	Russia	42.1432	47.095	SRR18125248	SAMN26179411
32.B	Russia	42.1432	47.095	SRR18125247	SAMN26179412
33.A	USA	NA	NA	SRR18125246	SAMN26179413
34.A	USA	NA	NA	SRR18125245	SAMN26179414
34.B	USA	NA	NA	SRR18125244	SAMN26179415
35.A	Russia	NA	NA	SRR18125243	SAMN26179416
36.A	Russia	43.1198	131.8869	SRR18125241	SAMN26179417
37.A	USA	NA	NA	SRR18125240	SAMN26179418
38.B	China	44.9188	130.5244	SRR18125239	SAMN26179419
39.A	Iran	36.3394	59.4698	SRR18125238	SAMN26179420
3A	China	47.1216	128.7382	SRR18125237	SAMN26179421
40.B	Iran	36.3394	59.4698	SRR18125236	SAMN26179422
41.B	Iran	32.4279	53.688	SRR18125235	SAMN26179423
42.A	Iran	32.4279	53.688	SRR18125234	SAMN26179424
43.A	Iran	32.4279	53.688	SRR18125233	SAMN26179425
44.B	Turkmenistan	37.9153	58.0897	SRR18125232	SAMN26179426
45.A	Turkmenistan	37.9153	58.0897	SRR18125230	SAMN26179427
46.A	Turkmenistan	37.9153	58.0897	SRR18125443	SAMN26179428
47.A	Turkmenistan	37.9153	58.0897	SRR18125442	SAMN26179429
48.B	Turkmenistan	37.9153	58.0897	SRR18125441	SAMN26179430
49.B	Turkmenistan	37.9172	58.0907	SRR18125440	SAMN26179431
4A	China	47.1216	128.7382	SRR18125439	SAMN26179432
5.B	China	47.1216	128.7382	SRR18125438	SAMN26179433
50.A	Turkmenistan	37.9172	58.0907	SRR18125437	SAMN26179434
51.B	Turkmenistan	37.9601	58.3261	SRR18125436	SAMN26179435

52.A	Turkmenistan	37.9601	58.3261	SRR18125435	SAMN26179436
53.B	USA	40.1605	-103.2144	SRR18125433	SAMN26179437
54.A	USA	40.1605	-103.2144	SRR18125432	SAMN26179438
55.B	Ukraine	48.3794	31.1656	SRR18125431	SAMN26179439
56.A	Kazakhstan	43.3667	68.4094	SRR18125430	SAMN26179440
57.A	Iran	34.7608	48.3988	SRR18125429	SAMN26179441
58.A	Iran	35.6892	51.389	SRR18125428	SAMN26179442
59.B	Kazakhstan	43.3667	68.4094	SRR18125427	SAMN26179443
6.B	China	47.1216	128.7382	SRR18125426	SAMN26179444
60.A	Kazakhstan	42.2663	68.1431	SRR18125425	SAMN26179445
61.A	Uzbekistan	41.2995	69.2401	SRR18125424	SAMN26179446
62.A	Uzbekistan	41.2995	69.2401	SRR18125422	SAMN26179447
63.A	Uzbekistan	41.2995	69.2401	SRR18125421	SAMN26179448
64.B	Uzbekistan	41.2995	69.2401	SRR18125420	SAMN26179449
65.B	Uzbekistan	41.2995	69.2401	SRR18125419	SAMN26179450
66.B	Uzbekistan	41.2995	69.2401	SRR18125418	SAMN26179451
67.A	Uzbekistan	41.2995	69.2401	SRR18125417	SAMN26179452
68.A	Uzbekistan	41.2995	69.2401	SRR18125416	SAMN26179453
69.A	Uzbekistan	40.4915	68.7811	SRR18125415	SAMN26179454
70.A	Uzbekistan	39.627	66.975	SRR18125414	SAMN26179455
71.A	Uzbekistan	39.627	66.975	SRR18125413	SAMN26179456
72.A	Uzbekistan	39.627	66.975	SRR18125411	SAMN26179457
73.B	Uzbekistan	39.627	66.975	SRR18125410	SAMN26179458
74.A	Uzbekistan	39.627	66.975	SRR18125409	SAMN26179459
75.A	Uzbekistan	39.627	66.975	SRR18125408	SAMN26179460
76.A	Uzbekistan	41.2995	69.2401	SRR18125229	SAMN26179461
77.A	Uzbekistan	39.7681	64.4556	SRR18125228	SAMN26179462
79.B	Uzbekistan	39.7681	64.4556	SRR18125227	SAMN26179463
7A	China	47.1216	128.7382	SRR18125226	SAMN26179464
8.B	China	47.1216	128.7382	SRR18125225	SAMN26179465
81.B	Afghanistan	34.1769	61.7006	SRR18125224	SAMN26179466
82.B	Afghanistan	34.1769	61.7006	SRR18125222	SAMN26179467
83.A	Afghanistan	34.1769	61.7006	SRR18125221	SAMN26179468
84.A	Afghanistan	34.1769	61.7006	SRR18125220	SAMN26179469
85.A	Afghanistan	34.1769	61.7006	SRR18125219	SAMN26179470
86.A	Afghanistan	36.6153	66.9293	SRR18125218	SAMN26179471
88.B	Afghanistan	NA	NA	SRR18125217	SAMN26179472
89.B	Afghanistan	33.9391	67.71	SRR18125216	SAMN26179473
90.B	Uzbekistan	NA	NA	SRR18125215	SAMN26179474
91.A	Japan	35.719	139.7456	SRR18125214	SAMN26179475
92.A	Japan	35.719	139.7456	SRR18125213	SAMN26179476

93.B	Armenia	40.0691	45.0382	SRR18125211	SAMN26179477
94.A	Iran	35.102	59.1042	SRR18125210	SAMN26179478
95.A	Azerbaijan	40.4093	49.8671	SRR18125209	SAMN26179479
96.A	Azerbaijan	40.1431	47.5769	SRR18125208	SAMN26179480
97.A	Turkmenistan	39.0041	63.5688	SRR18125207	SAMN26179481
98.B	Panama	9.3593	-79.8999	SRR18125206	SAMN26179482
99.A	Panama	9.3593	-79.8999	SRR18125205	SAMN26179483
99.B	Panama	9.3593	-79.8999	SRR18125204	SAMN26179484
9A	China	47.1216	128.7382	SRR18125203	SAMN26179485
M7.A	India	31.5204	74.3587	SRR18125202	SAMN26179486

Supplementary file 2. Outgroup *f*3 statistics among all possible combinations of genetic group pairs

Outgroup (C)	**Source1 (A)**	**Source2 (B)**	***f*3**	**Standard error**	**Z-score**	**Significant**
sublobata	CA	EA	0.232	0.005	42.66	Yes
sublobata	CA	SA	0.209	0.005	38.41	Yes
sublobata	CA	SEA	0.213	0.005	39.03	Yes
sublobata	EA	SA	0.209	0.005	38.79	Yes
sublobata	EA	SEA	0.218	0.005	40.75	Yes
sublobata	SA	SEA	0.211	0.005	39.41	Yes

Abbreviations: SA, South Asia; SEA, Southeast Asia; EA, East Asia and CA, Central Asia (*f*3 statistics with Z-score > |3| are considered significant)

Supplementary file 3. Admixture *f*3 statistics among all possible population trios

Target (C)	**Source1 (A)**	**Source2 (B)**	***f*3**	**Standard error**	**Z-score**	**Significant**
EA	SA	CA	0.005	0.001	4.82	Yes
EA	SEA	CA	-0.001	0.001	-0.51	No
EA	SEA	SA	0.020	0.002	13.48	Yes
SEA	CA	EA	0.030	0.002	14.7	Yes
SEA	SA	CA	0.014	0.002	8.82	Yes
SEA	SA	EA	0.009	0.001	6.86	Yes
SA	CA	EA	0.032	0.002	16.66	Yes
SA	CA	SEA	0.011	0.001	9.02	Yes
SA	EA	SEA	0.017	0.001	12.91	Yes
CA	EA	SA	0.011	0.001	9.55	Yes
CA	EA	SEA	0.016	0.002	10.37	Yes
CA	SEA	SA	0.031	0.002	15.65	Yes

Abbreviations: SA, South Asia; SEA, Southeast Asia; EA, East Asia and CA, Central Asia (*f*3 statistics with Z-score > |3| are considered significant, but only negative *f*3 statistics denote the target population being admixed from source1 and source2.)

Supplementary file 4. Pearson's correlation coefficient between pairs of bioclimatic variables (denoted in lower triangle)

Bioclimatic variable	Bio1	Bio2	Bio3	Bio4	Bio5	Bio6	Bio7	Bio8	Bio9	Bio10	Bio11	Bio12	Bio13	Bio14	Bio15	Bio16	Bio17	Bio18	Bio19
Bio1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Bio2	0.087	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Bio3	0.732	0.321	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Bio4	-0.814	0.011	-0.876	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Bio5	0.872	0.258	0.455	-0.449	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Bio6	0.971	-0.038	0.779	-0.911	0.749	1	-	-	-	-	-	-	-	-	-	-	-	-	-
Bio7	-0.773	0.225	-0.784	0.973	-0.377	-0.896	1	-	-	-	-	-	-	-	-	-	-	-	-
Bio8	0.595	-0.066	0.383	-0.398	0.522	0.530	-0.392	1	-	-	-	-	-	-	-	-	-	-	-
Bio9	0.901	0.122	0.663	-0.759	0.803	0.896	-0.715	0.257	1	-	-	-	-	-	-	-	-	-	-
Bio10	0.915	0.129	0.472	-0.513	0.983	0.808	-0.472	0.590	0.815	1	-	-	-	-	-	-	-	-	-
Bio11	0.977	0.050	0.814	-0.918	0.760	0.994	-0.881	0.544	0.894	0.811	1	-	-	-	-	-	-	-	-
Bio12	0.237	-0.513	0.244	-0.397	-0.030	0.327	-0.477	0.293	0.121	0.073	0.303	1	-	-	-	-	-	-	-
Bio13	0.276	-0.341	0.289	-0.403	0.040	0.332	-0.438	0.342	0.142	0.124	0.330	0.926	1	-	-	-	-	-	-
Bio14	-0.084	-0.620	-0.151	-0.011	-0.205	0.013	-0.154	0.039	-0.120	-0.126	-0.048	0.494	0.233	1	-	-	-	-	-
Bio15	0.258	0.528	0.405	-0.263	0.208	0.191	-0.128	0.302	0.156	0.189	0.262	-0.024	0.213	-0.521	1	-	-	-	-
Bio16	0.271	-0.364	0.283	-0.406	0.028	0.333	-0.446	0.330	0.141	0.115	0.328	0.950	0.992	0.258	0.178	1	-	-	-
Bio17	-0.050	-0.639	-0.110	-0.058	-0.194	0.052	-0.203	0.062	-0.089	-0.110	-0.009	0.555	0.294	0.988	-0.508	0.321	1	-	-
Bio18	-0.031	-0.453	-0.011	-0.119	-0.257	0.027	-0.210	0.245	-0.184	-0.144	0.015	0.805	0.741	0.392	0.016	0.766	0.438	1	-
Bio19	0.177	-0.270	0.266	-0.279	0.048	0.263	-0.335	-0.010	0.218	0.080	0.227	0.460	0.353	0.468	-0.196	0.356	0.490	0.115	1

Supplementary file 5. Comparison of bioclimatic variables among the four genetic groups analysed with multivariate analysis of variance (MANOVA)

Predictor	**Test statistic**	**Df**	**Observed value**	**F value**	**Num. Df**	**Den. Df**	***P***
Genetic group	Pillai	3	1.790	44.215	24	717	< 2e-16
	Wilks	3	0.024	74.690	24	688	< 2e-16
	Hotelling-Lawley	3	12.716	124.870	24	707	< 2e-16
	Roy	3	10.777	321.960	8	239	< 2e-16

Df = degree of freedom among groups; Num. Df = degrees of freedom of the model; Den. Df = degree of freedom of residual

Supplementary file 6. Summary of ANOVA for bioclimatic variables

Bioclimatic variable	**Df**	**Sum square**	**Mean square**	**F value**	***P***
Bio1 (Annual temperature)	3	183.688	61.229	235.97	<2.2e-16
Bio2 (Mean diurnal temperature range)	3	66.253	22.085	29.813	<2.2e-16
Bio3 (Isothermality)	3	188.031	62.677	259.34	<2.2e-16
Bio8 (Mean temperature of wettest quarter)	3	177.063	59.021	205.91	<2.2e-16
Bio12 (Annual precipitation)	3	157.890	52.630	144.11	<2.2e-16
Bio14 (Precipitation of driest month)	3	29.859	9.952	11.183	<6.6e-07
Bio15 (Precipitation seasonality)	3	119.810	39.938	76.62	<2.2e-16
Bio19 (Precipitation of coldest quarter)	3	44.212	14.737	17.732	< 1.9e-10

Df = degree of freedom among groups

Supplementary file 7. Correlation between eight bioclimatic variables and climatic PC axes 1 to 4

Bioclimatic variable	**PC1**	**PC2**	**PC3**	**PC4**
Bio1 (Annual temperature)	**-0.445**	-0.107	0.390	-0.056
Bio2 (Mean diurnal temperature range)	0.193	**-0.564**	0.062	0.253
Bio3 (Isothermality)	**-0.430**	-0.082	**0.492**	-0.184
Bio8 (Mean temperature of wettest quarter)	**-0.486**	0.042	-0.287	0.049
Bio12 (Annual precipitation)	**-0.401**	0.366	0.066	0.202
Bio14 (Precipitation of driest month)	0.017	**0.582**	-0.248	0.259
Bio15 (Precipitation seasonality)	-0.323	-0.365	-0.292	**0.667**
Bio19 (Precipitation of coldest quarter)	0.279	0.235	**0.607**	**0.587**

(Correlation coefficients with absolute values higher than 0.4 are in bold.)

Supplementary file 8. ANOVA table for all evaluated field traits (phenology, reproduction and size) as well as drought-related traits

Trait	Garden	Model r^2	Group *F*	Group *P*	SEA[1]	SA[1]	CA[1]	Tukey[2]
Phenology:								
Days to 50% flowering	Pakistan 2015	0.2388	7.2144	0.0019*	-0.3702	0.6296	-0.3525	B,A,B
Days to 50% flowering	Taiwan 1984	0.5266	25.5887	<.0001*	0.5723	0.3197	-1.0685	A,A,B
Days to 50% flowering	Taiwan 2018	0.4465	18.5544	<.0001*	0.0974	0.6569	-0.9633	A,A,B
Reproduction:								
100 seed weight, g	Pakistan 2015	0.4722	20.5761	<.0001*	0.9050	-0.6397	-0.2756	A,B,B
Pod length, cm	Pakistan 2015	0.2621	8.1698	0.0009*	0.6810	-0.2605	-0.4896	A,B,B
Pod length, cm	Taiwan 1984	0.7173	58.3615	<.0001*	1.0524	-0.1980	-1.0232	A,B,C
Pods per plant	Pakistan 2015	0.4471	18.5988	<.0001*	-0.6441	0.8455	-0.3062	B,A,B
1000 seed weight, g	Taiwan 1984	0.6248	38.3053	<.0001*	0.9979	-0.8380	-0.1340	A,C,B
Seed yield per plant, g	Pakistan 2015	0.4666	20.1225	<.0001*	-0.6210	0.8752	-0.3712	B,A,B
Seeds per pod	Pakistan 2015	0.1300	3.4372	0.0406*	-0.4875	0.2418	0.2806	A,A,A
Seeds per pod	Taiwan 1984	0.1611	4.4168	0.0176*	0.1413	0.3386	-0.6107	AB,A,B
Plant size:								
Petiole length, cm	Pakistan 2015	0.2943	9.5907	0.0003*	0.5435	0.0878	-0.7798	A,A,B
Plant height, cm	Pakistan 2015	0.0001	0.0024	0.9976	0.0075	0.0055	-0.0158	A,A,A
Plant height at flowering, cm	Taiwan 1984	0.3981	15.2115	<.0001*	0.4811	0.3024	-0.9705	A,A,B
Plant height at maturity, cm	Taiwan 1984	0.5472	27.8000	<.0001*	0.3480	0.5605	-1.1362	A,A,B
Primary leaf length, cm	Taiwan 1984	0.5454	27.5930	<.0001*	0.9813	-0.4212	-0.6253	A,B,B
Primary leaf width, cm	Taiwan 1984	0.6053	35.2773	<.0001*	1.0244	-0.6010	-0.4313	A,B,B
Terminal leaflet length, cm	Pakistan 2015	0.2186	6.4340	0.0034*	0.3062	0.2643	-0.7167	A,A,B
Terminal leaflet width, cm	Pakistan 2015	0.1680	4.6458	0.0145*	0.4361	0.0387	-0.5734	A,AB,B
Drought (PEG6000):								

Shoot dry weight (SDW), mg	NTU 2021	0.5998	36.7246	<.0001*	1.0508	-0.5607	-0.5483	A,B,B
Root dry weight (RDW), mg	NTU 2021	0.5964	36.2048	<.0001*	1.0299	-0.6933	-0.3336	A,B,B
Total dry weight (TDW), mg	NTU 2021	0.5934	35.7555	<.0001*	1.0448	-0.5883	-0.5028	A,B,B
Root:Shoot ratio dry weight (RSRDW)	NTU 2021	0.3261	11.8577	<.0001*	-0.2316	-0.4342	0.9112	B,B,A
Drought (Control):								
Shoot dry weight (SDW), mg	NTU 2021	0.5779	33.5453	<.0001*	1.0275	-0.4709	-0.6484	A,B,B
Root dry weight (RDW), mg	NTU 2021	0.5205	26.5962	<.0001*	0.9716	-0.6077	-0.3811	A,B,B
Total dry weight (TDW), mg	NTU 2021	0.5638	31.6722	<.0001*	1.0195	-0.5374	-0.5430	A,B,B
Root:Shoot ratio dry weight (RSRDW)	NTU 2021	0.1753	5.2083	0.0089*	-0.3036	-0.2004	0.6773	B,B,A

*Significant at $P < 0.05$; 1: least-square means of each group after inverse normal transformation of raw data; 2: levels not connected by same letter are significantly different.

Supplementary file 9. Mean of eight independent bioclimatic variables of the genetic groups

Bioclimatic variable	Northeast Asia (N = 37) Mean ± SD	Northwest Asia (N = 45) Mean ± SD	Southeast Asia (N = 45) Mean ± SD	South Asia (N = 49) Mean ± SD	Central Asia (N = 72) Mean ± SD
Bio1	62.49 ± 55.39	117.58 ± 54.30	256.47 ± 19.29	255.57 ± 14.80	128.72 ± 41.10
Bio2	115.22 ± 15.44	124.38 ± 20.14	102.02 ± 16.11	127.24 ± 16.12	130.08 ± 13.89
Bio3	25.14 ± 2.04	31.02 ± 4.47	51.58 ± 7.19	42.8 ± 4.58	32.4 ± 3.52
Bio8	207.86 ± 31.97	107.89 ± 67.90	271.47 ± 11.68	283.92 ± 23.02	92.04 ± 42.23
Bio12	821.59 ± 299.98	301.24 ± 201.00	1477.69 ± 380.18	750.39 ± 329.19	285.67 ± 145.24
Bio14	12.14 ± 11.72	5.18 ± 8.99	6.33 ± 4.34	2.47 ± 3.44	2.51 ± 4.98
Bio15	95.35 ± 24.52	65.4 ± 20.35	84.78 ± 7.25	124.47 ± 23.48	70.92 ± 12.92
Bio19	42.51 ± 38.23	88.33 ± 67.16	48.02 ± 24.91	34 ± 33.99	92.15 ± 45.19