Fifteenth century CE Bolivian maize reveals genetic affinities with ancient Peruvian maize

Huan Chen[1,2,4], Amy Baetsen-Young[3], Addie Thompson[2,3], Brad Day[1,2,3], Thelma Madzima[4], Sally Wasef[5], Claudia Rivera Casanovas[6], William Lovis[7,*], Gabriel Wrobel[7,*]

[1]Department of Genetics and Genome Sciences, Michigan State University, East Lansing, Michigan 48824, USA. [2]Graduate Program in Molecular Plant Sciences, Michigan State University, East Lansing, Michigan 48824, USA. [3]Department of Plant, Soil and Microbial Sciences, Michigan State University, East Lansing, MI 48824, USA. [4]Department of Plant Biology, Michigan State University, East Lansing, Michigan 48824, USA. [5]Genomics Research Centre, Queensland University of Technology, 60 Musk Ave, Kelvin Grove, QLD, 4059, Australia. [6]Universidad Mayor de San Andres, Avenida Villazón 1995, Monoblock Central, La Paz, Bolivia. [7]Department of Anthropology, Michigan State University, East Lansing, MI 48824, USA.

*corresponding authors: William Lovis, Gabriel Wrobel

Email: lovis@msu.edu and wrobelg@msu.edu

Author Contributions: HC, ABY, AT, and BD designed and conceived the experiments. HC, ABY, AT, BD, TM, SW, CRC, WL, and GW analyzed the data and wrote the manuscript. All authors commented and agreed on the manuscript before submission.

Competing Interest Statement: The authors declare no competing interests.

Classification: Biological Sciences and Social Sciences.

Keywords: archaeological maize, agriculture, domestication

Abstract

Previous archaeological and anthropological studies have demonstrated the myriad of ways that cultural and political systems shape access to food and food preferences. However, few studies have conducted a biocultural analysis linking specific genotypic/phenotypic traits as evidence of cultural selection in ancient contexts. Here, we provide insight into this topic through ancient genome data from Bolivian maize dating to ~500-600 BP, included as an offering with the mummified remains of a young girl. These data are compared to 16 previously published archaeological maize samples spanning at least 5,000 years of evolution, and 226 modern maize samples. Our phylogenetic analysis showed that the archaeological Bolivian maize (aBM) has the closest genetic distance to the archaeological maize from ancient Peru, which in turn shared the most similarities with archaeological Peruvian maize. During the period of interaction between the Inca state and local polities in the central Andes and consequent interactions with local agricultural traditions, the genetic diversity of maize increased. Ovule development in modern maize was selected and compared to those in archaeological specimens,

revealing evidence of targeted breeding strategies aimed at improving seed quality and yield. While the cultural origin of the maize – either Inca or local Aymara – is uncertain, we demonstrate that the samples are most similar to Peruvian maize and potential targeted selection strategies for enhanced growth were well established by the 15th century.

Significance Statement

Maize has been improved through selective breeding delivering desirable horticultural, agronomic, and cultural characteristics, related to environment, nutrition, etc. Inca culture was closely associated with maize diversity, but there is little evidence to show how and why culture influenced that diversity and modern maize biogeographic patterns in South America. We show that in the 15th century CE, maize diversity in the central Andes was enhanced through selection for specific traits associated with reproduction. We hypothesize that this may have contributed to maize becoming a staple under the Inca, as happened previously with expanding Tiwanaku interactions and influence during the Middle Horizon.

Introduction

Modern maize (*Zea mays* ssp. *mays L.*) is one of the most important and productive global food crops[1]. Prior to European contact in the Americas, maize had been adapted for a wide range of environments. Its versatility is clear from its extensive geographic distribution today, ranging from 58° north latitude to 40° south latitude, and growing below sea level as well as 3,600 meters above sea level in the Andes[2]. In Bolivia, there is empirical evidence that small maize varieties can grow at altitudes of 3,800-3,900 meters above sea level (masl) in some areas of the Lake Titicaca Basin[3], as well as in other sheltered areas of Oruro and Potosí, although with lower levels of production[4, 5]. Studies of archaeological samples and modern molecular data indicate that maize originally evolved in Mexico from the flowering species of grass, teosinte (*Zea mays* ssp. *parviglumus*) ~9,000 years before the present (cal. BP) [6, 7]and spread into South America by ~7,000 cal BP[8, 9] from the lowland and Eastern North America by ~2500 cal BP[10]. During this domestication process there was hybridization between maize and mexicana (*Zea mays* ssp. *mexicana*)[11]. The dispersal of maize to the rest of the world followed European colonization of the Americas in the 15th and 16th centuries AD[2, 12]. The evolution and diversity of maize has been shaped by both cultural and natural selection in a wide range of environmental and social contexts. For example, previous research has shown that temperate adaption in modern maize is characterized by early flowering[13], evidence has also shown that cultural preferences were a factor in maintaining otherwise undesirable traits[14, 15]. Maize seeds were selected and retained by farmers for use in subsequent growing years to maintain or enhance specific morphological traits, such as color and texture, based on changing cultural preferences, sometimes at the cost of reduced cultivability and/or nutrition[16].

Politics and culture have had a strong influence on crop planting and food preferences in ancient (and modern) civilizations. Indeed, in the Andes, previous research showed that under the Inca empire, maize was fulfilled multiple contextual roles. In some cases, it operated as a sacred crop[17], symbolic of political power and tightly associated with high-status or elite social groups[6, 18]. It was also an important element in numerous cultural events and rituals[19]. From an agriculture-economic point-of-view, planting a crop on the most suitable land takes priority if a farmer wishes to maximize the output-to-input ratio. However, in certain civilizations, including Andean groups, maize may not necessarily have been a crop for which yield was considered a deciding factor. For example, in Andean highland communities, maize was not the primary food crop during pre-Inca times[20], not only because maize was ill-adapted to arid highland conditions and its cultivation was risky during the short growing season, but also because planting maize did not yield a return on investment. In the Andes during the Spanish conquest, the chronicler Cobo observed that, “Indians dropped all that they were doing in order to produce a little maize, even though it cost them more than it was worth”. It seemed to him that work in the fields was "…one of the major forms of recreation and festivals…”, and he was impressed by the "extraordinary fondness for farming"[21, 22]. While Indigenous agriculture and foodways would have been far more nuanced than Spanish chroniclers would have appreciated, this supports the fact that Andean farmers were not deterred from planting an abundance of maize in sub-optimal environments. In fact, while it was a desirable food, it could also have acted as a symbol of empire[17] and a ritual-feast crop, since its first introduction to the region around 2500 BCE[23].

The current study contributes to broader investigations documenting maize biogeographic patterns in South America by focusing on maize samples from a 15th century elite stone tomb burial context from south of La Paz, Plurinational State of BoliviaWe sequenced two archaeological Bolivian Maize (aBM) kernels with six libraries, using short read sequencing. In parallel, we used ^{14}C Accelerator Mass Spectrometer (AMS) radiocarbon dating to determine the approximate age of the samples. Phylogenetic analysis of aBM, 16 archaeological and 226 modern maize samples (*Zea mays* ssp. *mays L.*), 88 modern samples of Teosinte *(Zea mays* ssp*. parviglumis)*, 79 modern samples of Mexicana teosinte *(Zea mays* ssp*. mexicana)* and 1 *Tripsacum* genotype revealed genetic relationships among themselves (Table S1; Dataset S1). Finally, the unique single nucleotide polymorphisms (SNPs) in aBM infer that the selection imposed to enhance reproductive success in marginal highland growing environments resulted in increased maize diversity. Based on the data presented herein, we conclude that a combination the social and political needs of the Inca and local ethnic groups, and mitigation of certain natural environmental factors may have contributed to the specific preference for, and diversification of maize in the Central Andes. As such, our conclusions offer insight into the possible pathways that influenced maize genetic diversity, thus providing a vital resource to investigate further the factors that drove selection for maize domestication and diversity at the cusp of the cultural influence of the Inca empire.

Results

Archaeological Bolivian maize sample (aBM)

La Paz is a major city located in the highlands of west-central modern Bolivia, which is 16°30′S, 68°09′W, 3,650 masl. Dry conditions in this region and the adjacent Andes Mountain range have aided in the preservation of desiccated organic material. Our maize samples were found within a woven camelid fiber pouch that was one of many offerings associated with the mummified remains of a child reported as being found in a *chullpa* (stone tower tomb) south of La Paz, Plurinational State of Bolivia around 1890 (Fig. 1). Although it is impossible to know the exact location of the *chullpa* or the origin of the individual, the assemblage was acquired by the U.S. Consul to Chile and was sent as a gift to the Michigan State University Museum, where she was curated until 2019. Following a series of recent analyses, she has since been voluntarily repatriated to Bolivia[24]. Given the reported archaeological context of the mummy and her abundant offerings recorded in the MSU Museum intake records, it has been proposed that she might represent an elite member of society. However, the nature of the coarse fabrics, simple design motifs, and restricted color palette of her textiles would suggest a more common individual, perhaps with an affiliation with a local high-status group. The vast majority of the funerary towers that exist in a radius of 60 km south of La Paz city are made of mudbricks. To our knowledge, the only exception is an Inca “cushioned” (i.e., rounded edges) stone and mudbrick tower located in Uypaca, in the nearby Achocalla Valley, 8 km southwest of the city center[24]. Because of its characteristics, this tomb most likely belonged to a local (possibly non-Inca) high-status group and was part of a more extensive funerary site. Although it is impossible to know the exact provenience of the mummy, it would not be unreasonable to suppose that she originated from this or another similar tomb in the Achocalla Valley. Regardless, in the decades following her death, community members periodically visited the *chullpa* and left offerings. These included the pouch full of well-preserved maize from which we collected and analyzed samples from two kernels.

A single Accelerator Mass Spectrometer (AMS) date was obtained from one kernel, yielding a radiocarbon age of 400±26 BP (D-AMS-027148; Zea mays kernel; corrected for fractionation, no $\delta^{13}C$ reported). For the date 400±26 BP the two possible calibrated age ranges are 1455-1516 cal AD (p=0.489) and 1538-1627 cal AD (p=0.511), with a median age of cal AD 1534 (Calibrated at 2σ with Calib 8.2 [SHCal 20.14c]). Choice of the earlier age range is supported by other absolute dates on the assemblage[25, 26]: 447±45 BP (D-AMS-32518; Cucurbitaceae, $\delta^{13}C$ = -27.6) with two possible age ranges of 1443-1504 cal AD (p=0.848) and 1594-1616 cal AD (0.152) with a median age of 1474 cal AD; and 510±20 (PSUAMS-5947; Camelidae fiber, $\delta^{13}C$ = -18.9) calibrated to 1420-1454 cal AD (p=1.00) with a median age of 1438 (Both samples calibrated for southern hemisphere at 2σ with Calib 8.2 [SHCal 20.14c]). Ages on the squash and maize are statistically identical at p=.95 (t=1.70, x^2.05=3.84, df=1) with a pooled mean of the two ages of 424±18 BP calibrated to 1453-1505 cal AD (p=0.769) and 1593-1617 (p=0.231). Results on the squash, with highest probability between 1443-1504 cal AD, and camelid fibers with an age range of 1420-1454, as well as the pooled mean, reveal a greatest likelihood for a mid- to late 15th c age for the assemblage, consistent with the earlier of the two calibrated age ranges on the maize kernel.

Two associated maize kernels from the same pouch were subjected to molecular analysis. Genomic base modification patterns associated with ancient DNA (aDNA), including cytosine deamination damage patterns, have been identified. Observed position-specific substitutions at the ends of the sequence reads (e.g., C→T/G→A[27-31] (Fig. S1a), as well as an increase in adenine (A) and guanine (G) residues at the 5′ end, concomitant with a reduction of C and T residues[31-33] (Fig. S1b). From this, we evaluated all substitution types and read length (Fig. S2), including read length range[34] and substitution rate types, which are associated with aDNA genome data[35]. In total, these data are consistent with the radiocarbon results, supporting that 1) with the maize is in fact consistent with an archaeological biological sample, and 2) with based on the geographic origin of the sample, the kernels potentially descended from the period of the last Inca empire before the Spaniard Francisco Pizarro's conquest of the Inca capital, Cuzco, in A.D. 1533[36].

Our study focused on identifying the location from which aBM originally came, establishing and explaining patterns of genetic variability of maize, with a specific focus on maize strains that are related to our current aBM samples. We were especially interested in exploring how these patterns of variability found in both archaeological and modern samples reflect the influence of cultural systems of behavior on both the spread of variants across the ancient landscape and selection for phenotypic traits by local populations.

Genetic Identity and Genetic Relatedness

After Tupac Inca Yupanqui became the emperor of the Inca Empire in the 15th century, the territory of the Inca empire was greatly expanded across much of western South America, including the Qollasuyu, a broad territory located in what is now western Bolivia, southern Perú, northern Chile, and non-highland Argentina[37]. Different ethnic groups populated this territory forming polities that were confederated at the time of Inca arrival. Several Aymara Pakaje groups inhabited the highlands and the inter-Andean valleys south of La Paz, from where the maize samples derive[38]. Because of maize's central role in Inca society—as both a staple crop and a symbolically charged resource among diverse ethnic groups under Inca influence—its widespread distribution may reflect the expansion of Inca social and political hegemony across newly incorporated territories. Given the provenience of the aBM and its age, it is possible the samples were local or alternatively were introduced into western highland Bolivia from the Inca core area – modern Peru. To test this hypothesis, we first evaluated the genetic relatedness of archaeological and contemporary modern maize samples using a genome sequence approach to assist in identifying the origin(s) of aBM and the relatedness to other maize from different locations. Our f3-statistics results with *Tripsacum* as outgroup suggests that aBM is closely related to two archaeological lowland Peruvian maize (Z65 and Z61) among all other ancient maize and modern maize (Fig. 2). These results indicate that the closest relative of aBM is the archaeological maize that came from Peru. In addition, to predict the geographic location of aBM, we used spatial auto-correlations in genetic data, which allowed us to compare it to a set of archaeological maize samples of known

geographic origin[39]. Our results indicate the potential geographic location that aBM may have originally come from (locator.py –seed 549657840) and the predicted location is inside of Peru and very close to archaeological maize Z61 (Fig. 3; R2(x)=1.0, R2(y)=1.0). However, this did not indicate that aBM originally came from Inca core area, given that the results are based on predictions and the ages of archaeological samples vary. This suggests that aBM might not only genetically, but also potential geographically related to the archaeological maize from ancient Peru. This is interesting, as historically, descriptions of *capacocha* rituals showed that they were able to source their food from the stations connecting high-altitude ritual sites and other regions of the empire[36]. Indeed, data generated herein show that our aBM has a strong relationship with archaeological Peruvian maize in terms of both genetic identity and geographic location[40]. This finding is also consistent with the above previous research revealing that one of the maize groups from Peru during Inca peak times spread into newly conquered territories, then slowly diverged to fit the local environment[41] following Inca cultural influence[21]. After this, diverged groups were introduced outside of Inca conquered territories. Although the origin of the aBM – either Inca core area or local – is uncertain, as our results cannot determine the dispersal direction, they do indicate that aBM has a strong relationship with archaeological Peruvian maize.

To investigate the genomic data from the aBM in relation to other archaeological and modern maize, principal component analysis (PCA) was used. As expected, the results showed that all the archaeological maize clustered with our aBM in the same cluster (Fig. 4). SM3, 5, and 10 were excluded due to their limited data to meet requirements for the PCA analysis. Unexpectedly, there is one modern maize from Brazil in the ancient maize cluster that has overlap with archaeological Brazilian maize Z6, which indicates that certain genetic traits from ancient Brazilian maize might have been preserved in modern Brazilian maize populations. There is also one modern tropical maize very close to archaeological Peruvian maize Z65. Considering the geographic origin of Z65 and its lowland characters, it is not surprising that modern tropical maize shares some level of genome sequence similarity. Following the establishment of an important maize culture center in Peru, maize was domesticated and diverged into different groups, which then spread along with Inca culture[42]. We found that the Central American cluster has overlap with both North and South America, which supports the distribution route of maize[13, 43, 44]. This finding also is consistent with previous research revealing that the original maize came from teosinte in Mexico, then dispersed northward into North America and southward into South America[6, 7, 9, 45, 46]. We also found that a few types of maize from Europe have a much closer distance to the archaeological maize cluster compared to other modern maize, which indicates maize from Europe might expectedly share certain traits or evolutionary characteristics with ancient maize. It is also consistent with the historical fact that maize spread to Europe from multiple areas and time periods after Christopher Columbus's late 15th century voyages to the Americas[12]. But as shown, maize also has diversity inside the European maize cluster. It is possible that European farmers and merchants may have favored different phenotypic traits, and the subsequent spread of specific varieties followed the new global geopolitical maps of the Colonial era[47, 48].

Taken together, these results support the possibility that aBM was introduced into western highland Bolivia from the Inca core area – modern Peru, and aBM may possibly reveal a history of adaptation to tropical conditions through local agency and/or following cultural influence of the Inca empire[46, 49]. After this, maize, both as a primary food and as a symbol of power, was dispersed from Peru throughout the Inca empire, in the end enhancing maize diversity in South America.

Selection for aBM under Inca Culture Influence

After establishing the identity of aBM and its relatedness to other regional samples, we explored how aBM was possibly shaped by human behavior, and specifically how cultural selection within the Inca empire influenced maize diversity in South America. To address this question, we examined the evolutionary relationship between aBM, its wild ancestor, and extant landraces. We constructed a Neighbor-Joining (NJ) and maximum-likelihood (ML) phylogenetic trees using the common genome-wide polymorphisms shared among aBM and modern maize samples[50]. Our data included 226 samples of modern maize, 88 modern samples of Teosinte (*Zea mays* ssp*. parviglumis*), 79 modern samples of Mexicana teosinte (*Zea mays* ssp*. mexicana*), and 1 *Tripsacum dactyloides* as an outgroup, totaling 28,588 genome-wide SNPs. As shown in Fig. S3a and Fig. S3b, both phylogenetic trees indicate that aBM lies outside the diversity of modern maize yet clusters within a specific clade alongside one modern tropical maize. This suggests that aBM shares a closer genetic relationship with modern tropical maize while being genetically distinct from other modern maize. Considering modern tropical maize is adapted to tropical climates exhibiting traits such as drought tolerance, heat resistance, and the ability to thrive in low-fertility soils, it is plausible that aBM might share these stress response characteristics with tropical maize[51, 52].

To investigate the selection preference on aBM under Inca cultural influence, we compared the allele frequency between aBM and other ancient maize samples. We identified 18,668 SNPs unique to aBM. Notably, two genes - Zm00001eb123120 and Zm00001eb178600-associated with traits “internode length below ear” and “nodes above ear” traits[53] contain several unique SNPs in aBM (Dataset S2). This suggested that height related traits in aBM possibly may have been selected under Inca cultural practices. Additionally, variations in the 5 or 3 untranslated regions UTR) can significantly affect gene expression. We found 83 target genes harboring unique aBM SNPs in their UTR regions (Dataset S3). Gene Ontology (GO) results showed that 3 of these genes are involved in glycosyltransferase activity, while serval of others is involved in defense response to biotic and abiotic stress and starch biosynthetic processes (Dataset S4). Previous researches in maize evolution implied that multiple loci are involved in shaping traits variation[54, 55]. Combining all this information, we inferred those traits associated with plant development and stress response processes might have been selected in maize during the period of Inca cultural influence, although the selection direction is uncertain.

Finally, to understand positive selection in modern maize compared to ancient maize, we investigated the selective sweep using cross-population extended haplotype homozygosity (XP-EHH) method. Following the same method of previous research[56], the cutoff metric for significant signatures of selection was set at a value of 6 for 5 kb windows

across the genome. We only identified one target gene (Fig. 5): Zm00001eb105060, whose biological process functions include plant ovule development, chromosome segregation and asparaginyl-tRNA aminoacylation. Ovule development plays a crucial role in improving maize breeding strategies via higher seed production and hybrid vigor[57]. The positive selection of this gene in modern maize suggests that characteristics aiming for higher seed production were selected during maize diversification after aBM. This finding might relate to breeding efforts to improve seed yield in modern maize compared to ancient varieties.

In conclusion, the aBM included in the funerary accoutrements of a young elite Andean girl belongs to the family of ancient Peruvian maize groups, and likely was introduced to the Aymara region following Inca expansion in the late 15th century. Following its arrival in the area of western Bolivia, the Peruvian maize variety was further modified by the local population. Some genomic changes reflect selection to mitigate local environmental conditions, including response to stress. Thus, this case study supports the idea that patterns of regional diversity in pre-Contact South America maize reflect complex biocultural processes. These data may also inform subsequent studies about Colonial dispersals and the origin of global maize varieties[12].

Discussion

Previous archaeological and anthropological studies have demonstrated that cultural and political systems shaped access to and preferences for food. In our study we explored the evidence for the contribution of Inca culture to maize diversity in South America by analyzing 16 archaeological maize samples spanning at least 5,000 years of evolution, and 226 modern maize samples. Recognizing their shared central Andean origins, we propose that the aBM sample potentially came from ancient Peruvian archaeological maize. While our findings are consistent with both genetic and archaeological evidence, they raise several questions. Notably, what specific traits were selected in aBM, and how this selection occurred under Inca cultural practices is unclear, especially given our limited aBM sample size and the lack of the same genotype in archaeological maize under non-Inca culture influence.

Cultural preferences are often a factor in maintaining certain aesthetically desirable traits[14, 15], such as color and texture, even at the cost of reduced cultivability or nutrition[16]. This suggests it is possible that culture played an important role in maize evolution and diversity. To better understand how exactly cultural interactions influenced maize diversity in the Central Andes, we explored the possible origin of aBM and its closest genetic relationships to ancient maize. We identified that aBM potentially have originated from ancient Peru, and archaeological maize from Peru has the closest genetic relationship with aBM, indicating that aBM may be a product of Inca cultural dissemination into new territories[21].

We further investigated which traits were possibly selected under Inca culture by analyzing unique SNPs in aBM. The results show that traits related to plant development,

357 and stress response were selected. These traits can aid in resisting drought and frost in
358 the relatively harsh conditions of the Andean highlands. The selected traits could facilitate
359 fermentation for the creation of *chicha* to meet the consumption requirement of elite
360 lifeways[18]. However, we are uncertain if these traits were directly selected under Inca
361 culture due to the limited aBM sample size, which prevented us from identifying positive
362 selection directly between aBM and other archaeological maize groups.
363
364 Traditional breeding systems have increased tolerance to biotic and abiotic stress and
365 contributed to yield in crops[58, 59]. In this study, we compared modern maize to
366 archaeological maize across the entire Western Hemisphere and found that the ovule
367 development traits were selected for breeding to improve maize seed production during
368 its evolution. However, it is uncertain whether this selection happened directly in modern
369 maize when compared to ancient maize, or if it happened during the process of modern
370 improvement.
371
372 Our results not only highlight the influence of culture on maize diversity in South America
373 but also point to the adaptive characteristics of maize in improving maize seed production
374 during evolution. This provides a potential source for maize diversity studies and breeding
375 programs. Most importantly, this work suggests that cultural influence plays an important
376 role in aiding maize diversity, alongside the traits selected by early farmers.
377
378 **Materials and Methods**
379
380 **Plant material**. The two archaeological Bolivian maize (aBM) kernels were collected prior
381 to 1890 AD from the area south of modern La Paz, Bolivia, and later curated at the
382 Michigan State University Museum until their repatriation in 2022[25]. AMS assay dates
383 reveal a mid-late 15th century date for the maize samples. In addition, data from 16
384 archaeological samples collected from previous published research were also used,
385 including two from Chile dating from 750 to 1,100 BP, two from Brazil dating from 510 to
386 690 BP, three from Peru dating from 600 to 1,000 BP, two from Argentina, dating from
387 980 to 1,040 BP and from 70 to 130 BP, three from Honduras dating from 1,740 to 2,300
388 BP, and three from Mexico dating to 5,310 BP (Table S1)[40, 60].
389
390 **aDNA extraction**. Archaeological maize kernels were processed in a clean laboratory
391 environment at Michigan State University. Whole kernels were crushed in a mortar and
392 pestle, to which 600 uL of fresh PTB (*N*-phenacylthiazolium bromide) buffer (0.4 mg/mL
393 proteinase K, T2.5 mM PTB, 50 nM dithiothreitol) was added. The sample was then added
394 to 1260 uL of lysis buffer. An additional 600 uL of PTB buffer was used to rinse the mortar
395 and added to the lysis buffer. The individually ground maize kernels were rotated
396 overnight at 37 °C. The remaining DNA extraction followed Swarts et al., 2017[13].
397
398 **Library construction, amplification, and sequence**. DNA extracts were converted to
399 Illumina-compatible paired-end DNA libraries in a clean setting using SMARTer
400 ThurPLEX DNA-seq from Takara Bio and amplified with 7 polymerase chain reactions
401 (PCR) cycles. The generated libraries were cleaned to remove remaining adaptors with
402 AxyPrep Mag beads (Fisher Scientific) and analyzed on a 2100 Bioanalyzer (Agilent

Technologies) to check for quality. The libraries were indexed to facilitate pooling on the NovaSeq SP at the University of Illinois (Urbana-Champaign).

Geographic location map. The geographical coordinates of each sample were obtained from previously published studies, as indicated (Table S1). Utilizing latitude and longitude information, the samples were plotted on a geographic map, resulting in the successful mapping of 17 ancient samples. Geographic data visualization was carried out in R using the ggplot2, sf, leaflet, rnaturalearth, rnaturalearthdata, ggspatial, and rnaturalearthhires packages.

Genome analysis. For the aBM sequence samples data with six libraries, we combined them into a single composite sample, referred to as aBMComb. This was achieved by mapping each individual aBM sequence sample to the B73 V5 soft-masked maize genome and subsequently removing duplicate reads before merging them. We merged the sequence sample to obtain higher coverage for the analysis was needed for this study.

Subsequently, we used MapDamage v.2.2.1[61] verified cytosine deamination profiles consistent with ancient DNA, and estimated the misincorporation frequencies. Based on these results we hard-masked 5′ thymine and 3′ adenine residues within 5nt of the two ends, where deaminations was most concentrated.

Data for 16 ancient samples with specific geographic location information (maize landraces) obtained from previously published work[40, 60, 62] by downloading sequencing from Sequence Read Archive (SRA) (https://www.ncbi.nlm.nih.gov/sra/)[63]. To ensure consistency and accuracy, we downloaded the raw sequence (SRA format) for each sample and converted it into FASTQ format using fastq-dump.

For the archaeological maize samples, adapters were removed and paired reads were merged using AdapterRemoval[64] with parameters --minquality 20 --minlength 30. All 5′ thymine and 3′ adenine residues within 5nt of the two ends were hard-masked, where deamination was most concentrated. Reads were then mapped to soft-masked B73 v5 reference genome using BWA v0.7.17 with disabled seed (-l 1024 -o 0 -E 3) and a quality control threshold (-q 20) based on the recommended parameter[65] to improve ancient DNA mapping. Duplicated reads were removed by GATK tools Picard (https://gatk.broadinstitute.org/hc/en-us). The coverage of each nucleotide position was estimated by bam-readcount (https://github.com/genome/bam-readcount) (Table S2), and the overall coverage of the assembled genome sequence was measured using Qualimap v2.2.1[66].

Variant Calling. We used SequenceTools pileupCaller (v 1.5.4.0; https://github.com/stschiff/sequenceTools) to generate pseudohaploid calls for 17 archaeological maize samples. The commands executed were: samtools mpileup -R -B -q20 -Q20 & pileupCaller -- sampleNames <ancient sample name> randomHaploid --singleStrandMode. This process yielded 16,815,782 single nucleotide polymorphisms (SNPs).

We future filtered the SNPs using estimated information from bam-readcount. SNPs supported by at least two reads were retained for each individual archaeological maize sample. We then combined the filtered SNPs from each sample, keeping only those SNPs that were present in at least one sample. This resulted in a final dataset of 2,808,917 SNPs for the 17 archaeological maize samples.

For all subsequent analyses, the ancient genotype data was merged with the genotype dataset for 394 samples from Grzybowski et al, ("Feb 03, 2023 version files" in Dryad repository: https://doi.org/10.5061/dryad.bnzs7h4f1). The merged dataset included 2,635,047 SNPs from chromosomes 1-10 that were common in both archaeological and modern maize samples, which were used for downstream analysis.

***f3* statistic and phylogenetic analyses**. We created a genotype file by combining 17 archaeological maize and publicly available SNP dataset form Grzybowski et al, resulting in a total of 17-archaeological and 226-modern maize, 88-modern samples of Teosinte *(Zea mays* ssp*. parviglumis)*, 79-modern samples of *Mexicana teosinte (Zea mays* ssp. *mexicana)*, and 1-*Tripsacum* genotypes.

Next, we used plink v1.9[67] to prune for linkage disequilibrium with the parameters --indep-pairwise 50 5 0.1, following previous research[45], to prepare the dataset for Principal Component Analysis (PCA) using "plink -pca". The final results were plotted in R using the ggplot2 package[68].

We calculated the *f3* statistic[69, 70] using the admixr package[71] , which is part of the package of ADMIXTURE software suite[72]. The outgroup f3 statistics was used to measure how closely aBM and each test group are related to each other. The final results were plotted using Python.

A total of 28,588 SNPs present in both aBM and all modern maize, out of a total of 2,626,087 SNPs, was used to build the phylogenetic tree. A maximum likelihood (ML) phylogenetic tree was constructed using SNPhylo[73] with parameter: -v snps.vcf -r -o tripsacum -P tree -b 1000; A Neighbour-Joining (NJ) phylogenetic tree was constructed using VCF2PopTree[74] with the "number of differences" model. Both ML and NJ phylogenies trees were inferred and visualized using FigTree v1.4.4 (http://tree.bio.ed.ac.uk/software/figtree/).

Geographical location prediction. To predict the possible geographical location of aBM, we applied a deep neural network method[39] using only 17 ancient maize samples, as all the archaeological maize clustered in the same cluster. A total of 2,800,190 SNPs were used to predict the possible geographical location of aBM. The command used was: locator.py --vcf SNP_file --sample_data sample_data.txt –out name.

Infer selection on aBM. Due to the lack of archaeological maize with the same genotype as aBM grows outside the influence of Inca culture, it was impossible to directly identify the selection that occurred on aBM under Inca cultural influence. To determine if any of our SNPs are related to known traits, we utilized existing information on SNP-trait

associations[53]. To achieve potential unique selection on aBM, we calculated the allele frequency for each SNPs between aBM and other ancient maize, resulting in allele frequency data for 49,896 SNPs. Of these,18,668 SNPs were unique to aBM. We consulted SNPVersity 2.0 from MaizeGDB[50, 75] and found that 84 of these unique SNPs were classified as "3_prime_UTR_variant" or "5_prime_UTR_variant". These SNPs corresponded to 83 target genes, for which we retrieved Gone Ontology (GO) terms.

Identification of selection sweeps. To detect genomic signatures of recent selective sweeps in modern maize compared to ancient maize groups, SNPs that present in at least two archaeological samples and modern samples were used. We applied the cross-population extended haplotype homozygosity (XP-EHH)[76] method. A commonly used threshold $-\log_{10}(p) = 6$ was set as the cutoff threshold for identifying the signal of significant selection. The regions with -log10(p) >= 6 were designated as candidate sweeps for candidate genes located within 5 KB of these regions identified, following the approach used in previous research[56]. MaizeMine from MaizeGDB[77] was used to obtain putative gene function information.

Data availability

The authors declare that all data supporting the findings of this study are included in the manuscript and its supplementary files or are available from the corresponding author upon request. Source data are provided with this paper. The genome sequence data of ancient Bolivian Maize has been deposited in the NCBI database under BioProject accession PRJNA886637. Custom scripts and single nucleotide polymorphism (SNP) calls are available on Dryad (DOI: https://doi.org/10.5061/dryad.w6m905qtd).

Acknowledgements

We are grateful to all participants who were involved in this project. We are thankful for the support of the Michigan State University Cloud Fellowship for computational skills training. This work was supported in part through computational resources and services provided by the Institute for Cyber-Enabled Research at Michigan State University. We thank Jennifer Wai, University of Chicago, for her help with DNA extraction and library preparation. We also thank Emily Josephs, Michigan State University, and Logan Kistler, Smithsonian Institution of National Museum of Natural History, for their help with the DNA analysis. Thanks to José Capriles Flores for his insightful reading and comments. The MSU Museum provided maize samples and images for documentation and analysis prior to repatriation to Bolivia. Research in the laboratory of Brad Day was supported by the MSU Research Foundation.

References

1. Ranum, P., Pena-Rosas, J.P. & Garcia-Casal, M.N. Global maize production, utilization, and consumption. *Ann N Y Acad Sci* **1312**, 105-112 (2014).

2. Bonavia, D. *Maize : origin, domestication, and its role in the development of culture*. (Cambridge University Press, Cambridge, NY; 2013).
3. Chavez, S.J.a.R.G.T. Early Maize on the Copacabana Peninsula: Implications for the Archaeology Introduction. *Histories of Maize*, pp. 415-428 (2006).
4. Hastorf, C., Whitehead, W., Bruno, M. & Wright, M. The Movements of Maize into Middle Horizon Tiwanaku, Bolivia Introduction. *Histories of Maize*, pp. 429-448. (2006).
5. Suca Gómez, A. Caracterizacion de granos de maiz andino(Zea mays L.) de colectas de germoplasma en la Facultad de Agronomia -UMSA. *Trabajo dirigido para optar por el título de licenciado en Ingeniería Agronómica.* (2011).
6. Doebley, J. The genetics of maize evolution. *Annu Rev Genet* **38**, 37-59 (2004).
7. Matsuoka, Y. *et al.* A single domestication for maize shown by multilocus microsatellite genotyping. *Proc Natl Acad Sci U S A* **99**, 6080-6084 (2002).
8. Grobman, A. *et al.* Preceramic maize from Paredones and Huaca Prieta, Peru. *Proc Natl Acad Sci U S A* **109**, 1755-1759 (2012).
9. Lombardo, U. *et al.* Early Holocene crop cultivation and landscape modification in Amazonia. *Nature* **581**, 190-193 (2020).
10. Hart, J.P. & Lovis, W.A. Reevaluating What We Know About the Histories of Maize in Northeastern North America: A Review of Current Evidence. *Journal of Archaeological Research* **21**, 175-216 (2013).
11. Hufford, M.B. *et al.* The genomic signature of crop-wild introgression in maize. *PLoS Genet* **9**, e1003477 (2013).
12. Rebourg, C. *et al.* Maize introduction into Europe: the history reviewed in the light of molecular data. *Theor Appl Genet* **106**, 895-903 (2003).
13. Swarts, K. *et al.* Genomic estimation of complex traits reveals ancient maize adaptation to temperate North America. *Science* **357**, 512-515 (2017).
14. Bellon, M.R. The dynamics of crop infraspecific diversity: A conceptual framework at the farmer level. *Econ Bot* **50**, 26-39 (1996).
15. Knapp, G. Changing fortunes: Biodiversity and peasant livelihood in the Peruvian Andes. *Geogr Rev* **87**, 568-570 (1997).
16. Louette, D. & Smale, M. Farmers' seed selection practices and traditional maize varieties in Cuzalapa, Mexico. *Euphytica* **113**, 25-41 (2000).
17. Mintz, S.W. *Sweetness and power : the place of sugar in modern history*. (Viking, New York, N.Y.; 1985).
18. Bray, T.L. Inka pottery as culinary equipment: Food, fasting, and gender in imperial state design. *Lat Am Antiq* **14**, 3-28 (2003).
19. Ceruti, M.C. Frozen Mummies from Andean Mountaintop Shrines: Bioarchaeology and Ethnohistory of Inca Human Sacrifice. *Biomed Res Int* **2015**, 439428 (2015).
20. Burger, R.L. & Vandermerwe, N.J. Maize and the Origin of Highland Chavin Civilization - an Isotopic Perspective. *Am Anthropol* **92**, 85-95 (1990).
21. Doutriaux, M. Power, ideology and ritual: the practice of agriculture in the Inca Empire. *Pap Kroeber Anthropol Soc*, 91-108 (2001).
22. Cobo, B. & Hamilton, R. *Inca religion and customs*, Edn. 1st. (University of Texas Press, Austin; 1990).
23. Pearsall, D.M. Phytolith analysis of archeological soils: evidence for maize cultivation in formative ecuador. *Science* **199**, 177-178 (1978).

24. Lovis, W.A., J. M. Capriles & D. Trigo Rodríguez La repatriación de una momia andina del Museo de la Universidad Estatal de Michigan al Estado Plurinacional de Bolivia. *Textos Antropológicos* **21(1):23-41** (2023).
25. Lovis, W.A. A Mummy Returns Home. *MSU Today, MSU 360, Faculty Voice* (2019).
26. Hogg, A.G. *et al.* SHCal20 Southern Hemisphere Calibration, 0–55,000 Years cal BP. *Radiocarbon* **62**, 759-778 (2020).
27. Handt, O., Krings, M., Ward, R.H. & Paabo, S. The retrieval of ancient human DNA sequences. *Am J Hum Genet* **59**, 368-376 (1996).
28. Krings, M. *et al.* Neandertal DNA sequences and the origin of modern humans. *Cell* **90**, 19-30 (1997).
29. Hansen, A., Willerslev, E., Wiuf, C., Mourier, T. & Arctander, P. Statistical evidence for miscoding lesions in ancient DNA templates. *Mol Biol Evol* **18**, 262-265 (2001).
30. Gilbert, M.T. *et al.* Characterization of genetic miscoding lesions caused by postmortem damage. *Am J Hum Genet* **72**, 48-61 (2003).
31. Dabney, J., Meyer, M. & Paabo, S. Ancient DNA damage. *Cold Spring Harb Perspect Biol* **5** (2013).
32. Briggs, A.W. *et al.* Patterns of damage in genomic DNA sequences from a Neandertal. *Proc Natl Acad Sci U S A* **104**, 14616-14621 (2007).
33. Stiller, M. *et al.* Patterns of nucleotide misincorporations during enzymatic amplification and direct large-scale sequencing of ancient DNA. *Proc Natl Acad Sci U S A* **103**, 13578-13584 (2006).
34. Paabo, S. Ancient DNA: extraction, characterization, molecular cloning, and enzymatic amplification. *Proc Natl Acad Sci U S A* **86**, 1939-1943 (1989).
35. Prufer, K. *et al.* Computational challenges in the analysis of ancient DNA. *Genome Biol* **11**, R47 (2010).
36. Wilson, A.S. *et al.* Stable isotope and DNA evidence for ritual sequences in Inca child sacrifice. *Proc Natl Acad Sci U S A* **104**, 16456-16461 (2007).
37. D'Altroy, T.N. The Incas, (Malden, Mass. : Blackwell, Blackwell Publishing; 2003).
38. Wilson, D.J. *Indigenous South Americans of the Past and Present: An Ecological Perspective*. (Westview Press; 1999).
39. Battey, C.J., Ralph, P.L. & Kern, A.D. Predicting geographic location from genetic variation with deep neural networks. *Elife* **9** (2020).
40. Kistler, L. *et al.* Multiproxy evidence highlights a complex evolutionary legacy of maize in South America. *Science* **362**, 1309-1313 (2018).
41. Vallebueno-Estrada, M. *et al.* Correction: Domestication and lowland adaptation of coastal preceramic maize from Paredones, Peru. *Elife* **12** (2023).
42. CooK, O.F. Peru as a Center of Domestication: Tracing the Origin of Civilization through the Domesticated Plants. *Journal of Heredity* **16**, 95-110 (1925).
43. Wang, L. *et al.* Molecular Parallelism Underlies Convergent Highland Adaptation of Maize Landraces. *Mol Biol Evol* **38**, 3567-3580 (2021).
44. Dillehay, T.D. *et al.* Monte Verde: seaweed, food, medicine, and the peopling of South America. *Science* **320**, 784-786 (2008).
45. van Heerwaarden, J. *et al.* Genetic signals of origin, spread, and introgression in a large sample of maize landraces. *Proc Natl Acad Sci U S A* **108**, 1088-1092 (2011).
46. Mercer, K., Martinez-Vasquez, A. & Perales, H.R. Asymmetrical local adaptation of maize landraces along an altitudinal gradient. *Evol Appl* **1**, 489-500 (2008).

631 47. Haberer, G. *et al.* European maize genomes highlight intraspecies variation in repeat and
632 gene content. *Nat Genet* **52**, 950-957 (2020).
633 48. Tenaillon, M.I. & Charcosset, A. A European perspective on maize history. *C R Biol* **334**,
634 221-228 (2011).
635 49. Cerda-Hurtado, I.M. *et al.* Climatic adaptation and ecological descriptors of wild beans
636 from Mexico. *Ecol Evol* **8**, 6492-6504 (2018).
637 50. Grzybowski, M.W. *et al.* A common resequencing-based genetic marker data set for global
638 maize diversity. *Plant J* **113**, 1109-1121 (2023).
639 51. Chakradhar, T., Hindu, V. & Reddy, P.S. Genomic-based-breeding tools for tropical maize
640 improvement. *Genetica* **145**, 525-539 (2017).
641 52. Menkir, A. *et al.* Approaches and progress in breeding drought-tolerant maize hybrids for
642 tropical lowlands in west and central Africa. *Plant Genome* **17**, e20437 (2024).
643 53. Wallace, J.G. *et al.* Association mapping across numerous traits reveals patterns of
644 functional variation in maize. *PLoS Genet* **10**, e1004845 (2014).
645 54. Doebley, J. & Stec, A. Genetic analysis of the morphological differences between maize
646 and teosinte. *Genetics* **129**, 285-295 (1991).
647 55. Lukens Ln, D.J. Epistatic and environmental interactions for quantitative trait loci involved
648 in maize evolution. *Genetical Research* **74(3):291-302** (1999).
649 56. Brodie, A., Azaria, J.R. & Ofran, Y. How far from the SNP may the causative genes be?
650 *Nucleic Acids Res* **44**, 6046-6054 (2016).
651 57. Yang, X. & Tucker, M.R. Establishing a regulatory blueprint for ovule number and
652 function during plant development. *Curr Opin Plant Biol* **63**, 102095 (2021).
653 58. Galluzzi, G., Seyoum, A., Halewood, M., Lopez Noriega, I. & Welch, E.W. The Role of
654 Genetic Resources in Breeding for Climate Change: The Case of Public Breeding
655 Programmes in Eighteen Developing Countries. *Plants (Basel)* **9** (2020).
656 59. Kim, K.H. & Lee, B.M. Effects of Climate Change and Drought Tolerance on Maize
657 Growth. *Plants (Basel)* **12** (2023).
658 60. Kistler, L. *et al.* Archaeological Central American maize genomes suggest ancient gene
659 flow from South America. *Proc Natl Acad Sci U S A* **117**, 33124-33129 (2020).
660 61. Jonsson, H., Ginolhac, A., Schubert, M., Johnson, P.L. & Orlando, L. mapDamage2.0: fast
661 approximate Bayesian estimates of ancient DNA damage parameters. *Bioinformatics* **29**,
662 1682-1684 (2013).
663 62. Vallebueno-Estrada, M. *et al.* The earliest maize from San Marcos Tehuacan is a partial
664 domesticate with genomic evidence of inbreeding. *Proc Natl Acad Sci U S A* **113**, 14151-
665 14156 (2016).
666 63. Chia, J.M. *et al.* Maize HapMap2 identifies extant variation from a genome in flux. *Nat*
667 *Genet* **44**, 803-807 (2012).
668 64. Lindgreen, S. AdapterRemoval: easy cleaning of next-generation sequencing reads. *BMC*
669 *Res Notes* **5**, 337 (2012).
670 65. Schubert, M. *et al.* Improving ancient DNA read mapping against modern reference
671 genomes. *BMC Genomics* **13**, 178 (2012).
672 66. Okonechnikov, K., Conesa, A. & Garcia-Alcalde, F. Qualimap 2: advanced multi-sample
673 quality control for high-throughput sequencing data. *Bioinformatics* **32**, 292-294 (2016).
674 67. Purcell, S. *et al.* PLINK: a tool set for whole-genome association and population-based
675 linkage analyses. *Am J Hum Genet* **81**, 559-575 (2007).
676 68. Wickham, H. *Ggplot2 : elegant graphics for data analysis*. (Springer, New York; 2009).

69. Green, R.E. *et al.* A draft sequence of the Neandertal genome. *Science* **328**, 710-722 (2010).
70. Durand, E.Y., Patterson, N., Reich, D. & Slatkin, M. Testing for Ancient Admixture between Closely Related Populations. *Molecular Biology and Evolution* **28**, 2239-2252 (2011).
71. Petr, M., Vernot, B. & Kelso, J. admixr-R package for reproducible analyses using ADMIXTOOLS. *Bioinformatics* **35**, 3194-3195 (2019).
72. Alexander, D.H. & Lange, K. Enhancements to the ADMIXTURE algorithm for individual ancestry estimation. *BMC Bioinformatics* **12**, 246 (2011).
73. Lee, T.H., Guo, H., Wang, X., Kim, C. & Paterson, A.H. SNPhylo: a pipeline to construct a phylogenetic tree from huge SNP data. *BMC Genomics* **15**, 162 (2014).
74. Subramanian, S., Ramasamy, U. & Chen, D. VCF2PopTree: a client-side software to construct population phylogeny from genome-wide SNPs. *PeerJ* **7**, e8213 (2019).
75. Schnable, P.S. *et al.* The B73 maize genome: complexity, diversity, and dynamics. *Science* **326**, 1112-1115 (2009).
76. Sabeti, P.C. *et al.* Genome-wide detection and characterization of positive selection in human populations. *Nature* **449**, 913-918 (2007).
77. Lawrence, C.J., Dong, Q., Polacco, M.L., Seigfried, T.E. & Brendel, V. MaizeGDB, the community database for maize genetics and genomics. *Nucleic Acids Res* **32**, D393-397 (2004).

Figures and Tables

Fig.1. Location and appearance of archaeological Bolivian maize (aBM). a Map of maize sample collection and location information. b Photographs of kernels showing morphological characteristics.

Fig. 2. Admixture f3-statistics. In the form f3 (aBM; Test, tripsacum) where Test represents archaeological and modern samples.

Fig. 3. Predicted geographic location of archaeological Bolivian maize (aBM). The blue point is the predicted locations of aBM based on the SNPs from all archaeological maize. The pink points are the archaeological samples.

Fig. 4. Principal Component Analysis (PCA) of nuclear genomic data from archaeological and modern maize. Samples with greater affinity to one another cluster closer together. Samples with the same color and shape indicate they came from the same country.

Fig. 5. Genome-wide distribution of ancient maize specific selective sweeps. a Signal of selection of modern maize compared to archaeological maize population. Each point indicates a SNP. The blue horizontal line shows the genome-wide significance level ($p=1 \times 10^{-6}$).

Fig. S1. Ancient DNA (aDNA) damage pattern of archaeological Bolivian maize (aBM). a Cytosine deamination damage patterns for the combined bam file of six aBM sequence samples and individual six aBM sequence samples. The position specific substitutions from the 5' end (red) and the 3' end (green) of a read. The red line corresponds to C to T substitutions, the green line corresponds to G to A substitutions, and the blue line represents other types of substitutions. b Ancient DNA damage profile. The four upper plots show the base frequencies inside and outside of a read, where the open grey box corresponds to a read. The two lower plots show the position specific substitutions from the 5' end and the 3' end of a read. The red line corresponds to C to T substitutions, the blue line corresponds to G to A substitutions, and the fade line represents other types of substitutions.

Fig. S2. Archaeological Bolivian maize (aBM) DNA read length. a Read length distribution of combined aBM bam files prior to hard-masked 5′ thymine and 3′ adenine residues within 5nt of both ends.

Fig. S3. Phylogenetic trees of archaeological Bolivian maize (aBM). a Neighbour-Joining tree with VCF2Pop. b Maximum likelihood (ML) tree with SNPhylo. Parv (*Zea mays* ssp. *parviglumis*), Zmex (*Zea mays* ssp. *mexicana*), Europe (modern Europe), SweetC (model sweet corn), Ztrol (modern Tropical maize), mMexico (modern Mexico), mParaguay (modern Paraguay), mBrazil (modern Brazil), mPeru (modern Peru), mEcuador (modern Ecuador), mGuatemala (modern Guatemala), and mColombia (modern Colombia). Black color is Tripsacum. Red color is the aBM. Red brown color is modern maize (*Zea mays ssp. mays L.*). Green color is Teosinte (*Zea mays ssp. parviglumis*). Blue color is Mexicana teosinte (*Zea mays ssp. mexicana*).

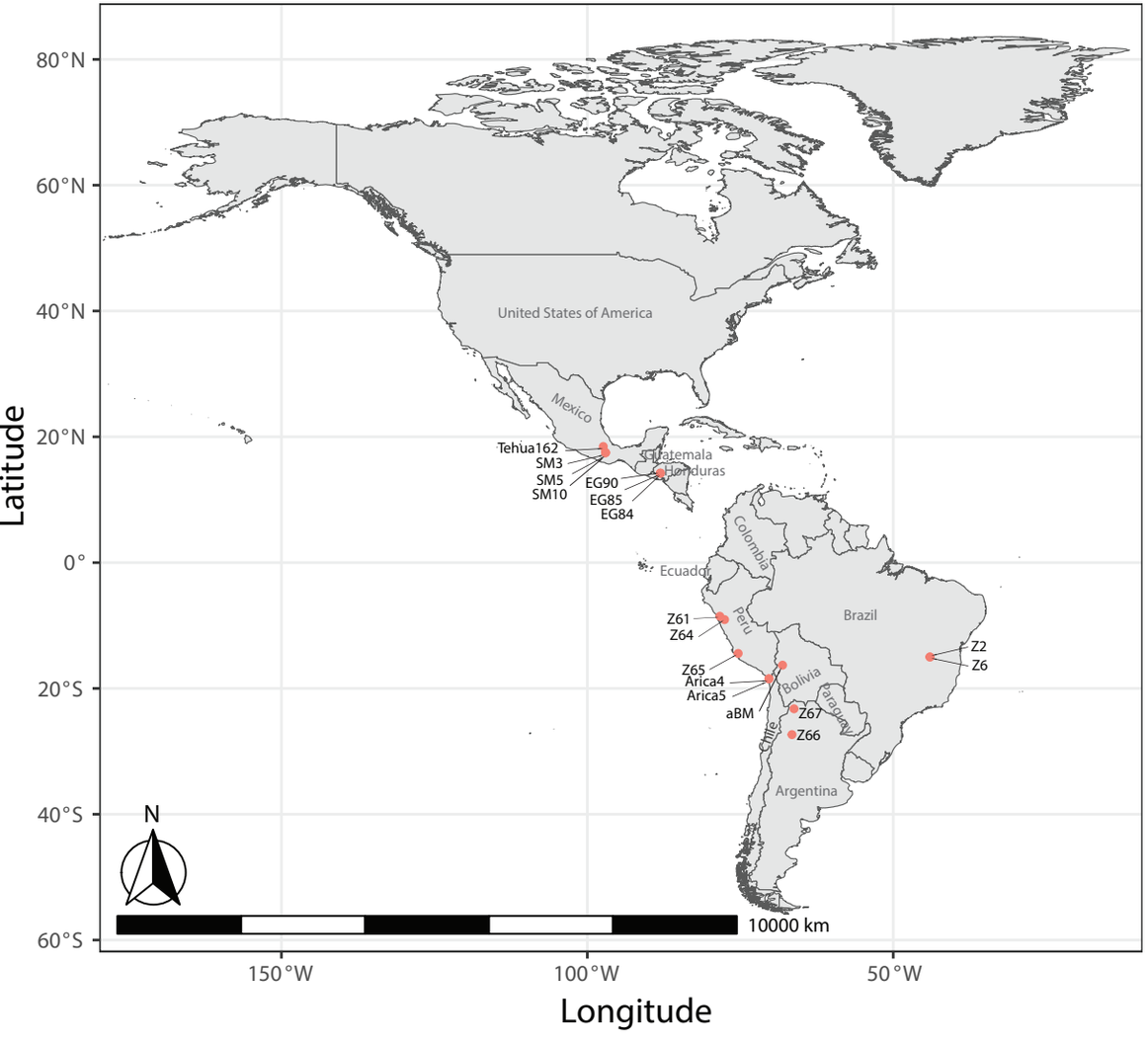
Fig. S4. Q-Q plot for genome-wide selection in modern maize compared to archaeological maize. The Q-Q plot between modern and archaeological maize. Each point indicates a value from expected and observed. Red line represents the expected distribution of the p-value, while the blue trend represents the observed distribution.

Table S1. Geographical information of the archaeological maize samples used in this study.

Table S2: Paleogenomic characterization of archaeological Bolivian maize sequence samples with six libraries.

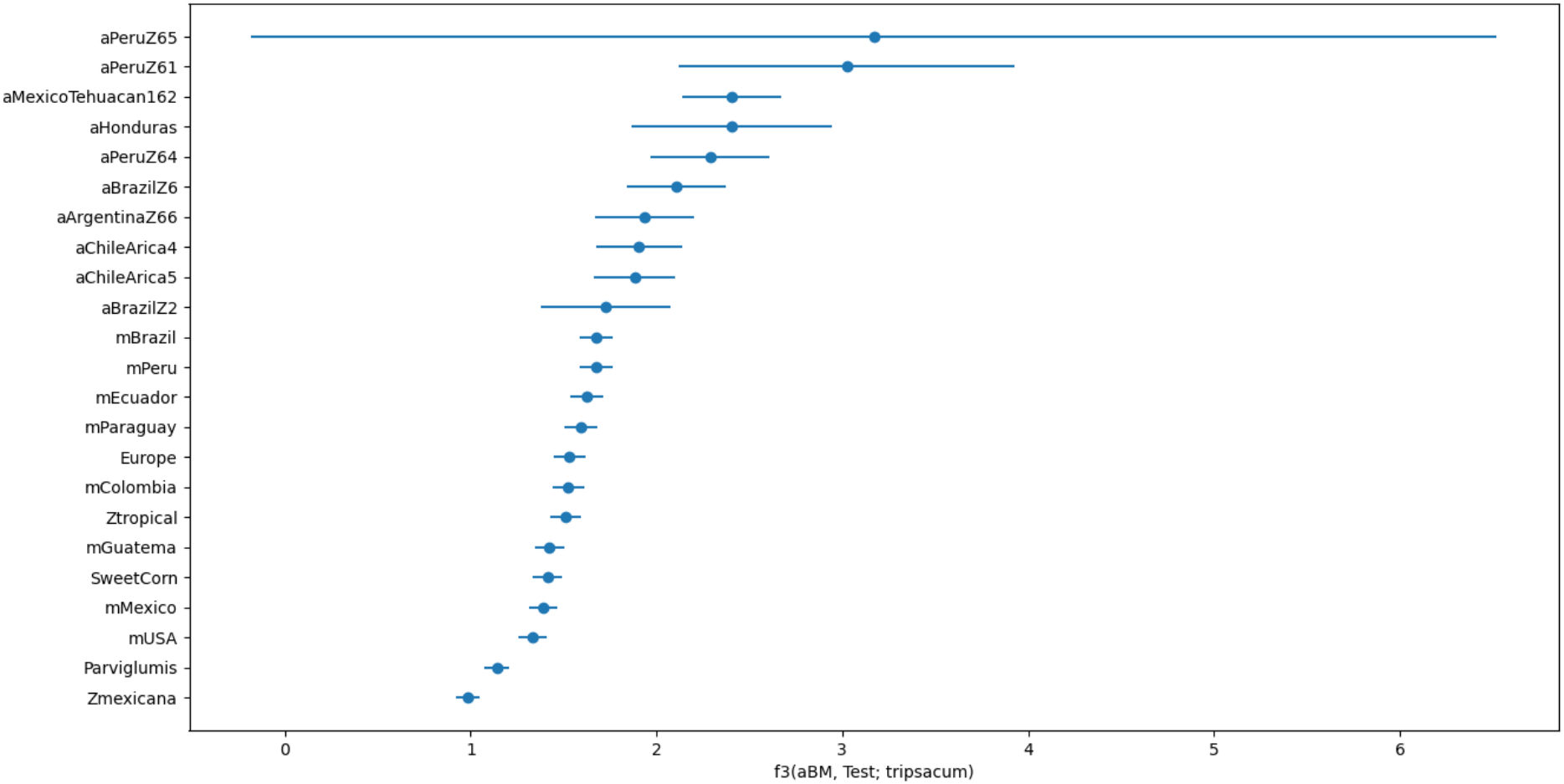
Table S3. The percentage of genomic sites covered at variable depths in the archaeological Bolivian maize (aBM) sample (aBMComb_rm5nt.rmDR.bam).

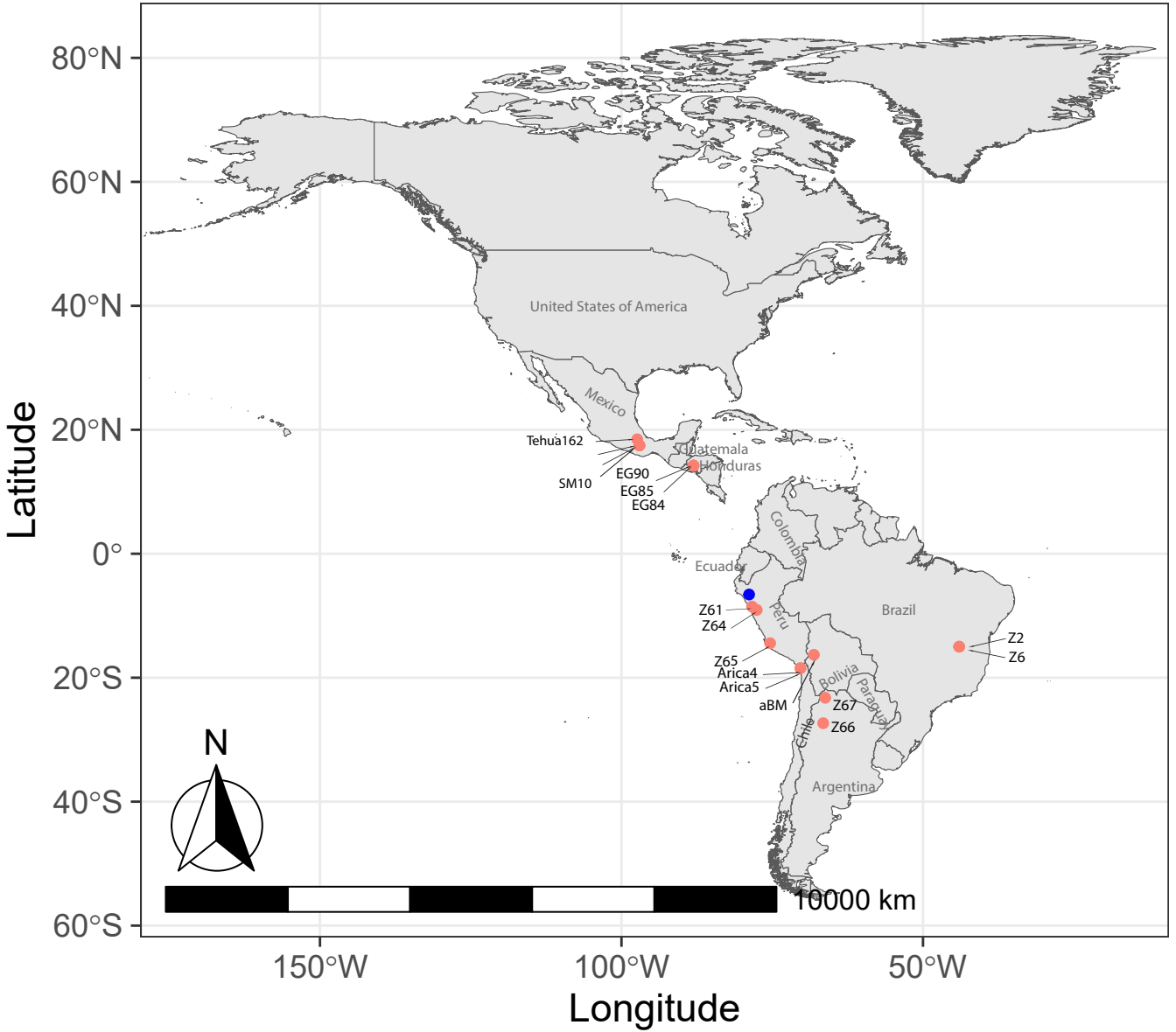
a

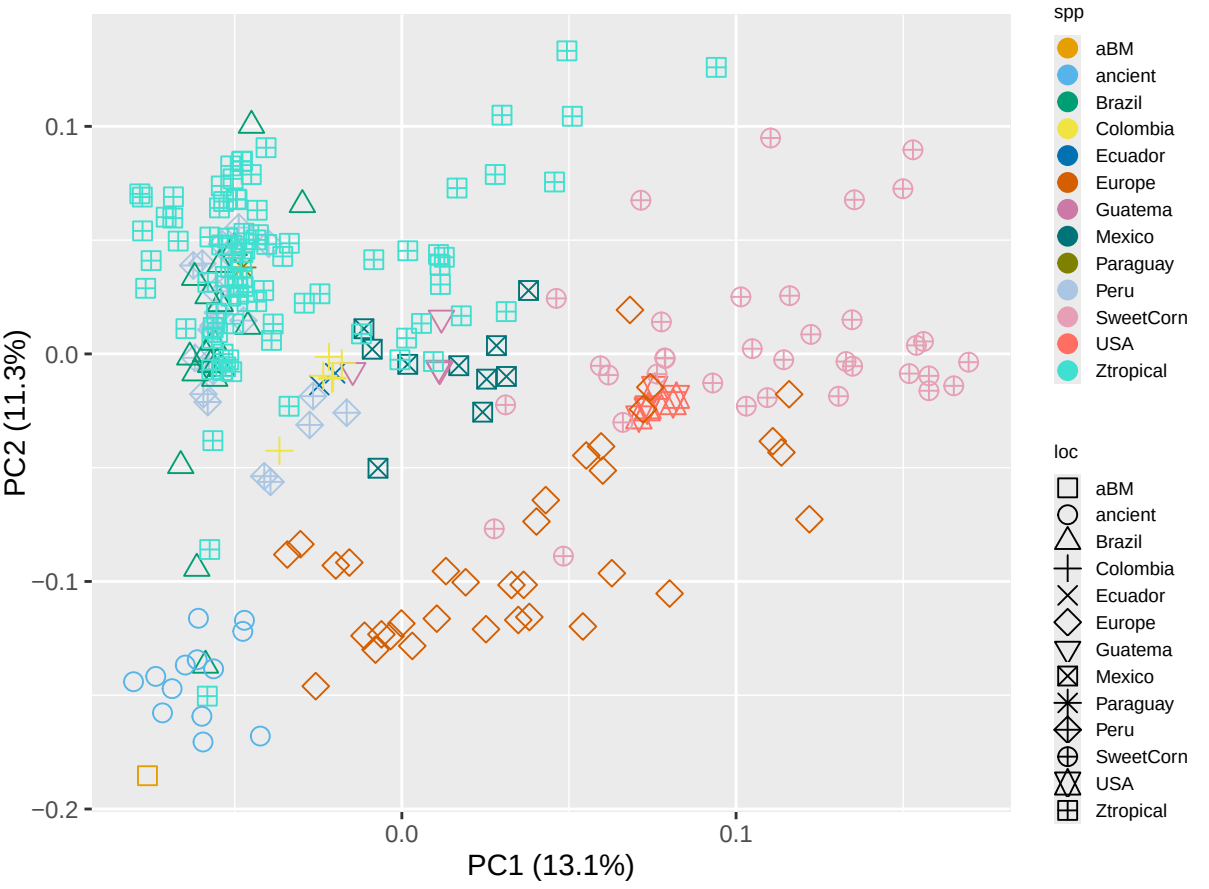

80°N
60°N
40°N
20°N
0°
20°S
40°S
60°S
Latitude
150°W
100°W
50°W
Longitude
United States of America
Mexico
Guatemala
Honduras
Tehua162
SM3
SM5
SM10
EG90
EG85
EG84
Colombia
Ecuador
Peru
Brazil
Z61
Z64
Z65
Arica4
Arica5
aBM
Bolivia
Paraguay
Chile
Z67
Z66
Z2
Z6
Argentina
N
10000 km

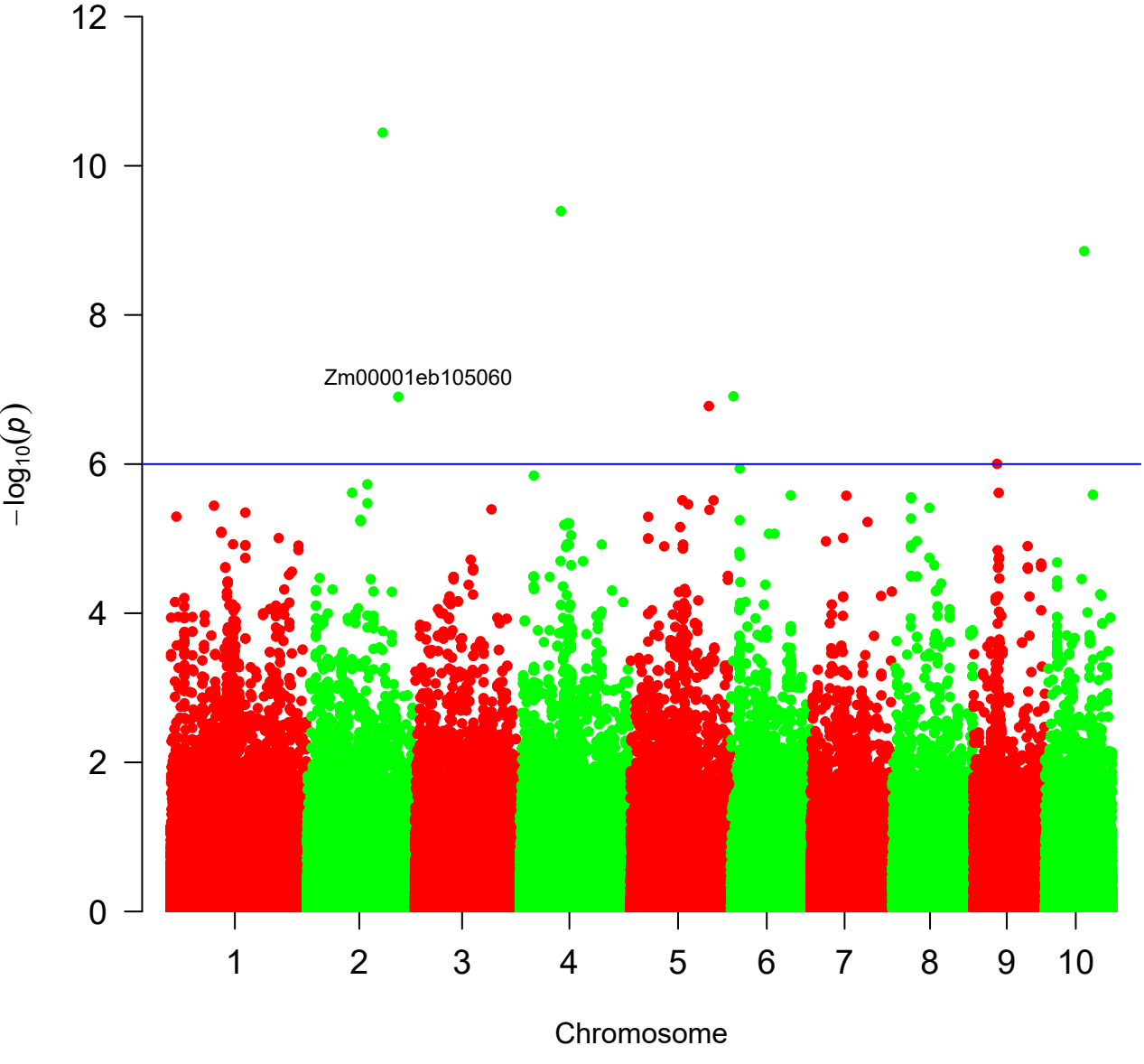
b

10
cm


aPeruZ65
aPeruZ61
aMexicoTehuacan162
aHonduras
aPeruZ64
aBrazilZ6
aArgentinaZ66
aChileArica4
aChileArica5
aBrazilZ2
mBrazil
mPeru
mEcuador
mParaguay
Europe
mColombia
Ztropical
mGuatema
SweetCorn
mMexico
mUSA
Parviglumis
Zmexicana
0
1
2
3
4
5
6
f3(aBM, Test; tripsacum)


80°N
60°N
40°N
20°N
0°
20°S
40°S
60°S
Latitude
150°W
100°W
50°W
Longitude
United States of America
Mexico
Guatemala
Honduras
Colombia
Ecuador
Peru
Brazil
Bolivia
Paraguay
Chile
Argentina
Tehua162
SM10
EG90
EG85
EG84
Z61
Z64
Z65
Arica4
Arica5
aBM
Z67
Z66
Z2
Z6
N
10000 km


spp
aBM
ancient
Brazil
Colombia
Ecuador
Europe
Guatema
Mexico
Paraguay
Peru
SweetCorn
USA
Ztropical
loc
aBM
ancient
Brazil
Colombia
Ecuador
Europe
Guatema
Mexico
Paraguay
Peru
SweetCorn
USA
Ztropical
0.1
0.0
−0.1
−0.2
PC2 (11.3%)
0.0
0.1
PC1 (13.1%)


12
10
8
6
4
2
0
$-\log_{10}(p)$
Zm00001eb105060
1
2
3
4
5
6
7
8
9
10
Chromosome