

## ANCIENT DNA

# Genomic estimation of complex traits reveals ancient maize adaptation to temperate North America

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By 4000 years ago, people had introduced maize to the southwestern United States; full agriculture was established quickly in the lowland deserts but delayed in the temperate highlands for 2000 years. We test if the earliest upland maize was adapted for early flowering, a characteristic of modern temperate maize. We sequenced fifteen 1900-year-old maize cobs from Turkey Pen Shelter in the temperate Southwest. Indirectly validated genomic models predicted that Turkey Pen maize was marginally adapted with respect to flowering, as well as short, tillering, and segregating for yellow kernel color. Temperate adaptation drove modern population differentiation and was selected in situ from ancient standing variation. Validated prediction of polygenic traits improves our understanding of ancient phenotypes and the dynamics of environmental adaptation.

The temperate U.S. maize landraces known as “Northern Flints” are one of two maize germ plasm pools that contributed to the development of the agronomically dominant Cornbelt Dent of the United States (1) and were also critical for adapting maize to Europe (2). Morphological similarity (3) and early genetic evidence (4, 5) support the origin of the Northern Flints in the southwestern United States. The environmentally diverse Southwest region sits just above the geographically constricted North American tropics and is the first point where pre-Hispanic maize agriculturalists would have had to contend with greatly reduced growing seasons. Maize in the southwestern United States today is culturally important to indigenous peoples (6), reflected in its morphologic and genetic diversity (7).

Maize was introduced to the Southwest from Mexico by 4000 years before the present (yr B.P.) (Fig. 1A), a finding supported by evidence from both the temperate highlands of the Colorado Plateau and the lowland deserts of southern Arizona (8–12); a recent study suggests an inland, rather than coastal, Mexican route (13). Despite evidence of experimentation with maize in the highlands (10–12, 14), maize agriculture was not fully adopted as a primary subsistence system until between 2400 and 1800 yr B.P. (14). By contrast, soon after

introduction, peoples in the southern lowlands rapidly committed to maize agriculture (8, 9). This notable temporal difference between highland and lowland adoption may result from insufficient adaptation (15).

Growing degree days (GDD) are used as a measure of maize development, normalizing heat accumulation across environments. For example, Blanding, Utah (temperate plateau), is geographically and altitudinally near early temperate sites with archaeological maize and has only 46% of the available GDD for maize growth relative to the Tucson basin (desert lowland), 725 km distant [(16); Fig. 1A]. To extend the growing season, farmers developed agronomic practices to exploit substantial microsite variation over time (6, 17). However, temperate adaptation in modern maize is characterized by early flowering (Fig. 1B); we suspect that the delay in full agricultural adoption in the uplands was due to a lack of adaptation to temperate environments (15) in the earliest introduced germ plasm and that agricultural adoption in the uplands transitioned with the introduction of early flowering varieties.

Turkey Pen Shelter (TPS) is a dry-cave shelter on the edge of Grand Gulch in temperate southwestern Utah (40 km from and at a similar elevation,

1830 m, to Blanding weather stations); it has evidence for established agriculture and was occupied 1800 to 2000 years ago during agricultural intensification in the uplands (16, 18). We assessed the degree of temperate adaptation in early maize agriculture by predicting days to flowering on the basis of the genotypes of archaeological TPS maize from a modern inbred panel representing a global collection of 2648 inbred lines held in Ames, Iowa [henceforth Ames Inbred Diversity (AID) panel]. Because ancient samples cannot be directly phenotyped, we validated predictions on a modern landrace panel from the southwestern United States. Genotypes of modern landraces and TPS maize were then used to refine the demographic history of maize in the Americas.

Preservation of genetic material in TPS maize was excellent—10 of the 21 samples contained >80% endogenous maize DNA (Fig. 1C, fig. S1, and table S1). Shallow sequencing of unrepaired libraries showed damage patterns typical of ancient DNA (fig. S1) (19). Subsequently, we prepared repaired DNA libraries for 15 samples with >20% endogenous DNA; whole-genome resequencing resulted in 5 to 20× coverage (fig. S1). All samples pursued for deep sequencing were dated with a median probability date of 1844 yr B.P. [(16); Fig. 1C]. We called single-nucleotide polymorphisms (SNPs) on the 81 million maize variants discovered as part of Hapmap3.21 (20), with an average SNP coverage of 0.55 ± 0.16 (table S1).

Days to flowering in maize is a complex, additively inherited trait (21) critical for temperate adaptation (21, 22). We generated flowering predictions for TPS and a subset of the landraces representing 80 southwestern landrace accessions, phenotyped with three replicates in three environments [Fig. 2, A and B, fig. S2, and tables S2 to S4; (16)]. Maize is monoecious but has imperfect flowers, and flowering time was phenotyped by measuring both female flowering, as days to silking (DTS), and male flowering, as days to anthesis (DTA). Broad-sense heritability was 0.90 for DTS and 0.89 for DTA in the landrace panel (see fig. S2 for correlations across environments). Predictions with the genomic best linear unbiased predictor method were generated from the AID panel (23), with good cross-predictive ability in the phenotyped landrace panel (fig. S3) (prediction accuracy 0.72) (Fig. 2A and figs. S4 and S5). Although, the accuracies of predictions for TPS from AID cannot be evaluated directly, we assume similar accuracy to the modern landrace panel, which covers the parameter space of tropical- and temperate-adapted landraces in the southwestern United States (Fig. 2B and table S2).

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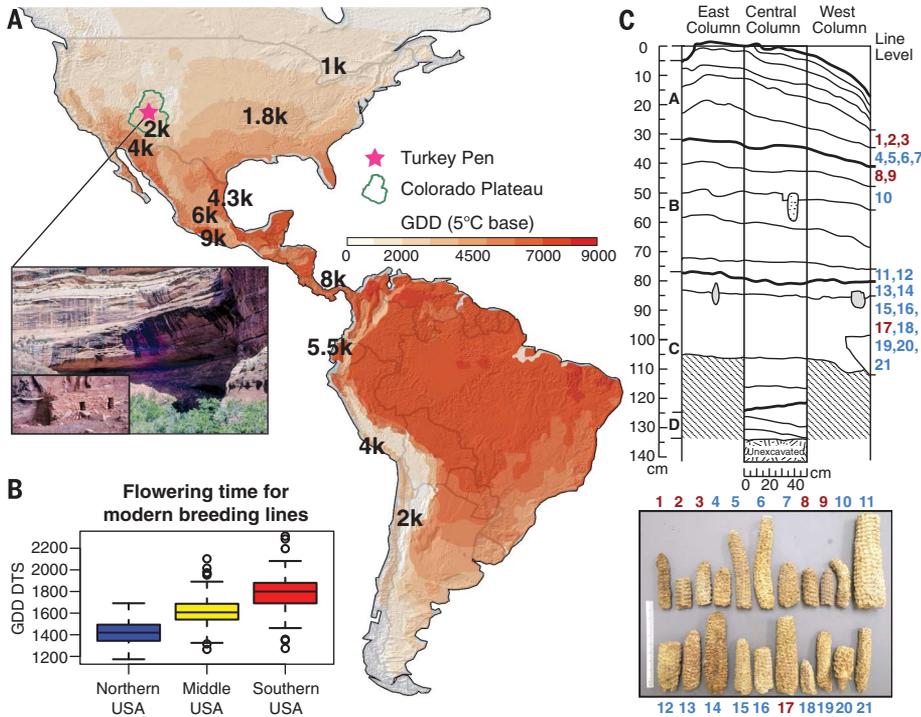
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TPS is located in the northern part of the Puebloan region of the Southwest, which is inhabited by the modern descendants of TPS. Predicted values for TPS from the AID panel were not significantly different than Puebloan predictions based on Wilcoxon rank-sum test and were one week earlier on average (although not significantly) than the desert-adapted southwestern samples (Fig. 2A, figs. S4 and S5, and table S4).

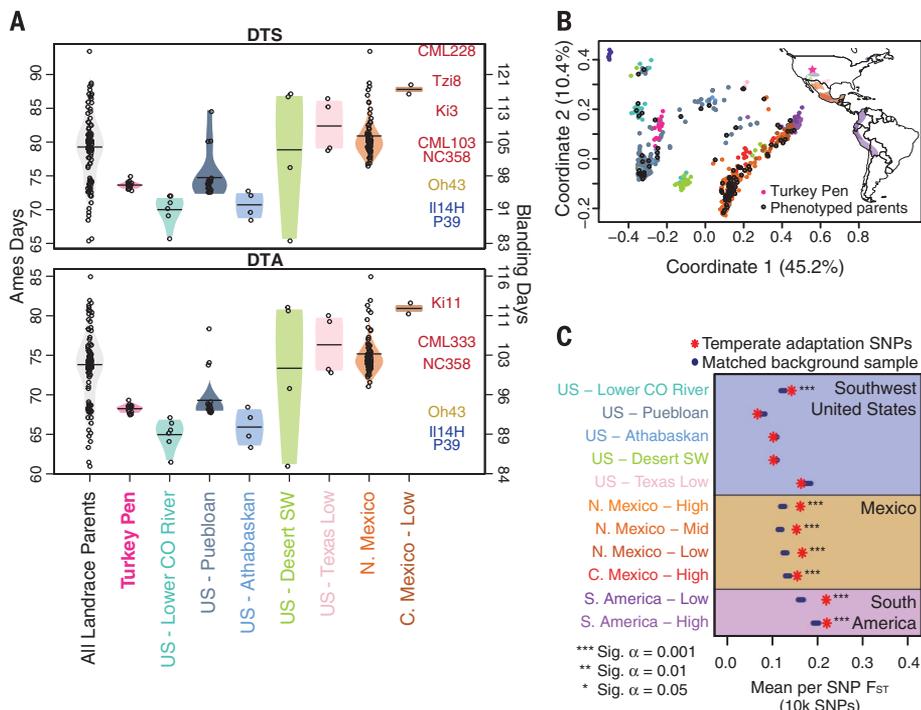
Although TPS individuals were predicted to flower at a time similar to that of most modern temperate inbred lines, they flower later than Northern Flint sweet corn inbred lines, the earliest flowering modern maize. Mean female flowering for TPS was predicted as 73.6 days from the AID panel. This prediction, situated in Blanding, Utah, translates to 96 days by means of GDD conversion (16). Assuming 55 days to physiological maturity (24),

TPS maize would take 151 days from planting to full physiological maturity. At 149 average frost-free days (25), TPS maize was therefore likely marginally adapted and, in some years, may have been harvested and had cobs dried off the plant to avoid frost.

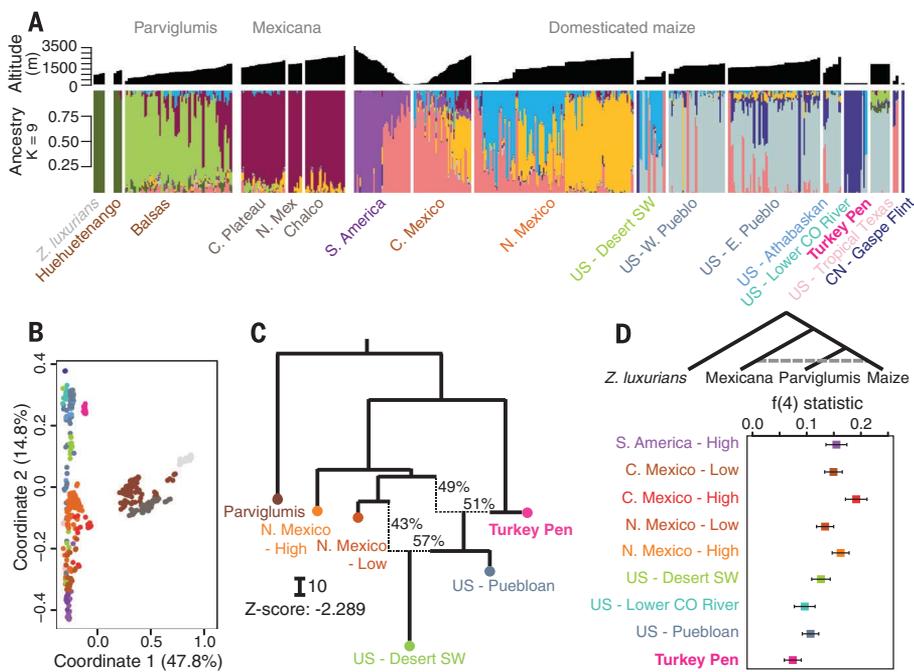
We also carried out prediction of two complex traits—height and tillering. As validated in two environments of the modern landrace population



**Fig. 1. Climatic and archaeological context of Turkey Pen Shelter (TPS).** (A) Modeled GDD (base 5°C) used by permission of the Center for Sustainability and the Global Environment, Nelson Institute for Environmental Studies, University of Wisconsin–Madison. Numbers in bold represent rough early dates for establishment of maize agriculture (not the first appearance) in yr B.P. TPS is located on the Colorado Plateau (~1500 m in altitude) in southeast Utah; see inset photographs. (B) Flowering time (GDD to silking) from inbred germ plasm in the AID panel generated from public breeding programs (23). Mean regional differences in flowering time are significant at  $\alpha = 0.001$  (Student's *t* test). (C) Stratigraphy taken from the central, unexcavated column of the midden; TPS samples were removed from the surrounding columns at the levels indicated. Photograph shows corncob specimens tested for sequencing (scale at 10 cm). Red numbers indicate samples with less than 20% endogenous maize DNA, which were not further pursued; blue numbers indicate samples that were deeply sequenced and radiocarbon dated. The mean calibrated radiocarbon age of samples 4 to 7 was  $1864 \pm 11$  calibrated radiocarbon yr B.P. and, for samples 15 to 21,  $1882 \pm 8$  yr B.P.



**Fig. 2. Days to flowering predictions in TPS maize.** (A) Predicted flowering for TPS and phenotyped southwestern landraces (tables S2 and S3). Predictive ability was 0.68 for both DTA and DTS, and prediction accuracy was 0.72. The left and right y axes show flowering time from the AID panel and corrected flowering time by means of GDD for Blanding, Utah, respectively. Labels at the right of the violin plots denote flowering time of inbred maize nested association mapping lines; the colors represent Northern Flint (blue), temperate (yellow), and tropical (red). (B) Genetic relationships modeled with the first two multidimensional scaling coordinates (fraction of variance shown in parentheses) of the landrace parent hybrid population used to validate predictions in TPS. (C) Comparison of  $F_{ST}$  values between TPS and modern landraces within high- $F_{ST}$  temperate-adaptation loci (red asterisk) and randomly sampled genomic background (overlapping blue points).  $F_{ST}$  values to TPS in temperate-adaptation loci for modern southwestern populations (except the lower Colorado River) are not significantly greater than background relatedness but are significantly greater for all other populations.



**Fig. 3. Relationship of TPS maize to modern landraces.** (A) Admixture analysis for maize and teosinte ordered by species/population and elevation (lowest error  $K = 9$ ; fig. S16). TPS is modeled with the dominant Puebloan component, with minor contributions from teosinte, specific to TPS among domesticated maize. Modern temperate southwestern U.S. samples include minor northern Mexican components. (B) MDS coordinates separate teosintes from domesticated maize and separate maize populations according to geography. (C) Best z-score five-population admixture graph (fig. S14) with Parviglumis as the outgroup. Continuous lines are scaled according to  $f(2)$  values (representing shared drift), and dotted lines illustrate admixture events, with estimated proportions shown above. Modern southwestern U.S. landraces are the result of admixture between TPS and ancestral northern Mexican populations. (D)  $f(4)$  statistics test analysis of four populations (Luxurians, Mexicana, Parviglumis, Test population) for Mexicana introgression into the landrace core populations (fig. S11). Values of  $f(4)$  for all populations are significantly different from zero (bars represent 2 standard errors based on block-jackknifing), which indicates introgression. All populations south of the modern United States have significantly more introgression than the U.S. samples, except the intermediate Desert Southwest.

and predicted by AID, TPS was relatively short, comparable to the median predictions for modern Puebloan landraces (fig. S6). TPS also was bushy and predicted to tiller more than the median of modern Puebloan landraces on the basis of the phenotyped landraces, as the AID panel is less suited to predict tillering (fig. S7).

We selected 10,000 SNPs with the highest fixation index ( $F_{ST}$ ) values between domesticated maize from the central Mexican lowlands and the Northern Flint landrace Gaspé Flint from Quebec, Canada. We then calculated  $F_{ST}$  between TPS and tropical and temperate landraces at these highly differentiated SNPs and tested this value against 1000 randomly selected sets of the same size from background SNPs. When compared to the genomic background controls for genetic drift, any deviation from the background suggests selection between TPS and test population. After controlling for drift, we show that temperate adaptation captured in the 10,000 differentiated SNPs is not shared with Mexican and South American populations but is shared with most temperate groups. These results are not consistent with the introduction of pre-adapted germ plasm from Mexico and suggest

instead an in situ temperate adaptation in the southwestern United States (Fig. 2C). The only modern northern sample that shows increased differentiation to TPS is the lower Colorado River germ plasm, a fast-cycle sweet corn from a particularly hot, arid desert region that relies on early flowering to escape heat but would not benefit from additional temperate adaptation.

A significantly higher proportion of the high- $F_{ST}$  temperate SNPs, compared with genomic background, segregate in two subspecies of teosinte, which are wild relatives of maize; 90% segregate in *Zea mays* spp. *parviglumis* (henceforth Parviglumis) from the Balsas River valley and 84% in the highland teosinte *Zea mays* spp. *mexicana* (Mexicana), 21 and 18 standard deviations above the genomic mean, respectively, suggesting that temperate adaptation was selected mainly from ancient standing variation (fig. S8). This is supported by known flowering and photoperiod loci in maize, where large-effect early flowering variants present in TPS also segregate in teosinte (fig. S9 and table S5). Additionally, the genome-wide estimate of nucleotide diversity in TPS is 0.0044, which is comparable to estimates for diverse pan-

American modern inbred landraces of 0.0049 (26), suggesting a large population during northward expansion, again consistent with long-term in situ adaptation. In contrast to quantitative traits, for large-effect genes affecting culturally and nutritionally important traits such as kernel color (e.g., *yl*), TPS has derived alleles, and neighbor joining trees at the *yl* locus suggest that high-carotenoid yellow kernel color, which is important for human nutrition, may have evolved de novo in the Southwest (fig. S10).

We genotyped 1316 individual teosintes and landraces (a superset of the landraces used for validation), with a focus on the southwestern United States and northern Mexico, using genotyping-by-sequencing. We clustered these on the basis of geographic location, altitude, and cultural affiliation for subsequent analysis (table S2) and obtained discrete populations for some analyses (fig. S11).

Admixture and multidimensional scaling analysis (MDS) (Fig. 3, A and B) place TPS with the samples from the temperate Southwest, and admixture graph analysis (Fig. 3C and figs. S12 to S14) suggests that modern Puebloan samples result from admixing TPS with ancestors of northern Mexican landraces. This admixture may reflect the influx of floury maize after TPS (13), which is consistent with a very low frequency of the low-diversity flour haplotype at the locus *su1* in TPS (fig. S15). The dominant southwestern U.S. admixture component does not derive from either lowland or highland northern Mexican germ plasm on the basis of the estimated  $F_{ST}$  (0.127 and 0.124, respectively; fig. S16), and the best fit admixture graph model places TPS on a separate lineage from the modern northern Mexican germ plasm. TreeMix results (fig. S17A) are consistent with the inference from Fig. 2C that adaptation to temperate environment occurred in situ in the Southwest.

Highland teosinte, Mexicana, commonly introgresses into domesticated maize (27), and chromosomal inversions have been implicated in highland adaptation and early flowering (28). Evidence for Mexicana introgression was observed across domesticated maize (Fig. 3D and figs. S18 and S19), but TPS received less Mexicana contribution than modern samples and genome-wide  $F_{ST}$  scans are not consistent with the presence of adaptive Mexicana inversions (fig. S20). Across modern maize, the lower ancestral levels of Mexicana admixture in northern Southwest samples (excepting the admixed desert population) relative to other maize populations is consistent with the primary topological split between the United States and all other germ plasm (fig. S17A).

TPS showed lower levels of Mexicana ancestry, but admixture and MDS analysis (Fig. 3, A and B) model a high proportion of generalized teosinte ancestry in TPS relative to modern landraces. TreeMix analysis commonly models an admixture edge to TPS from the teosintes (typically Balsas Parviglumis) (fig. S17). When we include an ancient maize sample from the Tehuacan Valley of Mexico (29) in TreeMix analysis, this TPS admixture edge transfers to the Tehuacan sample

(fig. S21), suggesting that the teosinte signal may be related to the age of TPS. Positive selection leading to modern maize after TPS at domestication and improvement loci (26) can partially explain this pattern (fig. S22).

Advances in ancient genomics and the excellent preservation at TPS allowed us to predict previously unknowable complex traits from archaeological samples. We show here that 1900-year-old maize already maintained the alleles conferring early flowering, although the lineage was likely only marginally adapted to the TPS environment. Integrating archaeological inference with modern and ancient genomics thus supports the hypothesis that ancestral Puebloan people selected for temperate-adapted maize for millennia in situ in the southwestern United States, and, additionally, that alleles for temperate adaptation were selected from preexisting standing variation in teosinte. Reliance on standing genetic variation suggests that maize retains its adaptive capacity and highlights the importance of germ plasm maintenance. However, temperate adaptation in the southwestern United States took 2000 years. In light of predicted climate change, precision breeding with genome-edited crops will be necessary to rapidly adapt modern germplasm.

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#### SUPPLEMENTARY MATERIALS

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### Estimating temperate adaptation in ancient maize

Maize as a staple food crop in temperate North America required adaptation to a shorter growing season. On its first introduction in the southwestern United States ~4000 years ago, maize was extensively grown in the lowlands. Cultivation in the temperate uplands did not occur for another 2000 years. Swarts *et al.* used ancient DNA data from 1900-year-old maize cobs found in a temperate cave in the southwestern United States and mapped the ancient flowering phenotype. The ancient maize samples were marginally adapted to temperate regions as a result of selection on standing variation.

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