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IDENTIFICATION OF CLIMATE-RESILIENT TEOSINTE POPULATIONS TO ASSIST MAIZE ADAPTATION IN THE FUTURE

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Abstract

Background: Climate change is a serious threat to biodiversity. Due to their reduced genetic diversity and increased genomic load, domesticated species might be very susceptible in the future.

Question: Can we use genomic tools and species distribution models to identify populations of teosintes that could act as sources of adaptive genetic variation for maize under future climatic conditions?

Studied species: *Zea mays* ssp. *mexicana*, *Zea mays* ssp. *parviglumis* and *Zea mays* ssp. *mays.*

Study site: Mexico.

Methods: For a dataset of 46 teosinte populations, we analyzed their neutral and adaptive genetic diversity, genomic offsets and species distribution models to predict how vulnerable the populations will be to climate change. Based on these layers, we estimated a climate change risk index. Next, we identified the teosinte populations with low-risk scores, making them potential donors of adaptive diversity for maize. Finally, we estimated regions where potential migrations (using Forward genomic offsets) would allow the introduction of adaptive diversity from teosintes to maize locations.

Results: We identified six teosinte populations that have a low-risk score. Moreover, we found that as climate warms, the teosinte populations could potentially help rescue a higher number of maize populations in the central part of Mexico.

Conclusions: This study highlights the importance of integrating genomic and environmental data to design assisted gene flow strategies, to help domesticated species adapt to climate change. However, further experimental validation will be needed to confirm the utility of these approximations.

Keywords: Assisted gene flow, climate change, genomic offset, genomics of populations, local adaptation, maize, teosintes.

Resumen

Antecedentes: El cambio climático es una amenaza para la biodiversidad. Debido a la reducción de la diversidad genética y al aumento de la carga genómica, las especies domesticadas podrían ser susceptibles en el futuro.

Pregunta: ¿Se pueden utilizar herramientas genómicas y modelos de distribución de especies para identificar poblaciones de teosintes que se podrían cruzar con el maíz para facilitar su adaptación en el futuro?

Especies estudiadas: *Zea mays* ssp. *mexicana*, *Zea mays* ssp. *parviglumis* y *Zea mays* ssp. *mays*.

Sitio de estudio: México.

Métodos: Para 46 poblaciones de teosinte, analizamos su diversidad genética neutral y adaptativa, compensación genética y modelos de distribución de especies para predecir su vulnerabilidad al cambio climático. Con base en estas capas, estimamos un índice de riesgo futuro. Identificamos poblaciones de teosintes con bajo riesgo, las cuales podrían ser donantes de diversidad genética adaptativa para el maíz. Finalmente, estimamos los costos de migración entre las poblaciones de teosinte y donde se cultiva maíz para identificar entrecruzamientos entre teosinte y maíz que pudieran introducir diversidad genética adaptativa.

Resultados: Encontramos seis poblaciones de teosinte con bajo riesgo ante el cambio climático. Además, encontramos que, las poblaciones de teosinte podrían ayudar a rescatar más poblaciones de maíz en la parte central de México.

Conclusiones: Este estudio muestra la importancia de integrar datos genómicos y ambientales para diseñar estrategias de flujo génico asistido, con el fin de ayudar a las especies domesticadas a adaptarse al cambio climático. Será importante realizar validaciones experimentales para confirmar la utilidad de estas aproximaciones.

Palabras clave: Flujo génico asistido, cambio climático, compensación genética, genómica de poblaciones, adaptación local, maíz, teosinte.

Climate change is a natural process that has occurred through the history of Earth due to natural factors. However, since the Industrial Revolution in the 19th Century, human activities have been the main cause of climate change. In the last two decades, the release of greenhouse gases has accelerated climate change and temperature is expected to increase between 2 and 4 ºC by the end of the century (IPCC 2021). This increase in temperature will also be joined by global changes in precipitation, including increased drought, and higher frequency of extreme weather events (Hannah 2021). The environmental change is causing shifts in the distribution of species, a reduction of the size of populations (Ceballos *et al.* 2017), modifications in the distribution overlap between interacting species (Zamora-Gutiérrez *et al*. 2021); and in consequence the extinction of many species (Parmesan 2006, Parmesan & Yohe 2003, Thomas *et al*. 2004).

As climate changes, species can respond in four different ways (Feeley *et al*. 2012). First, through phenotypic plasticity, species can tolerate the new environmental conditions. Second, if there is enough standing genetic variation, or new mutations arise, species can adapt to the new environmental conditions (Barrett & Schluter 2007). Third, species can migrate to track their niche. Finally, if populations are not able to tolerate, migrate or adapt, they will become extinct. A pessimistic prediction suggests that over 25 % of species could become extinct because of climate change (Thomas *et al*. 2004).

An important group of species that will be sensitive to climate change are the domesticated species for at least three reasons. First, during domestication, these species undergo strong bottlenecks, reducing their genetic diversity and increasing their genomic load (Gaut *et al.* 2018). A reduction in genetic diversity can affect their capacity to adapt to new conditions, while an accumulation of deleterious mutations can decrease their overall fitness (Aitken & Whitlock 2013, Frankham 2005). Second, during domestication, traits related to important agronomic traits are selected, but the management of species can modify the conditions where species grow and affect their capacity to respond to new environmental conditions (Purugganan 2019). Third, domesticated species are grown by farmers and producers in their own land. The possibility of actively migrating these domesticated species to locations where they could be well adapted can be problematic since it could affect farmers and impact natural systems (Salazar-Barrientos *et al*. 2016). Therefore, it is important to identify strategies that could accelerate the adaptation of vulnerable cultivated populations.

One possibility to help domesticated species adapt is to introduce, through assisted gene flow, adaptive diversity that will be important in the future by doing crosses between populations that will be vulnerable and resistant in the future (Aitken & Whitlock 2013, Hampe & Petit 2005). Most studies have used species distribution models (SDMs) to categorize the vulnerability or resistance of populations. However, this can be problematic because SDMs do not incorporate local adaptation (Aguirre-Liguori *et al*. 2021). Moreover, in the case of domesticated species, this is further complicated by the fact that they are managed. Alternatively, an option is to use multiple layers of information (Aguirre-Liguori *et al*. 2021, Dominguez *et al*. 2024) to inform the state of populations and define which ones would be the most vulnerable and the most useful to introduce adaptive diversity. For instance, genomic data and genome-environment associations can be used to identify outlier loci that could be related to local adaptation to warm and dry conditions (Bomblies & Peichel 2022, Tiffin & Ross-Ibarra 2014). Second, neutral genetic diversity can be used to identify populations with high genetic diversity, high effective population sizes and low inbreeding (Allendorf *et al.* 2010, Dominguez *et al*. 2024). Third, genomic offsets can be estimated to identify populations that will be sensitive in the future (Capblancq *et al*. 2020). Genomic offsets are estimated by comparing the predicted genetic composition of populations in the present and future, allowing the identification of populations that may need to adapt in the future (Fitzpatrick & Keller 2015). Populations with higher genomic offset are expected to experience greater environmental mismatch, or have inadequate genetic diversity, and therefore be more vulnerable in the future. In addition, forward genomic offsets, which measures the genetic and environmental mismatch caused by the migration of a population, can also be estimated to identify populations that could be moved in the future to other locations and would have low offset, suggesting that they could contain adaptive diversity in the new location (Gougherty *et al.* 2021). This approximation was used to identify potential crosses that could be done to introduce adaptive diversity in the Pearl Millet (Rhoné *et al*. 2020).

In the case of domesticated species, adaptive diversity could be introduced from their wild crop relatives (WCR) (Janzen *et al*. 2019, McCouch 2013, Warschefsky *et al*. 2014). The use of WCR is advantageous because they usually have higher genetic diversity than their domesticated relatives and they have adapted in situ to the local biotic and abiotic conditions. Also, WCR are adapted to the natural conditions where they grow, which may increase our capacity to identify outlier loci using genome environment associations. Interestingly, since many WCR and domesticated species exhibit introgression or incomplete lineage sorting, it is possible that some of adaptive diversity contributing to local adaptation in WCR populations can also be found in domesticated species (Flint-Garcia *et al*. 2023). In such cases, adaptive diversity can first be identified in WCR, then traced in domesticated species. This would allow performing crosses directly between domesticated populations, avoiding the complications associated with hybridization between domesticated and wild crops (Flint-Garcia *et al*. 2023).

Maize is one of the most important cultivated crops in the world. This species was domesticated in México from the lowland teosintes (*Zea mays* spp. *parviglumis*) ~10,000 years ago (Matsuoka *et al*. 2002). Since teosintes and maize grow in sympatry, teosintes could potentially be a very important source of adaptive diversity for maize since they have high genetic diversity (Fukunaga *et al*. 2005). Moreover, they show strong patterns of local adaptation to different abiotic conditions (Aguirre-Liguori *et al*. 2017, Aguirre-Liguori *et al*. 2019, Fustier *et al*. 2017, Pyhäjärvi *et al*. 2013) and they have been important for the adaptation of maize to different conditions. For instance, adaptive introgression between *Zea mays* ssp. *mexicana* and maize was important for the adaptation of maize to the highlands (Hufford *et al*. 2013, Yang *et al*. 2023).

In this study, we use a published dataset (Aguirre-Liguori *et al*. 2017) to characterize how 46 populations of teosintes (*Zea mays* ssp. *mexicana* and *Zea mays* ssp. *parviglumis;* hereafter *mexicana* and *parviglumis*) might respond to climate change, based on multiple layers of information. Based on these data, we develop a climate change risk index, to identify the teosinte populations with the lowest risk of being affected by climate change. Next, we evaluate the cost of migration for these low-risk teosinte populations to over 50,000 locations where domesticated maize is cultivated. Finally, we identify the teosinte populations that would most efficiently introduce adaptive diversity into the largest possible number of maize accessions. After experimental validations, low-risk populations, with low forward genomic offsets, could serve as effective sources for assisted gene flow between teosintes and maize. These strategies could increase the adaptive diversity of vulnerable maize populations in the future.

Materials and methods

Genomic Datasets. For this project, we downloaded the teosinte genomic datasets of Aguirre-Liguori *et al*. (2017). This data set was generated with the MaizeSNP50 Genotyping BeadChip from Illumina. Genotypes were called using the Genome Studio's Genotyping Module v. 1.0 (Illumina), applying a GC50 score threshold of 0.15. Each genotype was visually inspected to ensure quality, and monomorphic markers were removed (for more details see Aguirre-Liguori *et al*. 2017). The final dataset consisted of 33,464 SNPs distributed across the 10 chromosomes of teosintes, 646 individuals, 25 populations of *parviglumis* and 23 populations of *Mexicana.*

Geographic and environmental datasets. We obtained the geographic location of each population. We also downloaded from Worldclim2 (Fick & Hijmans 2017) the 19 bioclimatic variables for the present (from 1970 to 2000) and for the future conditions. We used the *CorSelect* function from the R (R Core Team 2023) package *fuzzySim* (Barbosa 2015) to select bioclimatic variables with a correlation below 0.8, using the Variance Inflation Factor (VIF). This factor helps identify the most relevant variables with low collinearity, which is essential to avoid model overfitting and improve result interpretation. In total, we retained 7 variables (BIOS 2, 3, 5, 15, 17, 18 and 19).

We also downloaded the 7 layers from 5 circulation models (GFDL-ESM4, IPSL-CM6A-LR, MPI-ESM1-2-HR, MRI-ESM2-0, UKESM1-0-LL), three time periods (2041-2060, 2061-2080, 2081-2100) and four Shared Socioeconomic Pathways (SSPs 126, 245, 370, 585), representing different gas emissions (Riahi *et al.* 2017). The set of general circulation models and SSPs was selected to incorporate uncertainty into future projections by capturing variability among climate models (Sanderson *et al*. 2015) and accounting for contrasting greenhouse gas emission scenarios. Whenever we wanted to pinpoint an example, we use the model UKESM1-0-LL, SSP 245 and year 2041-2060; since a previous study showed that genomic offset estimated with this layer correlates strongly with the different climatic models in the case of teosintes (Aguirre-Liguori *et al*. 2023).

Next, we used the *sp_occurrence* function in the geodata package (Hijmans *et al.* 2023) in R to download from GBIF all the locations of maize that have been reported in Mexico (GBIF 2025). For these locations, we used the coordinate cleaner package in R (Zizka *et al*. 2019) to remove potentially erroneous locations (*e.g.,* based on duplications, locations that fall in the sea, outlier distributions). Finally, for all locations (teosintes and maize datasets), we used the terra package in R (Hijmans 2024 to extract the environmental values for the present and future environmental data.

Evaluation of risk, FOLDS Model. To estimate the range of vulnerability of populations to climate change, we followed the logic behind the FOLDS model of Aguirre-Liguori *et al.* (2021). This model integrates multiple layers of information that predict responses to climate change. The FOLDS model was originally described using gene Flow, genomic Offset, genomic Load, Dispersal capacity and Species distribution models. However, it is a flexible model that can be used with other layers of information. In this study, we estimated the layers of information that we describe below and based on them we defined a climate change risk index for the teosinte populations.

Neutral genetic diversity.- Based on genetic data, various population genetics summary statistics were obtained to describe the genetic variation within populations. First, to analyze the genetic diversity of the populations, the *basic.stats* function from the Hierfstat package (Goudet 2005) was used to calculate, for each species and population, expected genetic diversity (H_S), observed genetic diversity (H_O), and inbreeding coefficient (F_{IS}). We selected these summary statistics, because they provide simple and informative estimates of genetic diversity and inbreeding of populations. Populations with higher genetic diversity experience less genetic drift and have a greater ability to respond to future environmental changes (Allendorf *et al*. 2010, Barrett & Schluter 2007). Lastly, these statistics are relevant for proposing management strategies (Allendorf *et al*. 2010), as the ideal approach would involve introducing genetic diversity to vulnerable populations, while avoiding introducing genomic load, that is more common in small populations.

We tested the correlation between the three summary statistics and found that the expected and observed genetic diversity had a high correlation (cor = 0.94). In contrast, we found that the expected genetic diversity and fixation index had a very low correlation (cor = 0.26). Therefore, we only retained H_S and F_{IS} for subsequent analyses.

Adaptive genetic diversity.- To identify patterns of local adaptation, outlier loci were detected using genome-environment association (GEA) methods. These methods seek significant associations between allele frequencies and climatic variables, while accounting for genetic structure. For this purpose, the Latent Factor Mixed Model (Frichot *et al*. 2013, Frichot & François 2015) was employed to identify outlier SNPs associated with any of the 7 uncorrelated bioclimatic layers. Specifically, we used the *lfmm_ridge* and *lfmm_test* functions of the lfmm package in R (Caye *et al*. 2019) to run the analyses. To control for latent factors, which are used to account for population structure, a PCA of genomic data was conducted to determine the number of genetic groups in the populations. The *prcomp* function was applied to all SNPs, and the number of latent factors was selected based on changes in the variation explained by each principal component (Frichot *et al*. 2013, Frichot & François 2015, Supplemetary Material 1 Figure S1). Finally, a genome inflation factor was used to control for an over inflation of outlier SNPs caused by genetic structure.

To adjust for multiple testing, the *qvalue* function from the R package qvalue (Storey *et al.* 2022) was used, applying a False Discovery Rate (FDR) threshold of less than 0.05 to identify loci that are candidates for selection. The number of polymorphic sites identified as candidate loci under selection was recorded, as well as how many were linked to one or more climatic variables. Finally, all unique polymorphic sites showing any signal of selection were used for subsequent gradient forest modeling.

Genetic offset.- Once the outlier loci were identified, we followed the approximation of Aguirre-Liguori *et al.* (2021) to create gradient forest models and estimate genetic offsets. Briefly, the *gradientforest* function from the Gradient Forest package (Ellis *et al*. 2012) in R was used to build models predicting changes in the genetic composition of populations based on the geographic landscape. To build these models, we used as predictive variables the seven bioclimatic variables, as independent variables the unique outlier loci identified by the GEA, and 500 trees.

Based on the GF models, we predicted the expected genetic composition of populations in the present and for the 54 models of climate change. Subsequently, multidimensional Euclidean distances between present and future genetic compositions were calculated to estimate the Genetic Offset (GO) of teosinte populations (Fitzpatrick & Keller 2015). GO measures the amount of genetic change that populations would need to maintain their local adaptation. Therefore, populations with higher GO are more susceptible to climate change, since they would need to adapt more in the future. Finally, we estimated the GO of each population for 54 models (see Supplemetary Material 2 Table S1 for all values across 54 layers and for all populations). We obtained the mean GO across models and then tested the Spearman correlation of the mean GO against each modelled GO. We found that the mean GO had a high correlation with most of the GO projections estimated across the 54 climate models (75 % of estimated GOs had a Spearman correlation > 0.8, Supplemetary Material 1 Figure S2). Therefore, for simplicity we only report the mean GO.

Species distribution models.- For each teosinte subspecies, we followed the approximation of Aguirre-Liguori *et al.* (2021) to estimate a species distribution model (SDM) and project them to the 54 models of climate change. Briefly, we set the geographic calibration area (M layer, following the BAM framework), based on the overlap between locations and the terrestrial ecoregions of the world (Olson *et al*. 2001). For each subspecies, we used the *CorSelect* function from the R package *fuzzySim* (Barbosa 2015) to select uncorrelated bioclimatic variables (see above). Next, we built the SDM using the R package Biomod2 (Thuiller *et al*. 2016) and four different algorithms (RF, GBM, GAM and the Maxent algorithm). Seventy-five percent of occurrences were used to calibrate the model, while the remaining 25 % were used for validation. Twenty bootstrap replicates were performed to evaluate the stability of the results. Model quality was assessed using the ROC curve (which evaluates the model's ability to distinguish between species presences and absences across different thresholds) and the True Skill Statistic (TSS, which offers a comprehensive measure of model accuracy) curve. Finally, we used the *BIOMOD_EnsembleModeling* and the *BIOMOD_EnsembleForecasting* functions to create and project the ensembled model based on the individual models with the highest performance. These ensemble models were also projected into the 54 layers in the future, allowing us to identify areas that are expected to contract, persist or colonize in the future.

Risk evaluation.- Once we had all the variables that describe the risk of populations to climate change, we categorized the risk of each population into four levels, with 1 indicating low risk and 4 indicating high risk. To do so, we used the *quantile* function in R to divide populations based on their quartile distributions (0-25 % equals 1-low risk; and 75-100 % equals 4-high risk). For H_S, low values of genetic diversity were associated with higher risk, while for GO and F_{IS} higher values of these statistics indicated greater risk in the future. Finally, for the SDM models, we summed the 54 projected future models. In this case, populations that were predicted more often in the future were considered to have a low-risk category. Since each layer could potentially have different impact on the response of populations to climate change, we also tested adding weights to the model. In this case, we assigned the highest weight to adaptive diversity (GO × 3), followed by genetic diversity and inbreeding ($(H_S + F_{IS}) \times 2)$) and finally for SDM (SDM × 1). Weighted and unweighted scores had a high correlation (cor = 0.96, Supplemetary Material 1 Figure S4), so we decided to present the results without weights to avoid subjective decisions in weighting the layers.

Finally, for each population we summed their categories of risk across the four layers. The population with the lowest risk category would have a score of 4; while the population with the highest risk category would have a risk value of 16.

Assisted gene flow.- Once we characterized the expected vulnerability of teosinte populations in the future based on their risk category, we proceeded to identify potential crosses that could be performed to introduce adaptive diversity from the source population of teosintes to the vulnerable populations of maize (GBIF dataset). To do so, we estimated the Forward Genetic Offset (FGO) between the source population and the receiver populations. In these cases, the Euclidean distances were estimated between the present genetic composition of teosinte populations and the genetic composition that would be expected if the teosintes were moved to a location where maize grows (Gougherty *et al.* 2021). For each population, potential migration sites were identified as those with an FGO lower than the local GO of the population. In other words, these are the locations where each teosinte population could potentially be relocated to find more optimal climatic conditions than if they remained in situ. Since these populations would be expected to be well adapted (low offset), we would expect them to have adaptive diversity that would be useful in that location.

We performed these analyses for all teosinte locations and for the set of locations with low risk to climate change (Risk Score < 8; middle risk value). Finally, we defined how many locations of maize could be rescued by all teosinte's locations; how many locations of maize could be rescued by each of the low-risk populations; and finally define the areas in Mexico where these crosses could be performed.

Results

In this study, we used five layers of information to identify populations of teosintes that could be resistant to climate change (adaptation to drought and warmer conditions). For this, we first estimated the genetic diversity of populations, their potential vulnerability to climate change based on genetic data, and species distribution models. We combined all statistics to define the risk of populations to climate change (Aguirre-Liguori *et al*. 2021). Finally, we identified potential crosses that could be performed to introduce adaptive diversity from teosintes to maize.

FOLDS model creation. Genetic diversity.- First, we estimated the genetic diversity of populations of teosintes (Figure 1, Table 1). We found that the expected genetic diversity was high in both teosintes, although it was slightly higher in *parviglumis* ($H_S = 0.23 \pm 0.05$) than in *mexicana* ($H_S = 0.22 \pm 0.02$). We also found that inbreeding was low in the two teosintes, although it was lower in *mexicana* ($F_{IS} = 0.06 \pm 0.05$) than in *parviglumis* ($F_{IS} = 0.08 \pm 0.04$). Although we found that genetic diversity was high and inbreeding was low, we found that there was substantial variation across populations (Figure 1, Table 1), with some populations presenting very low values of genetic diversity (mainly populations of *parviglumis* in Jalisco; $H_S = 0.1$, Table S2) and others presenting high values of genetic diversity ($H_S = 0.29$, Table S2). The same pattern was observed for inbreeding, where we found that F_{IS} ranged from 0.01 to 0.21 in *mexicana* populations (Supplemetary Material 2 Table S2).

Adaptive genetic diversity.- We used genome environment associations (GEA) to identify outlier SNPs. Since we were interested in identifying outlier loci associated with climatic gradients, we combined the two teosintes' datasets. A PCA analysis on genomic data showed that K = 4 was the most probable number of genetic clusters (Supplemetary Material 1 Figure S1). Next, we used LFMM2, a genomic inflation correction and an FDR < 0.05 to identify outlier SNPs across seven bioclimatic variables (Figure 2A, B). In total, we found 419 outlier SNPs that were distributed across five bioclimatic variables (BIO 18, 2, 15, 3 and 19). The number of outlier SNPs varied across variables (Figure 2B). The highest number of outlier SNPs was associated to BIO 18 (Precipitation of Warmest Quarter), followed by BIO2 (Mean Diurnal Range). We also found that the outlier SNPs had a different distribution pattern across the genome (Figure 2A, Supplemetary Material 1 Figure S3). For example, for BIO18 (Precipitation of Warmest Quarter) we found outlier SNPs distributed across the entire genome, suggesting that adaptation could be polygenic, while for BIO15 (Precipitation seasonality) we identified clear selective sweeps suggesting strong selection and loci of strong effect.

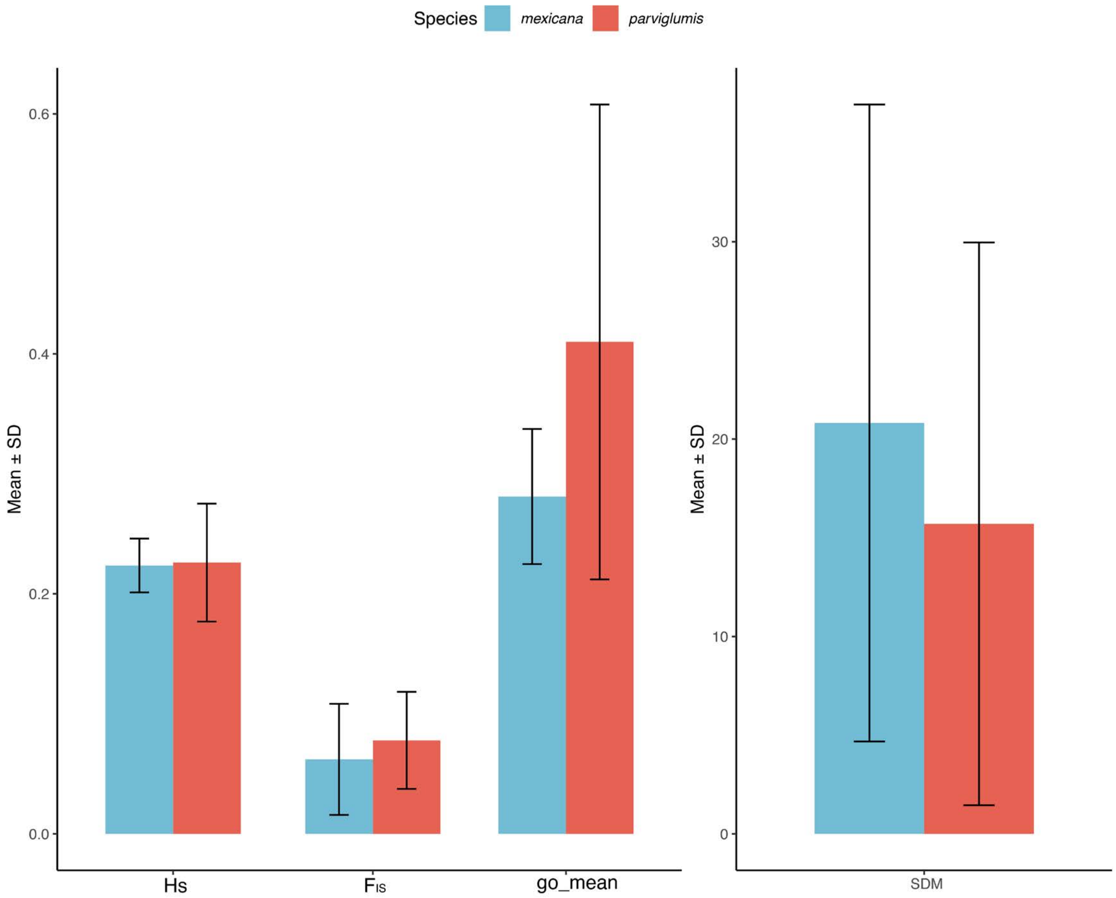

Figure 1. Barplots showing the summary statistics across genetic information and species distribution models. The barplot shows the mean value and the dispersion shows the standard deviation.

Table 1. Summary statistics of genetic diversity (H_S, F_{IS}), and mean genomic offset (GO) across 54 future climate change models and number of SDM models predicting the distribution of populations.

Taxa	N_{ind}	GO	H_S	F_{IS}	SDM
mexicana	22	0.28 ± 0.06 (0.15-0.38)	0.22 ± 0.02 (0.16-0.26)	0.06 ± 0.05 (0.01-0.21)	20.82 ± 16.13 (0-46)
parviglumis	24	0.41 ± 0.2 (0.2-1)	0.23 ± 0.05 (0.1-0.29)	0.08 ± 0.04 (0.02-0.19)	15.71 ± 14.25 (0-44)

The values in the table show the mean across populations ± standard deviation and the range in parenthesis (minimum-maximum values).

Genetic offset.- Once we had the outlier SNPs, we used gradient forest (GF) to build models of how the genetic composition varies across the landscape. For the teosintes model, we also found that the most important bioclimatic variables were BIO18 (Precipitation of Warmest Quarter) and BIO2 (Precipitation of Coldest Quarter) (inset in Figure 2C). We plotted the overall turnover function across BIO18 and found that the two subspecies of teosintes were clustered in different parts of the turnover function (Figure 2C). In other words, we found that *mexicana* populations were distributed and clustered in the lower values of BIO18, while *parviglumis* populations were in different parts of the turnover function. Indeed, three populations of *parviglumis* were in the superior limit of BIO18 and had a very divergent genetic composition (Figure 2C).

We used the GF models to estimate the genetic offset (GO) of populations. For this, we first predicted the genetic composition of populations in the present and the expected genetic composition across 54 future layers. Then we estimated the local genetic offset of populations across the 54 layers and their mean value. We found a high Spearman correlation across genetic offset and the mean value, so we only report the mean value of the genetic offset (Supplemetary Material 1 Figure S2, Supplemetary Material 2 Table S1). According to our models, *parviglumis* populations have a higher GO than *mexicana* populations (Figure 2D, E, Table 1). However, we also found substantial variation across populations and across the landscape, with higher offsets found in the warmer lowland populations (Figure 2D).

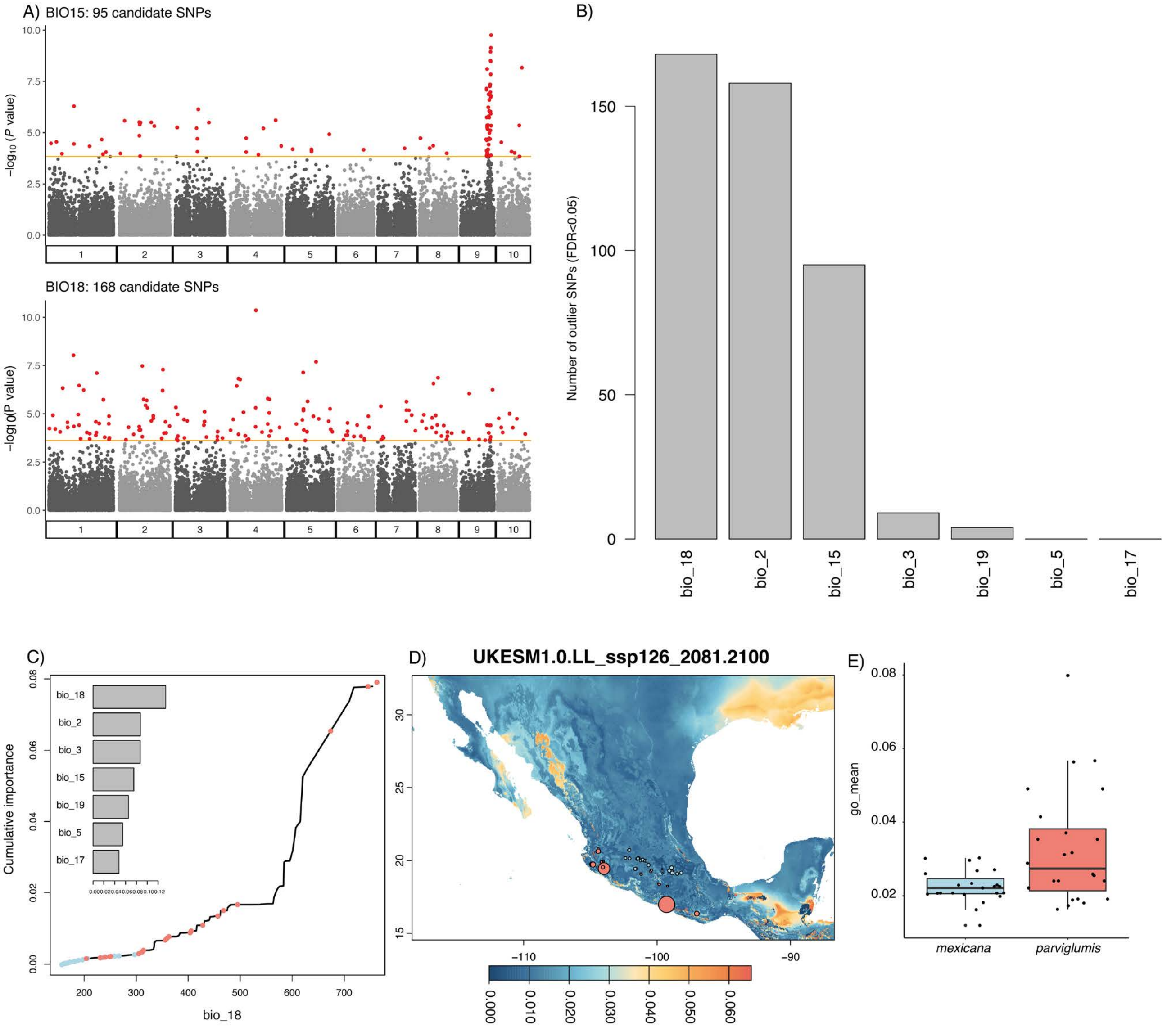

Figure 2. A) Manhattan plots showing the distribution of outlier SNPs associated to two Bioclimatic variables (BIO 15 and BIO 18, for 7 Bioclimatic variables see Figure S3). B) Barplot showing the number of outlier SNPs across all variables. C) Turnover function showing how the genetic composition changes across BIO18 (the variable that had strongest effect over the model). The inset shows the importance of each variable. D) genomic offset projected across the Mexican landscape. Warmer colors indicate higher offset, and the size of the dots showing the location of populations indicates the magnitude of the offset. E) Boxplots showing the distribution of genomic offset across populations. The dots correspond to the individual values of the populations. The salmon colors in C and D show populations of *parviglumis*, while the light-blue color show the populations of *mexicana*.

Species distribution models.- Finally, we also estimated the species distribution models (SDM) of teosinte populations. We projected the ensembled SDM to 54 models of future climate change. Figure 3 shows the sum of the future SDM distribution for each of the two taxa, with warmer values showing areas that are predicted by more models in the future.

We found that in average populations are predicted to persist in 20 scenarios in *mexicana* (range 0-46, Table 1) and in *parviglumis* only in 15 scenarios (range 0-44, Table 1). In all cases, we found that the locations of teosintes that will be more vulnerable in the future according to SDMs are peripheric populations.

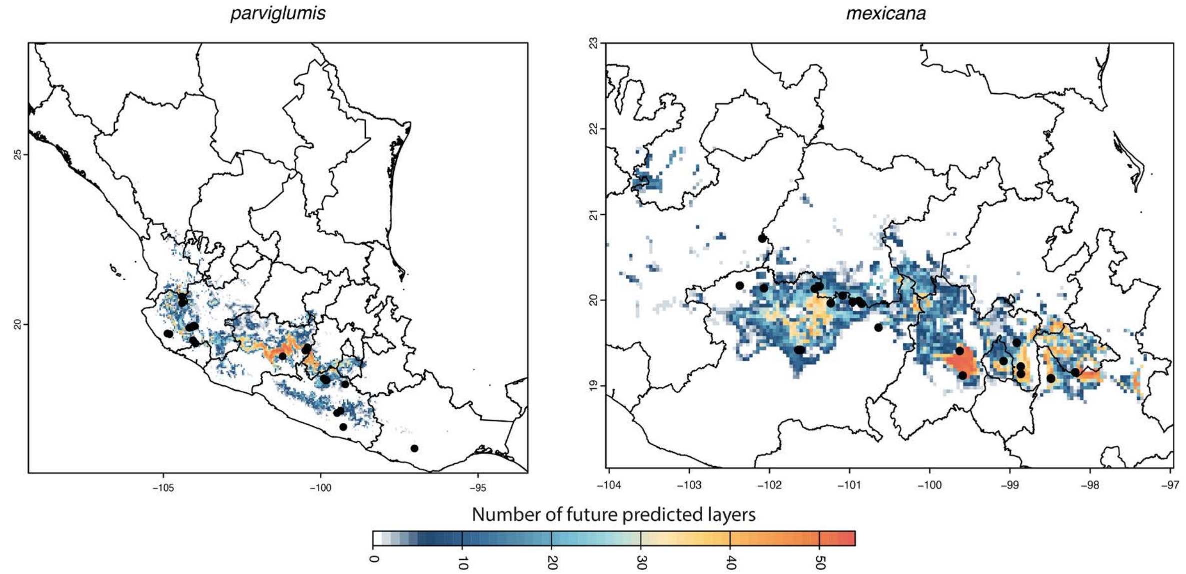

Figure 3. Species distribution models showing the projected distribution across 54 layers of climate change. The colors indicate how many models predict the persistence of populations in the future.

Climate change risk index. In total, we estimated five layers of information that are indicative of the risk of populations to climate change. These layers consisted of neutral and adaptive genetic diversity and species distribution models. While these variables are indicative of risk by themselves, they all have advantages and limitations. Therefore, we decided to combine the information to predict which populations are at higher risk according to different criteria. For this, we separated populations according to four quartiles and we set a value of 1 to the populations with the lowest risk, and 4 to the populations with the highest risk. Figure 4 shows the categorization of populations across the different layers of information for teosintes (four categories in H_S, F_{IS}, GO, SDM; Max = 16).

To estimate the climate change risk index, we summed the risk of each category for each population (Supplemetary Material 2 Table S2). We found that the risk of populations varied from four (the lowest possible value, in population Villa Seca) to 15 (out of 16, in populations Crucero Lagunitas, El Rodeo and San Cristobal Honduras). We selected the populations that had a risk category below eight (out of 16) and found that six populations of teosintes meet this criterion (risk value between 4 and 7), two populations from *parviglumis* and four populations from *mexicana* (Table 2).

Forward offset. Introducing adaptive diversity to vulnerable populations could help them adapt to climate change. We used populations of teosintes to estimate which ones could be introduced to other maize locations and that would have a lower FGO than their local GO. First, we evaluated how many maize populations could be rescued by all the teosintes or the low-risk teosinte populations (Figure 5A, B; Supplemetary Material 2 Table S3). We found that the number of maize populations that can be rescued depends on the circulation models, the time frame and the SSP

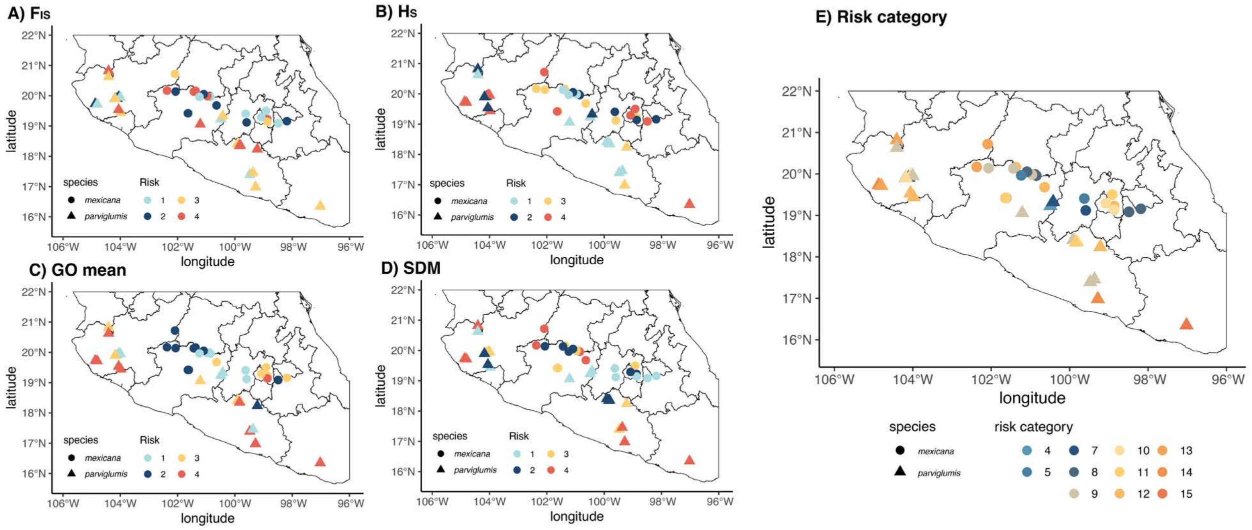

Figure 4. Maps showing the risk category of populations across the different layers of information (A-C) and the sum across layers (E). Warmer colors in the legends indicate a higher risk under climate change.

Table 2. Six populations having low risk score to climate change. Values scored across the four layers analyzed and their sum are shown

Species	Population	Longitude	Latitude	H_S	F_{IS}	GO mean	SDM	Risk category
mexicana	Calpan	-98.48	19.08	3	1	2	1	7
mexicana	Huandacareo	-101.24	19.96	1	1	1	2	5
mexicana	TenangodelAire	-99.59	19.12	3	2	1	1	7
mexicana	VillaSeca	-99.63	19.41	2	1	1	1	5
parviglumis	LosGuajes	-100.49	19.23	1	1	1	1	4
parviglumis	Zitacuaro	-100.42	19.33	2	3	1	1	7

projections. Interestingly, we found that as the climate becomes warmer (later in the century or higher SSP emissions), more populations of maize can be rescued according to our models (this is true for all teosintes or all low-risk populations). We also found that using 46 populations of teosintes, instead of the six low risk populations can rescue more maize locations (Figure 5A, B). For instance, we found that if we use all teosinte populations, we can rescue between 7,011 (model MRI.ESM2.0 ssp126 2041.2060) and 31,232 (model UKESM1.0.LL ssp585 2081.2100) maize locations (Table S3), while for the low risk populations we can rescue between 920 (model IPSL-CM6A-LR ssp126 2041-2060) and 12,599 (MRI.ESM2.0 ssp585 2081.2100) maize locations (Supplemetary Material 2 Table S4).

Finally, we evaluated how many maize locations could be rescued by each of the six low risk populations. We found that depending on the climate change models, the number of rescued locations could vary strongly between teosinte locations and between future climate change models (Figure 5C, Table 3, Supplemetary Material 2 Table S4). For instance, we found that for Villaseca_Otzoltepec population (*mexicana*) the range of maize populations that could be rescued would be very low (up to 1,889 locations), while for other teosinte populations, the range would vary a lot between models, but would be able to rescue up to 8,105 maize locations in model IPSL-CM6A-LR_ssp585_2081-2100 for population Los Guajes (Figure 5C, Supplemetary Material 2 Table S4). Moreover, we used the model UKESM1-0-LL_ssp245_2041-2060 to evaluate how the low-risk teosinte populations would be able to rescue the maize locations. We found that the number of rescued maize locations could range from 62 in Villaseca to 11,678 in Los Guajes (Figure 5D, Supplemetary Material 2 Table S4). Finally, we tested for each location of maize how many of the teosinte populations could be used to rescue them (Figure 5E). We were surprised to find that only populations in the center of Mexico would be rescuable by the teosinte locations and that the maximum number of teosinte populations that could be used to save a given maize location is four (out of the eight).

Discussion

Domesticated species tend to have high genomic load and low genetic diversity (Gaut *et al*. 2018). As they must adapt locally to the conditions where they are cultivated, this makes them vulnerable to climate change. A solution that could help domesticated species adapt in the future is by introducing adaptive genetic diversity via assisted gene flow (Aitken & Whitlock 2013). This adaptive diversity can be sourced either thought gene flow with their wild relatives (Warschefsky *et al*. 2014) or from adaptive alleles identified in wild relatives and that are polymorphic in the domesticated species (Flint-Garcia *et al*. 2023). To perform the assisted migration, the first step is to identify adaptive genetic diversity. Next, vulnerable populations must be identified, and finally potential crosses should be performed to introduce adaptive diversity. In this study, we used multiple layers of information to identify (Aguirre-Liguori *et al*. 2021) populations of teosintes that could be used to introduce adaptive diversity into maize populations.

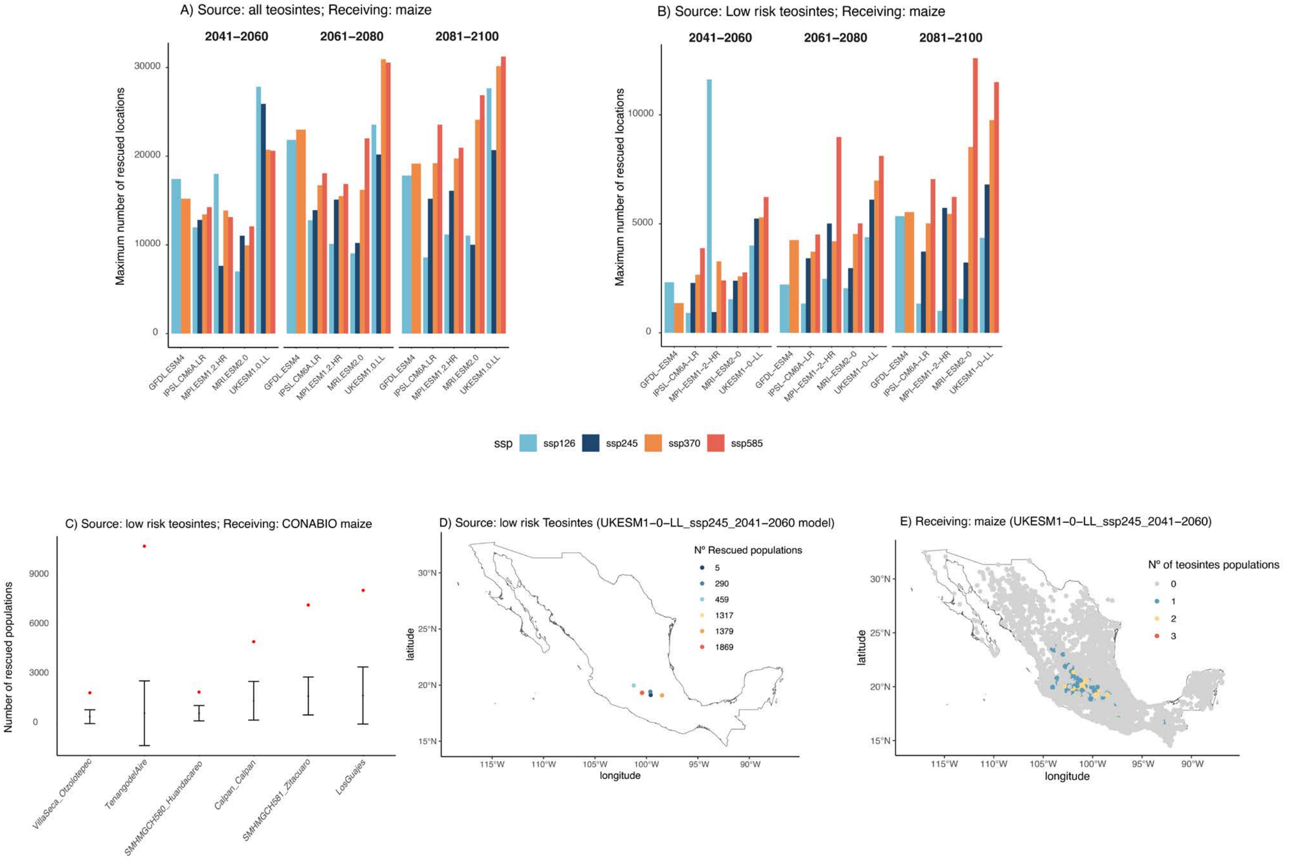

Figure 5. Barplots in the top show the number of maize locations that could be rescued from A) all the teosintes, B) the low-risk teosinte's locations. C) Scatterplot showing how many populations of maize each of 6 low risk teosintes could rescue. The dark dot shows the mean value across the 54 models of future climate change, the whiskers show the deviation, and the red dot shows the maximum value of populations that can be rescued. D) For model UKESM1-0-LL-ssp245-2041-2060 we show how many locations of maize the 6 low risk teosintes populations can save. E) for the same model, we show how many of the 6 teosintes locations can save each of the maize locations analyzed.

First, we estimated different layers of information that indicate how much genetic diversity and inbreeding occurs across populations of the two subspecies of teosintes. We found that both subspecies have similar levels of genetic diversity, although *mexicana* showed lower inbreeding and higher observed genetic diversity (Figure 1, Table 1, Table S2). However, we found some populations of *parviglumis* with very high genetic diversity and others with very low genetic diversity (Figure 1, Supplemetary Material 2 Table S2). These patterns of diversity have been widely documented in teosintes (Aguirre-Liguori *et al*. 2017, Aguirre-Liguori *et al*. 2019, Fukunaga *et al*. 2005, Fustier *et al*. 2017, Pyhäjärvi *et al*. 2013). It is important to identify populations with high genetic diversity and low inbreeding to avoid introducing genomic load and inbreeding depression into populations (Frankham 2005). Moreover, an additional objective in genetic crosses is to increase overall genetic diversity, since selection can act on standing genetic variation (Barrett & Schluter 2007).

Although neutral genetic diversity has been an important indicator of future response to climate change, it is not ideal, since it does not necessarily correlate with adaptive diversity (Allendorf *et al.* 2010). To incorporate adaptive diversity, we performed two analyses. First, we used LFMM to identify outlier loci across bioclimatic variables. We found 419 unique outlier loci. These loci were either distributed across the genome, indicating that they may be under selection for polygenic traits (*e.g.,* BIO18) or they showed signatures of hard sweeps (*e.g.,* BIO15) (Figure 2A, Supplemetary Material 1 Figure S3). Moreover, we found that most outlier SNPs were associated with BIO 18 (precipitation of the warmest quarter). These results indicate that precipitation is an important driver of local adaptation in teosintes. This is particularly relevant given that many future climate models predict an increase in drought across Mexico, especially those scenarios driven by human-induced climate change (IPCC 2021). Identifying outlier loci associated with drought tolerance may therefore be essential for introducing adaptive diversity in the future.

Adaptation to climate change depends not only on genomic diversity but also on how climate will change. Genomic offsets predict how populations will respond in the future if climate changes, depending on the adaptive genomic composition of populations (Capblancq *et al*. 2020, Fitzpatrick & Keller 2015). We measured genomic offsets first by estimating the turnover functions of populations using gradient forest. According to gradient forest, we also found that BIO18 (Precipitation of Warmest Quarter), followed by BIO 2 (Mean Diurnal Range) are the most important variables describing the model. Again, this supports that precipitation will play an important role in the adaptation of teosintes in the future. Next, we used GF to project the genomic offset across populations. The mean genomic offset across populations shows a large variation among them, with *parviglumis* populations (lowland teosintes) presenting higher levels of genetic offset (Figure 2E). This is consistent with other studies that have shown that *parviglumis* has higher offset (Aguirre-Liguori *et al*. 2019). This is interesting because it suggests that populations growing at the warmer end of the distribution are likely to be more sensitive to future climate warming (Hampe & Petit 2005). In contrast, *mexicana* populations will have a higher climatic tolerance for warmer and drier climate. Using *parviglumis* as a source of adaptive variation is interesting, as these populations are located at the rear edge of the teosinte's distribution (Hampe & Petit 2005). However, *mexicana* also represents an important source of adaptive diversity, given its adaptation to drier conditions (Aguirre-Liguori *et al.* 2016).

Table 3. Number of maize populations that can be rescued by the low-risk teosintes across the 54 models of climate change.

ind	mean	min	max	sd
VillaSeca_Otzolotepec	439.35	3	1,889	420.27
TenangodelAire	647.98	5	10,782	1,963.09
SMHMGCH580_Huandacareo	649.11	35	1,931	465.50
Calpan_Calpan	1,403.63	42	4,992	1,173.68
SMHMGCH581_Zitacuaro	1,694.24	367	7,224	1,153.56
LosGuajes	1,723.69	17	8,105	1,733.66

We identified four layers of information that can be used to predict how populations will respond in the future (Figure 4). However, the most interesting feature lies in integrating these layers to generate a better prediction of population responses. We followed the FOLDS framework (Aguirre-Liguori *et al*. 2021) to identify populations that are expected to respond more favorably to future conditions, based on SDMs, genetic diversity, and adaptive diversity. To do this, we classified populations according to four levels of risks for each layer and then summed their total risk across layers. This approach allowed us to estimate the risk of future climate change across 46 locations of teosintes (lowest risk 4 and highest risk 16). We also tested incorporating weights to the different layers of information, giving the highest weight to adaptive variation, followed by genetic diversity and finally SDMs. However, the weighted and unweighted risk scores were highly correlated. To avoid introducing bias, we proceeded with the unweighted scores (Supplemetary Material 1 Figure S4). Overall, we identified six locations of teosintes that have a risk below eight. Interestingly, four of these low-risk populations belong to *mexicana* and two populations of *parviglumis* (Table 2).

The FOLDS approximation allows to pinpoint populations that could have adaptive diversity, high genetic diversity, and be well-adapted in the future (low offset). However, this does not necessarily indicate that these populations could be successful donors of adaptive diversity if they were actively moved. A genomic offset can also be measured between a location in the present and another in the future, and this is called forward genomic offset (Gougherty *et al*. 2021). This has been estimated for pear millet (Rhoné *et al*. 2020) and indicates which potential cross could be used to introduce adequate genetic diversity from one population to the other. We estimated the FGO between teosintes populations and the maize locations. We performed this for all teosintes and for the low-risk teosintes. Overall, we found that as future climate becomes warmer and drier, making crosses between teosintes locations and maize would be more useful to protect maize populations (Figure 5). Unfortunately, under warmer climate scenarios, we found that using all teosinte populations versus only the low-risk populations leads to substantial differences in the number of maize locations that can be rescued (Figure 5A, B). Our results suggest that when different layers of information are considered to avoid introducing genetic load or inbreeding depression into target populations, the number of rescuable locations drops by two-thirds. Additionally, we also found that most maize locations that could be rescued by other teosintes occur only in the center of Mexico (Figure 5E). This is important because central Mexico is where most of the cultivation of maize occurs. However, for the peripheric populations of maize, it will be important to identify other sources of local adaptation that could be used to rescue them in the future. For instance, other maize populations may harbor important adaptive genetic diversity.

We found that not all low-risk teosinte populations are optimal for rescuing maize locations. For instance, we found that Villaseca, a *mexicana* population, could be useful to rescue in the best scenario up to 1,889 (minimum 3) locations of maize. If FGO had not been calculated, this population could have been a very strong candidate to perform potential crosses (risk value= 5). This shows the importance of incorporating different layers of information and projecting how populations might respond in the future if they were relocated actively. FGO are valuable as they might help identify crosses that are unlikely to result in outbreeding depression, an outcome that should be avoided in conservation efforts (Allendorf *et al.* 2010). Our findings may serve as a basis for developing strategies to enhance the resilience of domesticated species under future environmental change. However, it is important to note that these results are based on models integrating genetic diversity and environmental data. Since maize is an important crop, there are important steps before using this information for performing potential assisted gene flow crosses. First, experimental validations will be needed to show that GO and FGO are adequate predictors of the responses of maize and teosintes to climate change. While some experimental results suggest that GO are useful predictors (Fitzpatrick *et al*. 2021, Gain *et al*. 2023, Rhoné *et al*. 2020), there are still very few experimental studies showing their utility. Moreover, the GO workflow is still very young, and many theoretical aspects have not been evaluated yet, so caution when using these methods is important (Ahrens *et al*. 2023, Rellstab *et al*. 2021), especially for domesticated species. While sampling could also affect the estimations of GO (Aguirre-Liguori *et al*. 2023), in this study our sampling included enough populations and individuals per population. Third, many more layers could be used to increase the predictions of how teosintes and maize locations will respond in the future. For example, socioeconomic variables could be helpful predictors of risk of crop related species (Mouillot *et al*. 2024, Salazar-Barrientos *et al*. 2016). Finally, although we identified teosinte populations that could serve as sources of adaptive diversity for maize, crosses between crop wild relatives (CWR) and domesticated species can be challenging. For instance, hybrids between CWR and cultivated varieties may exhibit intermediate phenotypes lacking the desired agronomic traits, complicating selection protocols. In such cases, an alternative approach would be to identify the outlier loci associated with adaptation in teosinte, pinpoint the specific genotypes contributing to climate resilience, and then search for the adaptive variation present in maize (Flint-Garcia *et al*. 2023). This strategy could simplify the crosses that could introduce adaptive diversity in maize across Mexico.

Supplementary material

Supplemental data for this article can be accessed here: https://doi.org/10.17129/botsci.3680

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