A new evolution-based genomic prediction model forecasts yield performance across environments and future climates and identifies adapted maize landraces

Agustin O. Galaretto[1], Marie Pégard[2], Rosana Malvar[3], Laurence Moreau[1], Ana Butrón[3], Pedro Revilla[3], Delphine Madur[1], Valérie Combes[1], Carlotta Balconi[4], Cyril Bauland[1], Pedro Mendes-Moreira[5], Hrvoje Šarčević[6], Ana M. Barata[7], Danela Murariu[8], Beate Schierscher-Viret[9], Alex Stringens[10], Violeta Andjelkovic[11], Sandra Goritschnig[12], Brigitte Gouesnard[13], Alain Charcosset[1], Stéphane D. Nicolas[1*]

[1] Université Paris-Saclay, INRAE, CNRS, AgroParisTech, GQE - Le Moulon, 12 route 128, 91190, Gif-sur-Yvette, France
[2] INRAE, URP3F, Le Chêne, Lusignan, France
[3] Misión Biológica de Galicia Consejo Superior de Investigaciones Científicas, Pazo de Salcedo. Carballeira, 8 Salcedo, 36143 Pontevedra, Spain
[4] CREA- Council for Agricultural Research and Economics, Research Centre for Cereal and Industrial Crops, via Stezzano 24, 24126 Bergamo, Italy
[5] Agriculture School of the Polytechnic University of Coimbra (IPC-ESAC) and CERNAS – Research Centre for Natural Resources, Environment and Society Bencanta, 3045-601 Coimbra, Portugal
[6] University of Zagreb Faculty of Agriculture, Svetošimunska cesta 25, 10000 Zagreb, Croatia
[7] Banco Português de Germoplasma Vegetal, Quinta de S. José, S.Pedro de Merelim, 4700-859 Braga, Portugal
[8] Suceava genebank, b-dul. 1 Mai 17, 720224, Suceava, Romania
[9] Agroscope, Route de Duillier 60, Case Postale 1012, 1260 Nyon 1, Schweiz – Switzerland
[10] DSP -Delley Semences et Plantes SA, Route de Portalban 40, 1567 Delley, Switzerland
[11] Maize Research Institute Zemun Polje, Belgrade, Serbia
[12] ECPGR, Alliance of Bioversity International and CIAT, Via di San Domenico 1, 00153 Roma, Italy
[13] UMR AGAP Institut, Univ Montpellier, CIRAD, INRAE, Institut Agro, F-34398 Montpellier, France
* Corresponding author: Stéphane D. Nicolas (stephane.nicolas@inrae.fr)

Keywords

Genomic offset, Landraces, Genomic prediction, Genebanks, *Zea mays*, DNA pool genotyping

Short Title

Genomic prediction and offset to characterize maize landraces from genebanks

Teaser

Identify promising landrace adapted to new and future environments by combining genomic selection and offset

Abstract

Forecasting vulnerability of cultivated and wild species to climate changes is highly challenging. Evolutionary genomic models enable the prediction of mal-adaptation (genomic offset - GO) across environments and future climates under the assumption that populations are currently locally adapted but do not predict but the resulting phenotypic changes. To do so, we developed a new genomic prediction model (GP) integrating both genomic offset (GO) and within-population gene diversity (Hs) to capture genotype by environment interaction and inbreeding effects, respectively (GP-HO-Hs). As proof of concept, we applied this GP-GO-Hs model to a collection of 397 maize populations (landraces) evaluated across 25 environments in Europe using high-throughput DNA pool genotyping. GP-GO-Hs model accurately predicted yield, plant height and flowering time. It increased by 13% the predictive abilities of GP model for predicting yield of new landraces in new environments. GP-GO-Hs model also predicted that the more diverse the landrace, the more stable its agronomic performance across environments. GP-GO-Hs model generated phenotypic adaptive landscapes for each landrace in future climatic scenarios, enabling the identification of landraces with enhanced potential to adapt to future or emerging cultivation conditions. This GP-GO-Hs model could be easily applied to other wild and cultivated species.

Introduction

Adaptation of crops to changing growing conditions is critical to meet future food demands, as major crops are expected to be negatively impacted by climate change and variability (Ceccarelli et al., 2010; Challinor et al., 2014; Godfray et al., 2010; Minoli et al., 2022). This impact is expected to be variable across regions and crops (Jägermeyr et al., 2021; Rezaei et al., 2023). Maize is the world's most produced cereal and the one expected to be most highly demanded in the future for food, feed and fuel (OECD & Food and Agriculture Organization of the United Nations, 2022). Maize global production is expected to be negatively impacted by climate change with up to 11% of yield-loss expected in Europe (Heino et al., 2023; Jägermeyr et al., 2021; Knox et al., 2016; Zhao et al., 2017). Breeding for or introducing cultivars adapted to these future conditions could mitigate or even reverse this impact (Challinor et al., 2016; Minoli et al., 2022; Parent et al., 2018; Tsubo & Moeletsi, 2025). Therefore, there is an urgent need for characterizing the available genetic diversity to facilitate its utilization (Martini et al., 2021; Mascher et al., 2019; *FAO*, 2025).

Maize was domesticated in Mexico approximately 9000 years ago and adapted to wide uses and pedo-climatic conditions throughout America, Europe and the rest of the world leading to locally adapted open pollinated populations–landraces (Brandenburg et al., 2017; Matsuoka et al., 2002; Mir et al., 2013; Romero Navarro et al., 2017). Maize landraces have been cultivated in conditions ranging from 0 to 2900 m of altitude, 426 to 4245 mm of annual rainfall and 11.3 to 26.6°C of annual temperature and in latitudes from 58° N to 40° S (Hallauer et al., 2010; Ruiz Corral et al., 2008). After 1930s, modern hybrids replaced landraces in most parts of the world (Duvick, 2001). But few landraces have been used as the starting point of modern breeding programs and the pedigree of currently cultivated hybrids traces back to only a few founder lines (Arca et al., 2023; Smith et al., 2022).

Despite major genetic progress achieved for yield and abiotic stress tolerance, the narrow diversity of elite germplasm can jeopardize future genetic gains (Allier et al., 2019; Campos et al., 2006; Sanchez et al., 2023; Smith et al., 2022; Welcker et al., 2022) and cope with new traits required for sustainable agriculture (e.g., reduced nitrogen fertilization) or climate

change (e.g., increasing temperatures and more frequent droughts) (Hawkesford & Griffiths, 2019; Heino et al., 2023). Consequently, maize landraces are receiving increasing attention as a reservoir of favorable alleles to introduce useful diversity into breeding programs (Böhm et al., 2017; Gorjanc et al., 2016; Hoisington et al., 1999; Hölker et al., 2019; Mayer et al., 2020). However, the utilization of genetic resources is partially constrained by the lack of information, as only 22% of maize accessions have been characterized despite big efforts made by genebanks (*FAO*, 2025). Because the identification of promising accessions is crucial for pre-breeding programs, methods that allow one to predict performances of not yet phenotyped accessions, such as genomic prediction (GP), could have a major impact in breeding for adaptation (Böhm et al., 2017; El Hanafi et al., 2023; Mascher et al., 2019).

GP enables the estimation of breeding values for accessions without phenotypic records using molecular markers and it has long been proposed as a solution to avoid the evaluation of large number of genotypes (Bernardo, 1994; Meuwissen et al., 2001). GP has been widely adopted in maize breeding programs but its application to maize landraces remains limited (Gholami et al., 2021). Previous works have focused on using single plant genotyping to predict the performance of landraces or their derived doubled haploid lines in combination with testers (Böhm et al., 2017; Hölker et al., 2019, 2022; Li et al., 2025; Romero Navarro et al., 2017). These studies have yielded promising results to identify beneficial alleles and represent an important step towards integrating landraces into breeding programs. However, the use of tester may blur the adaptation signal of landraces (Li et al., 2025) and generating DH lines from landraces is a costly process that allows to explore only few selected landraces (Böhm et al., 2017). Thus, efficient GP approach that enable the prediction of landrace *per se* agronomic performance and adaptation in various environments and the identification of best landraces are needed. In addition, genotyping single plants is insufficient to represent within landrace diversity. This is because maize landraces are heterogeneous populations, thus sampling multiple individuals is necessary to accurately characterize each accession, leading to increased genotyping costs.

To cope with this issue, high-throughput pool genotyping (HPG) methods, such as DNA-pool genotyping or sequencing, offer a cost-effective alternative to individual genotyping

113 and could therefore enable the large-scale application of GP to maize landraces (Arca et al.,
114 2021). In forage crops, HPG-based genomic prediction has proven useful for predicting the
115 value of synthetics and natural populations (Cericola et al., 2018; Keep et al., 2020; Pégard et
116 al., 2023). DNA-pool genotyping enabled a detailed understanding of maize landraces' ge-
117 netic composition, the history of maize dispersion, within-population gene diversity, and the
118 mechanisms underlying adaptation to diverse environments (Arca et al., 2023; Balconi et al.,
119 2024; Mir et al., 2013; Rebourg et al., 2003; Tamang et al., 2024). DNA-pooling genotyping
120 also showed that within-population gene diversity of maize landraces greatly varied and
121 was positively correlated with their *per se* agronomic performance reflecting certainly in-
122 breeding depression effect (Rebourg et al., 2001). Despite previous work, HPG has not been
123 explored yet to perform GP for maize landraces *per se*.

124 In addition to GP, ecology-derived methods that predict (mal)adaptation to present or fu-
125 ture scenario climatic conditions are gaining attention and have been applied to identify
126 useful genetic resources (Fitzpatrick et al., 2025; Rellstab et al., 2021). These methods link
127 current patterns of adaptive genomic composition to climatic conditions. Ultimately, they
128 allow one to estimate the allelic frequencies shift required at certain loci for populations to
129 be adapted to a new environment, a concept known as genomic offset (GO) (Fitzpatrick &
130 Keller, 2015). Gradient Forest (GF) is one of the most used models to predict
131 (mal)adaptation (Capblancq et al., 2020; Ellis et al., 2012). For maize landraces, GF was used
132 to assess future (mal)adaptation for a set of Mexican and Himalayan landraces, raising con-
133 cern about their *in-situ* preservation (Aguirre-Liguori et al., 2019; Tamang et al., 2024). De-
134 spite the potential of GO to identify endangered or interesting genetic resources for substi-
135 tution or pre-breeding, the integration of the GO with GP to predict *per-se* maize landrace
136 performances remains unexplored (McLaughlin et al., 2024).

137 In this study, we investigated the use of GP in combination with GO as a tool to unlock ge-
138 netic diversity in gene banks by massively predicting maize landrace performances, particu-
139 larly for complex traits of agronomic and economic importance such as grain yield, flower-
140 ing time and plant height in various environments and future climatic scenarios. We com-
141 bined genotypic data obtained from cost-effective HPG, with the phenotypic performances

142 for three agronomic traits of 397 landraces evaluated across a sparse 25 environment net-
143 work within the ECPGR EVA Maize Network. First, we took advantage from the climatic
144 characterization of both landrace collection sites and field experiments to predict landrace
145 (mal)adaptation to each experiment using GO and how it was related to agronomic perfor-
146 mance. Second, we evaluated accuracy of GP based on HPG for male flowering time, grain
147 yield and plant height in three scenarios of increasing difficulty: (i) completing missing data
148 in the trial network, (ii) predicting the values of a new accession in different environments
149 within the network (iii) and predicting a new accession in a new environment. Third, we as-
150 sessed to which extent within-population gene diversity (Hs) and GO captured part of the
151 genotypic and the genotype-by-environment variation and their potential to improve GP
152 accuracy in these three different scenarios. Finally, we proposed an approach that combined
153 GP and eco-genetic statistics to identify promising accessions for adaptation to future cli-
154 mate scenarios across Europe.

155 # Results

156 ## Modelling landrace adaptation to past and future climates

157 To investigate the adaptation of landraces to local environments, we applied the Gradient
158 Forest (GF) approach to a panel of 470 European maize landraces (**Table S1**), combining
159 allelic frequency and climatic variables of landrace collection sites (**Table S2**). GF models
160 allelic frequency variation of loci along climatic gradients. Our GF model identified 243 SNPs
161 significantly associated with the variation of 55 climatic variables from WorldClim2.1 (R^2 >
162 0.47 –**Figure S1A**). Among these SNPs putatively involved in climatic response, we identified
163 *loci* known to be involved in flowering time and adaptation in previous studies such as *Vgt2*
164 (PZE-108070380; R^2 = 0.60), *Vgt3* (PZE-103098779; R^2 = 0.49) and *ZCN2* (PZE-104057075; R^2
165 = 0.47, **Table S3**). The GF model ranked the importance of climatic variables to predict allel-
166 ic frequency variations of these 243 SNPs. This enabled us to retain the top 15 complemen-
167 tary climatic variables (accuracy importance > 0.01; **Figure S1B, Table S2)**.

168 We then studied spatial genetic variation based on the GF model adjusted with the selected
169 243 SNPs and these 15 climatic variables (**Figure 1A**). The geographical distribution of ge-
170 netic composition predicted by GF differentiated several climatic regions. "Green" regions
171 represented the largest area in Europe and included all Eastern European Countries but also
172 Po Valley in North of Italy, Central Southern Spain and Turkey. "Orange" regions were main-
173 ly located along the Atlantic Ocean but also along the Mediterranean coast and southern
174 regions of Portugal, France and Italy, with a South-North gradient corresponding to de-
175 creasing temperature in summer (light to dark from South to the North). “Pink” regions in-
176 cluded Galicia, Northern Western Spain and South Western France. "Blue regions" were the
177 smallest area including mainly mountain regions (Alpes, Massif Central and Pyrenean) as
178 well as German regions. The biplot (**Figure 1B**) presents the grids (~4.5 x 4.5 km) of the ge-
179 ographical map with their corresponding color as well as the contribution of each variables
180 to PCA axis. In Figure 1B, the first PCA axis, linked with red color intensity, was associated
181 with winter temperature (*tmax_11)*, while the second axis, linked with green color intensity,
182 was associated with temperature seasonality (*bio_4)* and temperature annual range (*bio_7).*

The first axis discriminated landrace groups of the Iberian regions (SE-Spanish, Galician and Portuguese landraces), where winter temperature is soften by the oceanic effect, from landraces assigned to the Northern Flint (NF) and Corn Belt Dent (CBD) genetic groups (Balconi et al., 2024). The second axis discriminated landraces assigned to the CBD group, collected in continental regions where temperature varies greatly across the year, from NF and Galician groups. The geographic distribution of genetic groups strongly mirrored the genetic composition predicted by GF, suggesting local adaptation of genetic groups.

We used the GF model to estimate GO expected under future climatic scenarios for each grid of the map across Europe (local GO). To do so, we used GF-transformed climatic variables from WorldClim2.1 past (1970-2000) data and four future climatic scenarios derived from two CO_2 concentration ([CO2]) corresponding to two greenhouse gases emission trajectories (one optimistic -SSP126- and one pessimistic -SSP585) and two time periods (one at short term - 2041-2060 - and one at long term - 2080-2100) with 13 global circulation models (GCMs, **Table S4**). Mean local GO across 13 GCMs increased across Europe under all future climatic scenarios with the highest increase for SSP585 scenario in 2081-2100 horizon, in NE-France, Germany and E-Europe (**Figure S2**). This implies that landraces collected in these regions could be maladapted to future climatic conditions in these same regions.

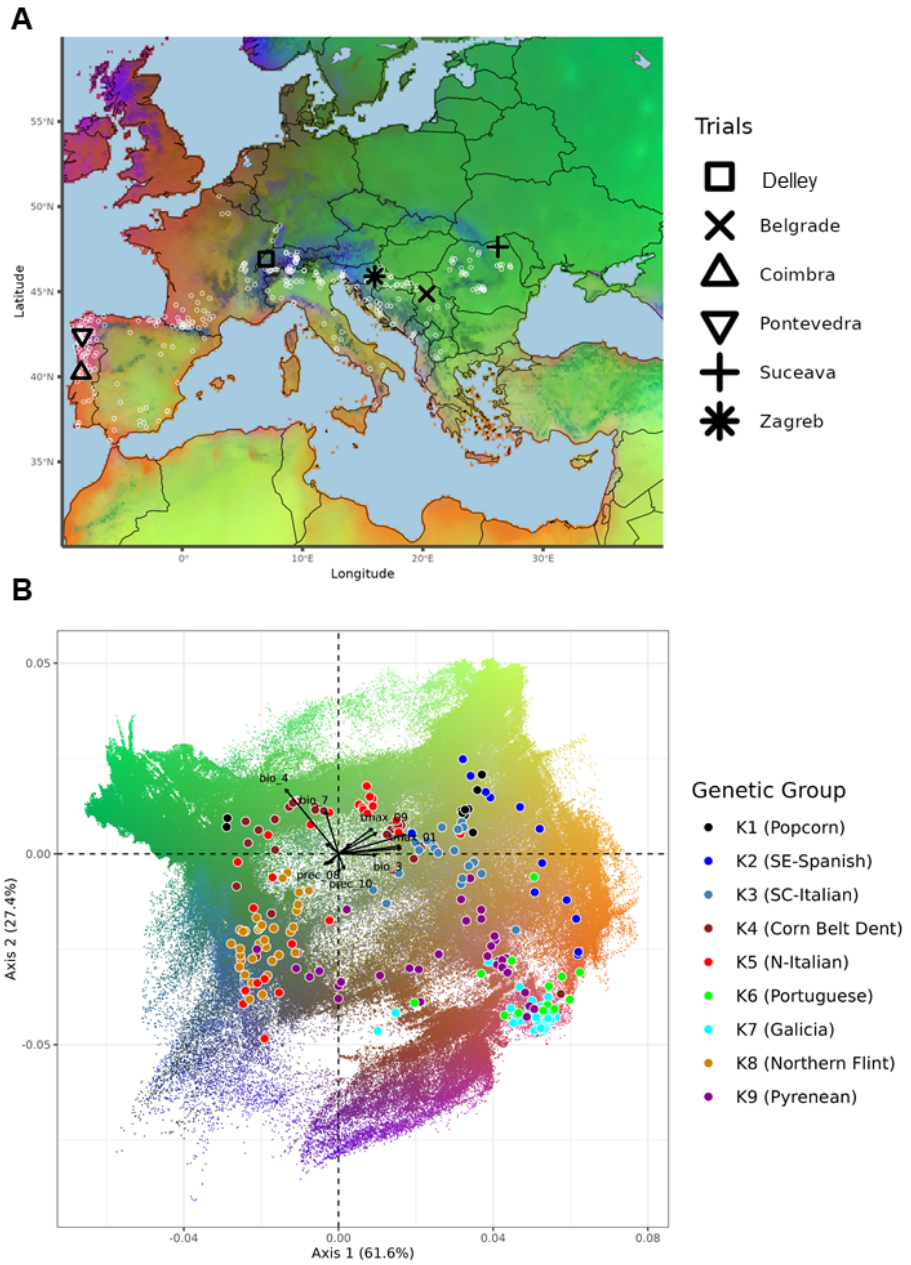

Fig. 1. Genetic adaptive landscape of maize landraces to past climatic conditions (1970-2000). (**A**) Adaptative landscape map of maize landraces is colored according to the first three axes of the Principal Component Analysis (PCA) on Gradient Forest (GF) transformed climatic variables from Worldclim 2.1 for period 1970-2000. The color at each grid (~4.5km^2) of the geographical map is based on a multivariate scale where each color is a mixture of red, green and blue with its intensity proportional to the first three PCA coordinates, respectively. As GF-transformed climatic variables represent adaptive allelic frequency variation, the different colors illustrate different adaptive genetic composition. Landrace collection sites and EVA Network field experiment sites are represented by white circles and black symbols, respectively. **(B)** The biplot of the first plan of PCA on GF-transformed climatic variables for the grids in the geographical map with their corresponding color and climatic variable vectors. Black symbols represent the projection of climatic conditions at field experiments. Colored circles represent the projection of collection site climatic conditions for landraces highly assigned to genetic groups (> 0.6).

Similarly, we used the GF model to predict the adaptive landscape for each landrace across Europe. The geographic distribution of GO predictions of four landraces representing different genetic groups showed contrasting patterns for past and future scenarios (**Figure 2**). For past climatic data, two landraces (ESP0148 and FRA0296) showed low GO (<0.03) in large geographic regions close to their collection sites, in Northern and Southern Europe, respectively. In contrast, for BIH0063 and FRA0491, geographic areas with low GO were more limited while those with high GO (> 0.07) were larger and included important maize production regions. Future climatic conditions had a negative impact on local adaptation for these 4 landraces irrespective of the period and the scenarios, with the highest negative impact observed for the 2081-2100 time horizon.

The pessimistic scenario (SSP585) led to an increase of the geographical area with high GO, and a reduction of geographical area with low GO. In contrast, under the optimistic scenario (SSP126), the model showed globally a small decrease in low GO area. The landrace BIH0063, assigned to CBD, was the most affected by climate change. In contrast, the SE-Spanish landrace ESP0148 showed less dramatic changes in GO for future scenarios. As GO relies only on climatic and genotypic data, no inference can be done in terms of loss of agronomic performance, limiting the interpretation of maladaptation predictions based on GO only.

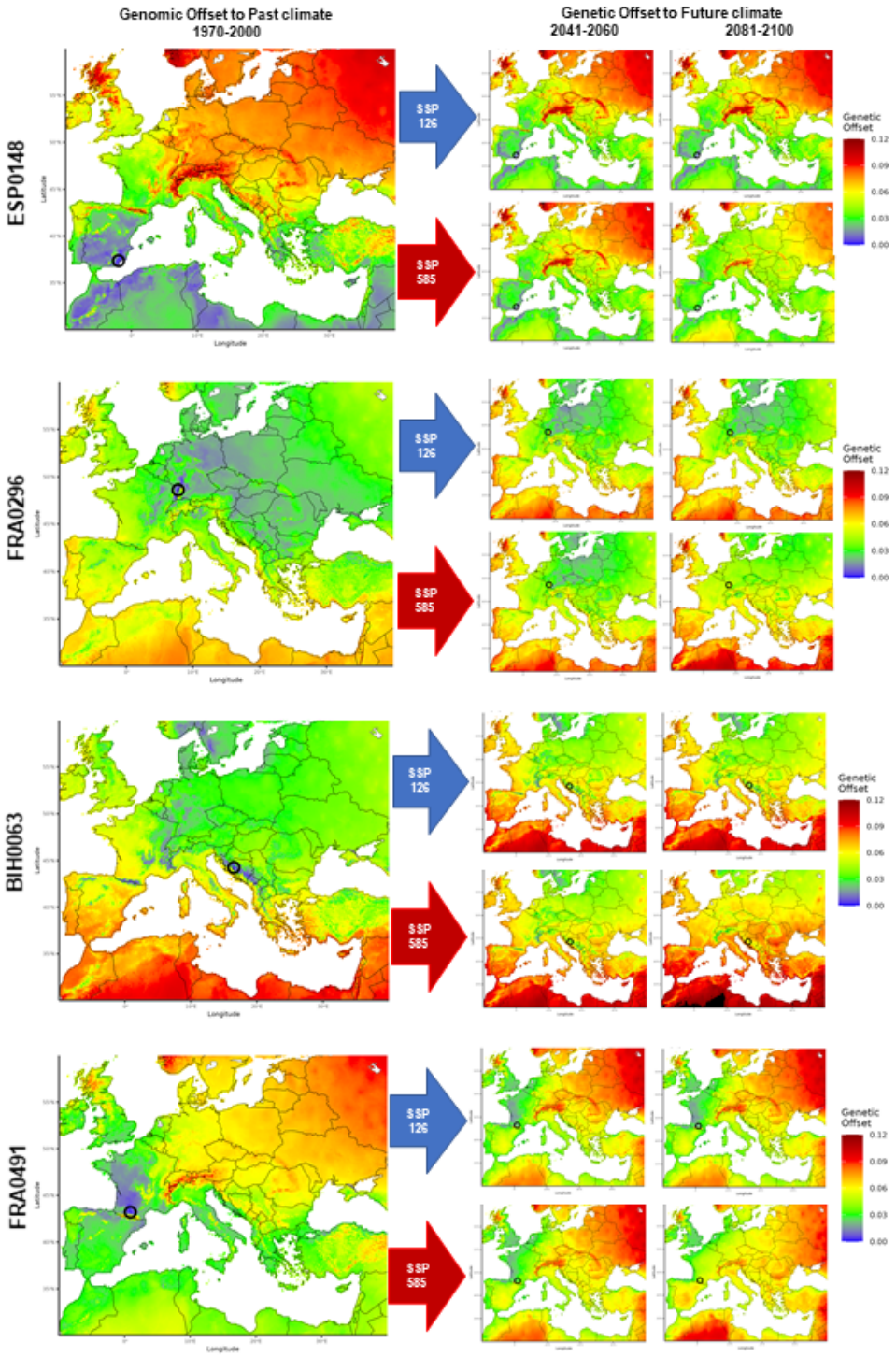

Fig 2. Prediction of (mal)adaptation (genomic offset) in past and future climatic conditions under different emission scenarios. The maps represent GO for four landraces under past (left) and future (right) climatic conditions. GO is defined as the Euclidean distance between GF-transformed past climatic variables of landrace collection sites (black circles) and climatic variables across Europe, in the past (left) or as predicted in the future (right). Because GF models the relationship between climatic variables and adaptive allelic frequencies, this distance represents the genetic distance to a theoretically-local adapted population (i.e adaptation gap). We selected for illustration four landraces representing different genetic groups: ESP0148 (SE-Spanish), FRA0296 (NF), BIH0063 (CBD), and FRA0491 (Pyrenean). Past climatic conditions are based on WorldClim 2.1 (1970-2000) while future climatic scenarios represent the combination of two time-horizons (2041-2060 and 2081-2100) with two emission pathways: SSP126 (blue arrows) and SSP585 (red arrows).

Effect of genomic offset and within-population gene diversity on agronomic traits

In order to test the effect of (mal)adaptation predicted by GO on agronomic performances, we evaluated the phenotypic response of 397 landraces to 25 environments for male flowering time (MF, in growing degrees units-GDU), plant height (PH, in cm) and grain yield (GY, in t/ha), using a sparse experimental design (**Table S5)**. The results of phenotypic evaluation are summarized in **Table 1** and **Table S6.** Means across the network were 788 GDU for MF, 183 cm for PH and 4 t/ha for GY (**Table 1**). Mean heritabilities were 0.96 for MF, 0.91 for PH and 0.86 for GY (**Table 1**). Significant variation of the three traits was observed between and within experiments (**Figure S3, Table S6).** The maximum GY was achieved at Zagreb (Croatia) in 2024 while the lowest one was recorded at Zagreb (Croatia) in 2022 (**Table S6**).

Table 1. Summary of EVA network environment means and heritabilities for male flowering, plant height and grain yield. Mean, standard deviation (SD), minimum and maximum is based on 25 environments of the EVA network.

			EVA network phenotypic data			EVA network heritability		
Trait	**Acronym**	**Unit**	**Mean (SD)**	**Min**	**Max**	**Mean (SD)**	**Min**	**Max**
Male Flowering	**MF**	GDU	788.64 (103.8)	624.84	1007.89	0.964 (0.03)	0.9	0.99
Plant Height	**PH**	cm	186.9 (32.51)	126.53	238.01	0.906 (0.09)	0.64	0.99
Grain Yield	**GY**	t/ha	3.82 (0.97)	2.09	5.63	0.855 (0.12)	0.44	0.99

To assess the adaptation of landraces to field experiment conditions, we used GF to estimate GO between environmental conditions of each experiment and each landrace collection site (**Table S7**). Our field trial experimental network covered well the range of climatic conditions of landraces' collection sites (**Figure 1B**). Maximum GO (corresponding to putatively the worst adapted accession) was 0.107 for the landrace "Vilariño" (ESP0142), collected in Galicia and evaluated at Suceava (Romania) in 2021 (SSR_2021_1A). In contrast, the lowest GO (putatively best adapted accession) was 0.015 for the Portuguese landrace "Milho Amarelo" (PRT0202) evaluated at Pontevedra (Galicia, Spain) in 2021 (CPS_2021_1A). The GO range for each landrace across the field trial experimental network (maximum GO – minimum GO) was highly variable (0.0002 to 0.0875, **Figure S4**), indicating that only part of the

landraces (~10%) was evaluated in contrasted conditions of low (<0.03) and high (>0.07) GO conditions. GO and the geographic distance between landrace collection sites and field experiments were correlated (**Figure S5**), indicating that the lowest GO were reached for landraces collected close to the experimental trials. This further supports the close relationship between local adaptation and the geographic distribution of genetic groups.

To assess the effect of GO estimation of maladaptation on phenotypic variation, we analyzed the relationship between GO and traits measured at each trial ($\bar{Y}_{grc}$). GO was slightly but significantly negatively correlated with GY (p < 0.001, b = -19 t/ha, R^2 = 0.05; **Figure 3A**) and PH (p < 0.001, b = -464 cm, R^2 = 0.06; **Figure S6A**). In the contrary, we observed no relationship between GO and MF (p = 0.173, R^2 < 0.001; **Figure S6B**). Focusing only on landraces that were evaluated under contrasting GO conditions (n = 46) increased the linear relationship between GO and GY (b = -27 t/ha, R^2 = 0.16), while this only had a limited or no effect for PH and MF, respectively (**Figure S7**). This suggests that the effect of GO on decreasing agronomic performance was certainly underestimated for the entire panel, since most landraces were evaluated in trials with weak contrasting GO contrast.

We also assessed the effect of inbreeding depression on phenotypic variation by studying the relationship between within-population gene diversity (Hs) and the three traits (**Figure 3B and Figure S8**). Mean Hs was 0.214 and it varied greatly among landraces, ranging from 0.075 (CHE0355 assigned to NF) to 0.299 (ITA0083 assigned to CBD) (**Table S1)**. Hs showed a significant and positive linear relationship with GY (p < 0.001, b = 15 t/ha, R^2 = 0.25; **Figure 3B**) and PH (p < 0.001, b = 321 cm, R^2 = 0.30; **Figure S8A**) but not with MF (p = 0.558, R^2 < 0.01; **Figure S8B**). This suggests that flowering time is less affected by inbreeding depression than GY and PH.

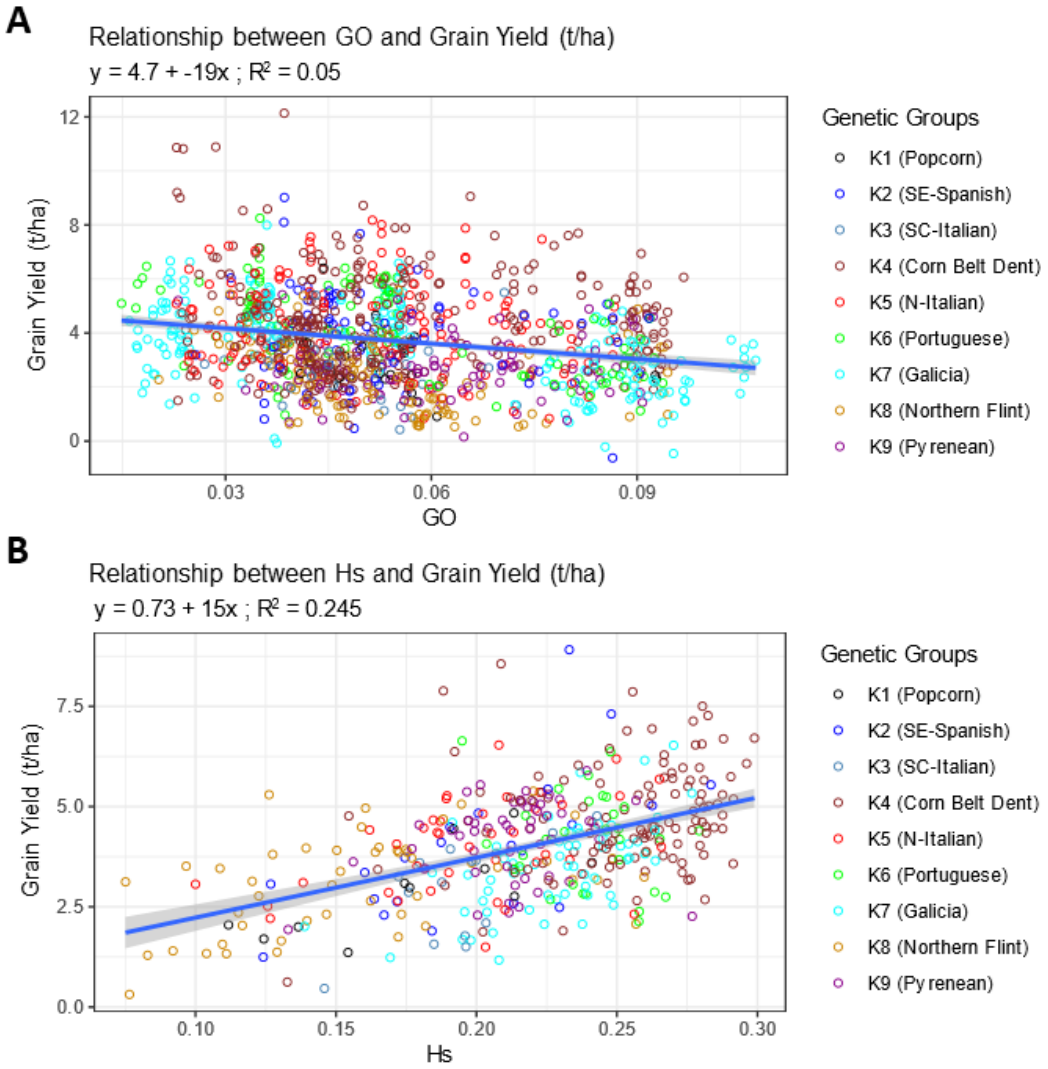

Fig. 3. Effect of within-population gene diversity (Hs) and genomic offset (GO) on grain yield (GY). **(A)** Relationship between genomic offset (GO) of each landrace to each field experiment and grain yield within experiment adjusted means. Each circle represents one landrace evaluated in one experiment. **(B)** Relationship between within-population gene diversity (Hs) with grain yield least square means across EVA Network field experiments. Each circle represents one landrace. In **A** and **B**, circles are colored by maximum assignment to 9 genetic groups.

Within-population gene diversity and genomic offset capture a part of genotypic and genotype-by-environment variance of grain yield and plant height

To evaluate the contribution of Hs and GO to the genotype and genotype by environment (G×E) variance components, we compared a first model (M1) accounting for the genotype and G×E effects with models also including either the GO effect (M2), or the Hs effect (M3) or both (M4). (**Table 2**).

Table 2. Variance decomposition of male flowering, plant height and grain yield for the four models. Base model M1 included genotype, genotype-environment interaction as random effects. M2 model included all terms of M1 model plus genomic offset (GO) as fixed effect. M3 model included all terms of M1 model plus within-population gene diversity (Hs) as fixed effect. M4 model included all terms of M1 model plus both GO and Hs as fixed effect.

Trait	Variance / Effect	M1	M2 (M1+GO)	M3 (M1+Hs)	M4 (M1+Hs+GO)
Male Flowering	σ^2_g	7356,78	7335,78	7287,96	7266,58
	σ^2_{ge}	1061,84	1060,17	1061,37	1059,61
	σ^2_e	481,37	481,86	481,52	482,02
	GO Effect	-	-112,36	-	-113,83
	Hs Effect	-	-	-256,43	-257,45
Plant Height	σ^2_g	828,02	816,07	762,54	750,12
	σ^2_{ge}	56,42	53,91	56,61	53,99
	σ^2_e	136,81	137,37	136,91	137,54
	GO Effect	-	-87,07	-	-88,10
	Hs Effect	-	-	215,38	214,97
Grain Yield	σ^2_g	1,13	1,11	0,91	0,89
	σ^2_{ge}	0,55	0,52	0,56	0,53
	σ^2_e	0,95	0,95	0,95	0,95
	GO Effect	-	-10,61	-	-10,72
	Hs Effect	-	-	10,97	10,96

For M1, the genotype variance (σ_g^2) accounted for 83%, 81% and 43% of the total variance for MF, PH and GY, respectively. The G×E variance (σ_{ge}^2) accounted for 12%, 6% and 21% of total variance for MF, PH and GY, respectively. This indicates that G×E contributed approximately two and four times more to GY variation than to MF and PH, respectively. When adding GO in the model (M2), σ_g^2 slightly decreased in reference to M1 for PH and GY (-1% and -2%, respectively). This decrease was stronger (-4% and -6%, respectively) for σ_{ge}^2, indicating that GO captured mainly G×E for both PH and GY. When Hs was included in the

model (M3), σ_g^2 decreased by 8% and 20% for PH and GY relative to M1, respectively, while there was no or a slight increase in σ_{ge}^2. This indicates that Hs captured mainly the genetic variation between landraces for PH and GY. Finally, when including both GO and Hs (M4), we observed a decrease of the genotypic and G×E variance for PH and GY which was much stronger for σ_g^2 (-9% and -22%, respectively) than for σ_{ge}^2 (-4% for both traits). Hs and GO captured therefore 19% and 10% of the genetic variance component for GY and PH, respectively. GO and Hs acted independently on trait variation since Hs and GO displayed similar effects irrespective of whether they were considered together in the model (M4) or as unique factors of variation (M2 and M3). With the model 4, an increase of GO by 0.1 reduced GY by 1.1 t/ha and PH by 88 cm, while an increase of Hs by 0.1 increased GY by 1.1 t/ha and PH by 214 cm (**Table 3**). This suggests that PH is proportionally more impacted by Hs than GO compared to GY (**Table 3**).

Table 3. Comparison of predictive abilities between four genomic prediction models for three traits that included or not within-population gene diversity and genomic offset and using different cross-validations schemes. Mean, standard deviation (SD) and gain of predictive abilities (PA) were estimated for the different genomic prediction models for the three traits and the three different cross validation schemes (CV). Four models for genomic prediction corresponded to the same models used in Table S2. Predictive abilities gains are estimated in reference to the model M1.

Trait	CV	PA	M1	M2 (M1+GO)	M3 (M1+Hs)	M4 (M1+Hs+GO)
Male Flowering	CV2	Mean (SD)	0.94 (0.01)	0.94 (0.01)	0.94 (0.01)	0.94 (0.01)
		Gain (%)	**-**	**0.0**	**0.1**	**0.1**
	CV1	Mean	0.89 (0.02)	0.89 (0.02)	0.89 (0.02)	0.89 (0.02)
		Gain (%)	**-**	**0.0**	**-0.2**	**-0.1**
	CV00	Mean	0.69 (0.19)	0.69 (0.19)	0.69 (0.18)	0.69 (0.18)
		Gain (%)	**-**	**-0.3**	**-0.3**	**-0.6**
Plant Height	CV2	Mean	0.92 (0.01)	0.92 (0.01)	0.92 (0.01)	0.93 (0.01)
		Gain (%)	**-**	**0.0**	**0.1**	**0.2**
	CV1	Mean	0.84 (0.04)	0.84 (0.04)	0.85 (0.03)	0.86 (0.03)
		Gain (%)	**-**	**0.2**	**2.0**	**2.1**
	CV00	Mean	0.53 (0.20)	0.54 (0.20)	0.58 (0.16)	0.59 (0.15)
		Gain (%)	**-**	**1.3**	**10.2**	**11.9**
Grain Yield	CV2	Mean	0.75 (0.03)	0.76 (0.03)	0.76 (0.03)	0.76 (0.03)
		Gain (%)	**-**	**0.4**	**0.5**	**0.9**
	CV1	Mean	0.69 (0.06)	0.69 (0.06)	0.71 (0.04)	0.72 (0.04)
		Gain (%)	**-**	**0.4**	**4.2**	**4.5**
	CV00	Mean	0.52 (0.18)	0.54 (0.18)	0.57 (0.15)	0.59 (0.14)
		Gain (%)	**-**	**3.7**	**9.5**	**13.5**

333 We used Model 4 to study the effect of within-population gene diversity (Hs) on grain yield
334 stability across various climatic conditions (Figure 4). The distribution of grain yield G×E best
335 linear unbiased prediction ($BLUP_{G\times E}$) across the EVA Network was highly variable across
336 landraces, suggesting that grain yield stability varied among landraces (**Figure 4A**). We then
337 analyzed the relationship between Hs and the standard deviation of $BLUP_{G\times E}$ for each land-
338 race predicted by the model M4 ($SD_{BLUPG\times E}$). Hs and $SD_{BLUPG\times E}$ were negatively linearly corre-
339 lated (b = -0.76, p < 0.001, R^2 = 0.191; **Figure 4B**), suggesting that landraces with the high-
340 est diversity were more stable across environments. In addition, $SD_{BLUPG\times E}$ was also positively
341 correlated with the landrace genetic value ($BLUP_G$), suggesting that high performing land-
342 races displayed also higher G×E (**Figure S9**). To test whether these relationships could
343 come from a spurious effect of our sparse design, we first analyzed if we accurately predict-
344 ed observed $SD_{G\times E}$ (**Figure S9**). Predicted $SD_{BLUPG\times E}$ was positively correlated with observed
345 G×E (b = 1.3, p < 0.001, R^2 = 0.05, **Figure S9**) and this correlation increased for landraces
346 evaluated in a high number of environments (b=2.2, r2=0.29 for landraces evaluated in at
347 least 4 environments). This suggests that our model predicted accurately $SD_{BLUPG\times E}$, and that,
348 as expected, this accuracy increased with the number of environments and that we certainly
349 underestimated $SD_{G\times E}$. (**Figure S9**). In addition, Hs, $SD_{BLUPG\times E}$ and observed G×E varied only
350 slightly according to the number of environments in which landraces were evaluated, indi-
351 cating that the effect of Hs on GY stability did not originate from an unbalanced distribution
352 of landraces with low or and high Hs across our sparse design (**Figure S10**).

353 We then compared 4 different previous models (M1, M2, M3, M4) for their ability to predict
354 GY, PH and MF of landraces across 25 environments using 3 cross-validation schemes corre-
355 sponding to 3 different prediction scenarios (**Figure S11**): (1) predicting a missing observa-
356 tion (unobserved landrace-environment combination) in a sparse experimental network
357 (CV2), (2) predicting a new landrace (never observed in any trial) in observed environments
358 of this network (CV1), and (3) predicting a new landrace in a new environment by hiding in
359 the calibration set a trial of this network (CV00).

360

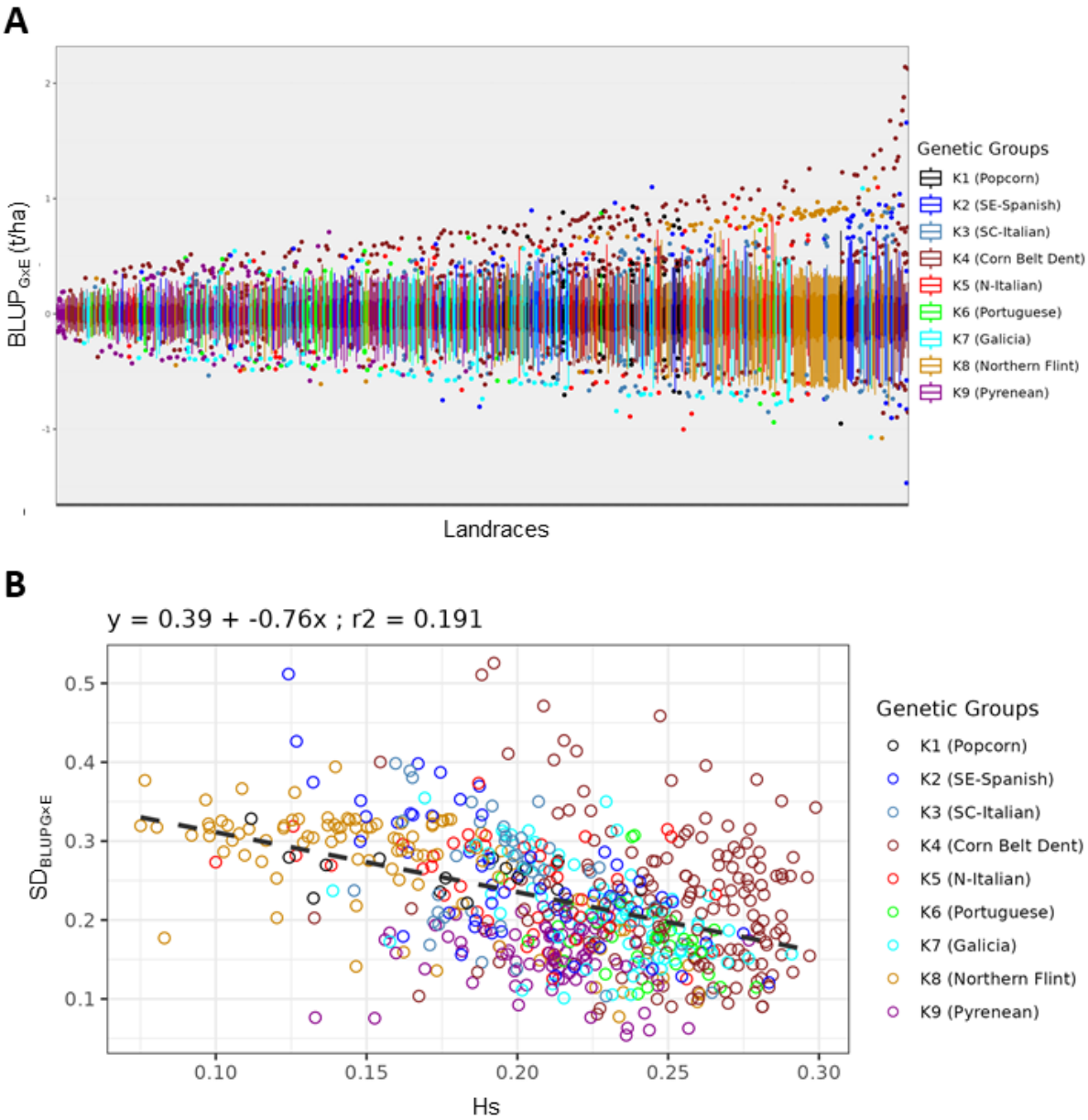

Fig. 4. Variation of grain yield stability across field trial network and how it relates with within-population gene diversity. (A) Variability for each landrace across 22 environments of grain yield genotype-by-environment interaction best linear unbiased predictors (BLUP$_{G\times E}$). **(B)** Relationship between within-population genetic diversity (Hs) and grain yield stability assessed using the standard deviation of BLUP$_{G\times E}$ (SD$_{BLUPG\times E}$). BLUP$_{G\times E}$ and SD$_{BLUPG\times E}$ were estimated using model 4 that included Hs and GO as covariables.

368 Predictive abilities (PA) obtained for the different traits were highest with the CV2 scenario,
369 followed closely by CV1 (**Table 3, Figure 5**). PA dropped strongly for all traits and models
370 when moving from CV1 to CV00. For instance, PA decreased from 0.89 to 0.69 for MF, from
371 0.84 to 0.53 for PH and from 0.69 to 0.52 for GY with model 1 (**Table 3**). Adding Hs and GO
372 in the models M2, M3 and M4 increased PA for GY and to a lesser extent PH under CV1 and
373 CV00 scenarios, while it did not increase PA for MF (**Figure 5**). The highest gain in PAs was
374 obtained with M4 under CV00 scenario (new landraces in new environments) with 11.9 and
375 13.5% of PA gain for PH and GY, respectively compared to M1 (**Table 3, Figure 5**). Including
376 Hs instead of GO in the model led to a higher gain in PA in CV00 scenario for PH (10.2 vs
377 1.3%) than for GY (9.5 vs 3.7%). For PH and GY, the gain in PA for M4 (Hs + GO) relative to
378 M1 could be obtained by adding the gain in PA of M2 (Hs) and M3 (GO), confirming that Hs
379 and GO contributed independently to trait variation. To test whether our GP models pre-
380 dicted more than the genetic structure, we compared PA obtained under M1 with predic-
381 tion using a multiple linear regression based on assignments to the nine genetic groups
382 (Table S1, Balconi, Galaretto et al., 2024). M1 outperformed multiple regression based on
383 genetic structure for all traits and all repetitions under CV2, and PA variability was strongly
384 reduced across repetitions (**Figure S12**).

385 PA distribution showed that PA increase for PH and GY in M3 and M4 was mostly driven by
386 PA increase of the worst predicted environments, leading to a decrease in PA variance (**Fig-**
387 **ure 5**). In particular, PA augmented in the three environments of Pontevedra (COS_2023_1B,
388 CES_2022_1B, and CES_2023_1B) for GY from 0.13, 0.26 and 0.29 in M1 to 0.51, 0.40 and 0.53
389 in M4, respectively (**Figure S13**). The same trend was evidenced for one experiment at
390 Delley (DDS_2024_2B3B), where PA increased from 0.20 in M1 to 0.30 in M4. This could indi-
391 cate that incorporating GO is most valuable for predicting GY in new environments, that are
392 difficult to predict because they differ from the ones included in the training set.

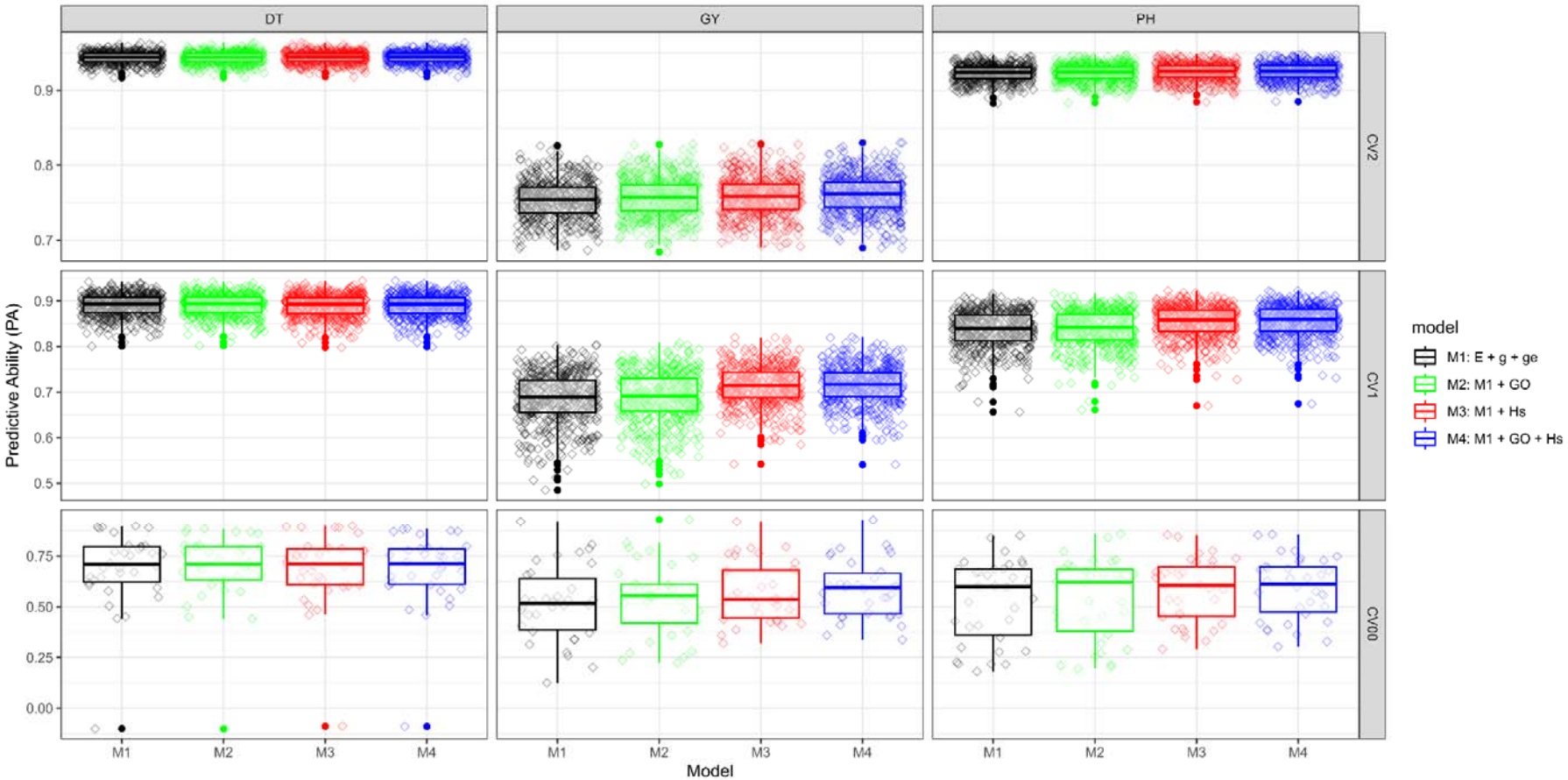

Fig. 5. Predictive ability for models and traits. Predictive abilities obtained using different genomic prediction models for male flowering (**MF – left**), grain yield (**GY - middle**) and plant height (**PH – right**) under **CV2** (**top**), **CV1** (**middle**) and **CV00** (**bottom**) cross validation scenarios. Under **CV2**, 20% of phenotypic observations (genotype-environment combinations) were randomly removed from the whole training set then predicted using 80% remaining training set. Under **CV1**, 20% of the genotypes were randomly selected and their phenotypic observations were removed across the dataset; as a consequence, genotypes to be predicted were not present in the training set. Under **CV00**, one trial is removed at each fold and their genotypes were removed also across other trials; as a consequence, both environment and genotype to be predicted were not present in the training set. Each point represents the correlation between observed and predicted values for one cross-validation fold.

Integrating genomic offset and genomic prediction enabled the identification of promising landraces adapted to future European climates

We investigated how to use the GF model in combination with the GP model integrating GO and Hs to identify landraces that could be adapted to future climatic scenarios. To do so, we devised a three-step scenario for selecting landraces that are well adapted (low GO), have a high grain yield (high genetic value) and are stable in fluctuating environments (low $SD_{BLUPG\times E}$) under a pessimistic (SSP585) long term (2081-2100) future climatic scenario. In a first step, we used GF model for selecting a list of landraces in the EVA panel with low GO (<0.03) under this future scenario conditions for two relevant target regions for maize production in Europe: NE-Romania and SW-France (**Figure 6**).

Across the EVA Panel, we identified 10 and 27 landraces presenting low GO for these two regions, respectively (**Tables S8-S9**). For NE-Romania, local landraces had high GO estimations (**Figure 6A**) while for SW-France, local landraces had low GO in future scenario (**Figure 6C**). This suggests that Romanian landraces will be maladapted under this future scenario and a stronger need for looking for non-local resources to breed for adaptation. In a second step, we used GP model integrating GO and Hs (M4) to predict agronomic performance of these landraces and to assess their yield stability using $SD_{BLUPG\times E}$ (**Figure S14, Tables S8-S9**).

For NE-Romania, predicted grain yield of selected landraces varied between 1.9 and 4.2 t/ha, while $SD_{BLUPG\times E}$ varied between 0.18 and 0.31 t/ha. None of these landraces were among the top 20% for both yield and stability (low $SD_{BLUPG\times E}$) (**Table S8**). For SW-France, predicted grain yield of selected landraces varied between 0.4 and 2.6 t/ha, while $SD_{BLUPG\times E}$ varied between 0.08 and 0.40 t/ha. Two landraces were among the top 20% for both yield and stability (**Table S9**). Following these two criteria (the highest performing and most stable), we identified PRT0537 and ITA0709 as promising landraces for NE-Romania and SW-France, respectively (**Figure S14**).

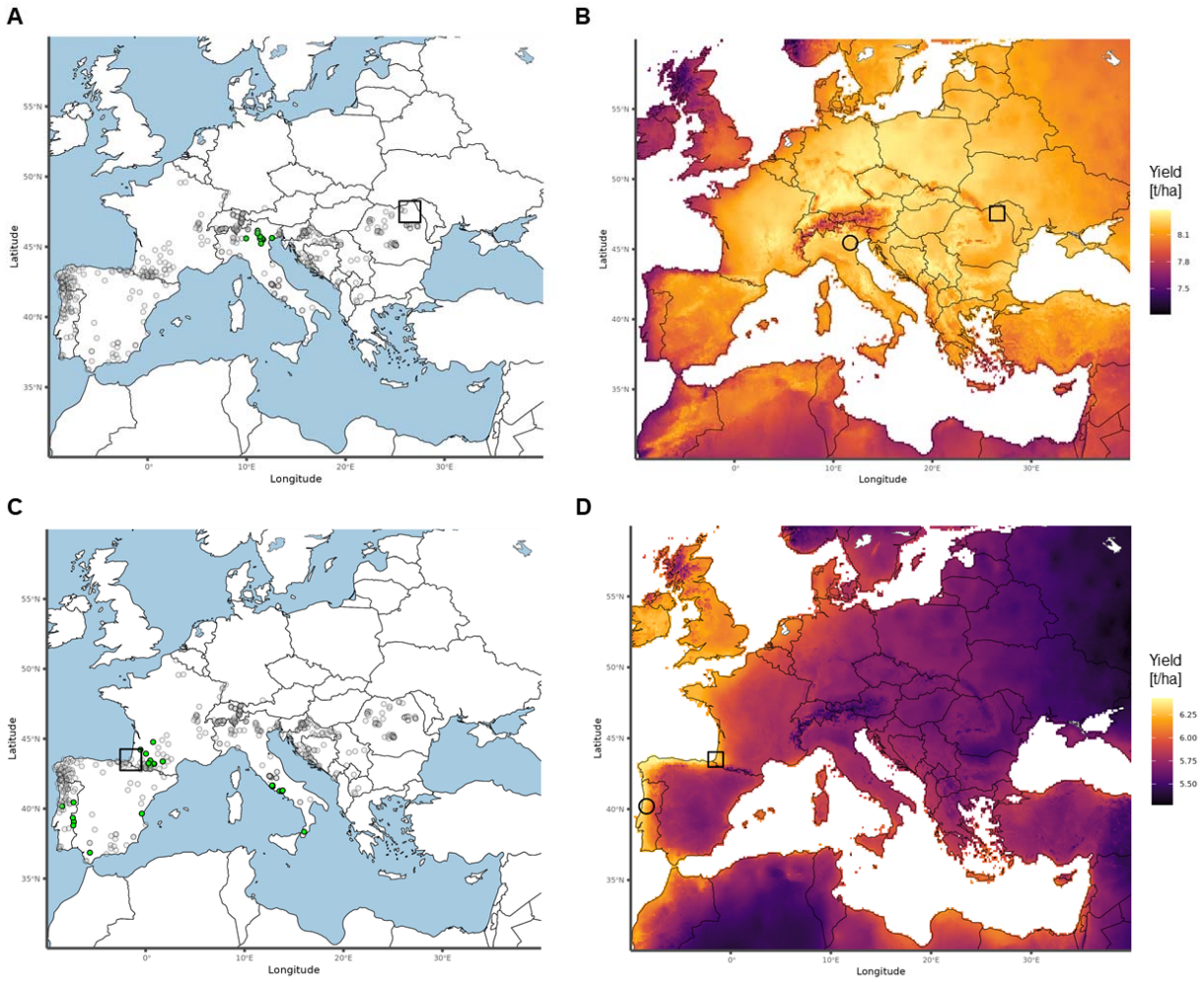

Fig. 6. Interesting landraces for future climatic scenario and yield variation due to genomic offset (GO). Identification of landraces with low genomic offset (GO <0.03; collection sites shown in green) for target regions (squares) of NE-Romania **(A)** and SW-France **(C)** under climatic conditions of SSP585 climate scenario for 2081–2100. Yield variation due to GO under this scenario is projected for two landraces selected considering predicted grain yield and stability, (ITA0709 and PRT0537) originating from countries different from the target regions (**B** and **D**, collection sites represented by circles). This example illustrates how combining GP with GO can support the identification of exotic genetic resources that satisfy different criteria.

We then illustrated yield variation of these two landraces across Europe in this future scenario. The Portuguese landraces PRT0537, displayed the best yield along the western coast of Portugal and Spain, in addition to SW France (target region) (Figure 6B). The Italian landrace ITA0709, displayed a good yield performance across all Europe except the Western Atlantic coast and the mountain regions in these future scenarios (Figure 6D). This landrace showed a low loss of performance for most part of the SE-European agricultural region, but a higher predicted yield loss due to increased GO in western France and most of Spain and Portugal.

We then investigated whether some landraces will be favored by climate change or not in regions across Europe with genomic prediction model M4. We estimated yield variation due to GO for four landraces representing different genetic groups and how it will evolve (yield gain/loss) in SSP585 at 2081-2100 as compared to the past climate. Whatever the landrace, we observed a higher yield loss in the region of origin of the landrace (or in regions with similar environment) which is expected since GO could only decrease in this region. Interestingly, yield change strongly depends on the landraces. For instance, the model predicted that the yield of Southern Spanish landraces (such as ESP0148) will strongly increase in the North of Europe above latitude 47° (>1t/ha) where they were not originally adapted (**Figure S15**). Similarly, the French Pyrenean landrace FRA0491 will lose yield in Western France but will gain yield in Germany and Eastern Europe. In contrast, no yield gain was observed for the Bosnian Landrace BIH0063 or the Northern Eastern French landrace FRA0296 suggesting that these landraces will be no longer adapted to any European region in the future. Taken together, our results showed that climate change may differently impact landraces, according to their region of origin and whether the environment corresponding to the landrace collection site will expand or reduce in the future.

Discussion

HPG-based genomic prediction is an efficient and cost-effective approach to characterize genebank collections of landraces

Exploiting genetic resources and adaptive alleles is essential for addressing future agricultural challenges (Godfray et al., 2010; Hoisington et al., 1999). Given the vast number of accessions preserved *ex-situ* in gene banks, efficient tools are needed to identify the most promising ones for pre-breeding programs (Böhm et al., 2017; Bohra et al., 2022; Gorjanc et al., 2016; Mayer et al., 2020; *FAO*, 2025). In our study, we investigated the potential of combining high throughput DNA-pool genotyping (HPG), genomic prediction (GP), genomic offset (GO) and within-population gene diversity (Hs) to predict performances of maize landraces for agro-morphological traits and their adaptation to future climatic scenarios. HPG enables to significantly reduce genotyping costs, becoming a feasible strategy for massive characterization of genebank collections, especially for heterogeneous population (Arca et al., 2021; Mascher et al., 2019).

Our GP models trained with a sparse evaluation network accurately predicted landrace agro-morphological traits in observed environments, in which they never were evaluated (prediction scenarios "CV2" and "CV1"). This corresponds to a typical genebank use case in which we would like to predict the phenotype of an unobserved landrace across various environments based only on their genotype and a training set of landraces that were both genotyped and phenotyped (El Hanafi et al., 2023; Keep et al., 2020; Mascher et al., 2019). Regarding traits, MF showed the highest predictive ability, followed by PH and GY, whatever the prediction scenario. These results are consistent with higher heritabilities and lower genotype by environment (GxE) effects for MF than for PH and GY (Hallauer et al., 2010). Integrating GO and Hs into the GP models was most useful for improving GP accuracy for the most challenging prediction scenario (predict a new accession in a new environment) and the most challenging trait (low heritability and high G×E) (**Table 1-3**).

Regardless of the model used, GP was robust and efficient in predicting landrace trait across environments under a sparse design (CV2), yielding high PA (0.75-0.94 depending on model

88 and traits, Table 4). This result is in agreement with PA obtained through HPG-based GP in
89 forage species (Cericola et al., 2018; Guo et al., 2018; Keep et al., 2021; Pégard et al., 2023).
90 Including GO and / or Hs neither improved nor reduced PA in this scenario, suggesting that
91 Hs and GO effects were already captured by genetic and G×E effects in this sparse design
92 scenario. Under CV2 scenario, the prediction of missing landrace-environment phenotypic
93 values is enabled by correlated information from other environments and related landraces
94 (Burgueño et al., 2012a).

95 Combining HPG-based GP with a sparse evaluation networks for evaluating traits such as
96 the ECPGR EVA Maize Network (Balconi, Galaretto et al., 2024) is therefore an efficient and
97 cost-effective strategy to characterize agro-morphological traits in various environments
98 (**Table 3**). In addition, the phenotyping cost could be reduced without affecting PA by op-
99 timizing training set of landraces and the field trial network for capturing G×E interaction.
100 Previous works suggest that it could be possible to optimize the training set composition of
101 landraces based on their genotyping without affecting PA but this approach remain to eval-
102 uate on landraces (Pégard et al., 2023; Rincent et al., 2012). Our result also paves the way for
103 reusing thousands of historical and patrimonial phenotyping experiments and field observa-
104 tions of maize landraces made by genebanks and research teams to train GP models and
105 therefore valorize this tremendous historical work. However, it required to genotype these
106 landraces and to digitalize this patrimonial field experiment.

107 **Within-population gene diversity contributes positively to agronomic performance**
108 **and stability**

109 Within-population gene diversity (Hs) had a strong positive effect on GY and PH but not on
110 MF. Hs captured 8% and 20% of PH and GY genotypic variation, respectively (Table 2). This
111 positive correlation of Hs with GY and PH is consistent with previous studies based on RFLP
112 markers on maize landraces (Rebourg et al., 2001). Although this effect is widely recognized
113 in maize, it is rarely included in GP models. Accounting for inbreeding depression in GP of
114 maize hybrids at individual level improved PA for height and yield (Roth et al., 2022). Our
115 study showed that this result obtained at individual plant level could be extended at the

population level to improve PA of landraces cultivated *per se*. For PH and GY, including Hs increased PA when predicting unknown landraces in known (CV1) and unknown (CV00) environments. The Hs effect was independent from GO effect, suggesting that Hs is mostly related to the potential intrinsic average performance of landraces while GO is mostly related to G×E. In addition, our results suggested strongly that landraces with higher Hs had more stable GY across the EVA field trial network, suggesting that within-population gene diversity partially determines the capacity of landraces to buffer fluctuating environmental conditions. This buffering environmental effect of within-population gene diversity was observed in several cultivated species and studies when comparing the yield of cultivar mixtures to monoculture, since the yield of cultivar mixtures outperformed monocultures, with a stronger effect in environments with biotic and abiotic stresses and in years with extreme weather (Reis and Drinkwater, 2017). This buffering effect could be due to the fact that landraces with larger population genetic diversity have more chance plants that are adapted to a given environment compensating the detrimental effect of plants that are not adapted but also that this heterogeneity limits disease propagation.

The Hs effect certainly originates from the well documented strong effects of inbreeding depression on these traits in maize (Hallauer et al., 2010) driven by exposing deleterious alleles or by decreasing the number of best-fitted heterozygotes (Crow & Kimura, 1970). In a random mating outcrossing population, Hs corresponds indeed to the expected mean heterozygosity of plants and therefore relates directly to their level of inbreeding. Low within-population gene diversity for some landraces maintained *ex-situ* could originate from several factors that reduce the effective size of the populations, thus creating a bottleneck. First, some landraces may have undergone loss of diversity before their collecting because they have been cultivated in small fields or gardens in which the number of plants was low. Second, they may have been collected initially with a number of ears that was too low to well represent landrace diversity. Third, not enough plants may have been used for regenerating landraces seed-stock in genebanks.

Whatever its origins, low within-population gene diversity has a very strong effect on decreasing agronomic performances, notably for yield and plant height. Farmers must account

for this inbreeding depression when cultivating and multiplying landraces, particularly when the field area is small. Inbreeding could be avoided by reintroducing genetic diversity by crossing with landraces that have similar agro-morphological characteristics coming from genebanks or other local farmers through seed exchange. The admixture between landraces from different genetic groups should mitigate inbreeding depression effects, improve performance at the population level and enhance adaptive potential required to cope with a changing climate (Aguirre-Liguori et al., 2019).

Genomic offset promises for maize landraces: some things to win, few things to lose, many to explore

Including GO increased PA of GY and PH only when both genotype and environment were unknown (CV00), capturing a part of G×E for these two traits (Table 2, Figure 4). As GO effect was negative, these results confirm the hypothesis that maize landraces are locally adapted and that maladaptation increases as climatic conditions diverge from those of the collection site. Our study likely underestimates the effect of GO on traits since only 10% of the landraces have been evaluated in field experiments with contrasted GOs (Figure S4). We observed that GO had no impact on PA of MF, consistent with lower magnitude of G×E for this trait (Hudson et al., 2022; Rogers et al., 2021). Contrary to our study, (Li et al., 2025) reported that climatic conditions of landrace collection site have limited importance when predicting landrace value for breeding. These contrasting findings are likely due to the fact that our study addresses *per-se* performance of landraces, while signals of adaptation may be blurred by testers in gamete capture experimental designs (Li et al., 2025). Secondly, we used DNA-pool genotyping approach which better captures within-population gene diversity while Li et al., 2025 used a single plant genotyping that could blur the relationship between allelic frequency and environmental gradient. In addition, GO signal of adaptation may be reinforced in our study by the use of gradient forest (GF) that ranked, selected, weighted climatic variables according to their effect on allelic frequency (Beck et al., 2025).

Nevertheless, the ability of the GO to capture G×E could be improved further by tackling several limiting factors from our study. First, our sparse testing design does not allow to op-

173 timally capture G×E effects for all landraces, since only a small set of landraces have been
174 evaluated in contrasted environments. Thus, more complete designs should improve G×E
175 quantification. Secondly, our GO analysis relied on full-year climatic variables, which coarse-
176 ly represent the actual growing conditions at field experiments and collection sites. Replac-
177 ing satellite-derived climatic data by local climatic records, and accounting for management
178 practices (e.g., planting date, irrigation) and plant phenology will certainly improve GO
179 measurement. Moreover, including additional environmental descriptors—such as solar ra-
180 diation, evapotranspiration, or soil properties could further improve environmental charac-
181 terization and therefore the measurement of GO. Ideally, experimental designs aiming to
182 establish the relationship between GO and phenotypic traits should target environments
183 that represent contrasting GO conditions (Lotterhos, 2024). Consequently, landraces would
184 likely be exposed to both high and low GO conditions, improving the assessment of GO
185 effects. Accordingly, using a subset of landraces with contrasted GO exposure in the field
186 network increased strongly GO effect on GY and PH (**Figures S7**). Complete experimental
187 designs would further enable the study of genotype-by-GO interactions, as we observed
188 that landraces may differ in their phenotypic responses to GO (data not shown).

189 Investigating how GO sensitivity relates to landrace history could also provide additional
190 insight for genetic resources. Lack of sensitivity to GO could be related to a weak natural
191 selection pressure due to the variability of climatic conditions at the collection site (Keep et
192 al., 2021) or specific management practices like irrigation that mitigate climatic effects. In
193 addition, *ex situ* multiplication of landraces by genebanks could have led to adaptation to
194 climatic conditions that differ from those at the original collection site. Maize landraces are
195 also subject to human selection for specific purposes, such as earliness illustrated by short-
196 cycle Italian landraces from central-southern regions that are cultivated after wheat or grain
197 quality, as reflected in the marked differences between landraces used for human consump-
198 tion (e.g., polenta, bread) and those intended for animal feed (birds, monogastrics). (Balconi
199 et al., 2024; Gouesnard et al., 1997; Redaelli et al., 2024). Prior knowledge related to the
200 original use and field management of the maize landraces could help to anticipate the rele-
201 vance of GO as an indicator of adaptation or its impact in GP model accuracy for certain

accessions.

Identify pre-adapted genetic resources for future climatic conditions by integrating genomic offset and genomic prediction

We also illustrated how GO predictions can be used to identify landraces with potential adaptation to future climatic scenarios. Our model predicted strong negative effects in specific regions of Europe that are consistent with results from different studies using crop-climate models (Heino et al., 2023; Jägermeyr et al., 2021; Knox et al., 2016). The utilization of GO to identify interesting genetic resources has been deployed in similar approaches like "optimal migration" for pearl Millet (Rhoné et al., 2020) or "reverse offset" for forest tree (Gougherty et al., 2021). GO predictions for a target region or climate scenario can provide a reduced list of promising genetic resources but they do not predict traits in these new target environments. A related strategy, the Focused Identification of Germplasm Strategy (FIGS), has successfully identified valuable sources of stress-tolerance variation (Stenberg & Ortiz, 2021) but similarly to GO, this approach does not predict traits of interest in new environments.

Our approach overcome the issue of two previous mentioned strategies by using a GP model integrating GO and therefore assigning a phenotypic scale to the GO change, allowing to provide the phenotypic landscape due to GO. Scaling GO for different traits is a major challenge in eco-genetics approaches that remains to be addressed (Fitzpatrick et al., 2025). Nevertheless, GO effect remains to be validated using adequate field experiments as it may be subject of different limitations (see above). Combining G×E in genomic prediction model with GO is an encouraging way to address this issue.

Our work opens several perspectives for ecological genomics as genomic forecasting of mal-adaptation through GO could be translated into phenotypic change through our prediction model. This prediction model could be improved since GO captured only a part of G×E interactions or environment-specific effects due to limits of our sparse design for evaluating GO relationship with traits for each landrace (see below). Since GO relationship with traits could be different between landraces or genetic groups (data not shown), including a

specific landrace or genetic group GO effect rather than an average effect in our model could allow to explore more detailed responses to GO. This would require a complete design rather than a sparse design. Integrating an environmental kinship in our model could also capture more complex G×E interactions that are not captured by GO. Another limitation of our approach relates to (as any GO model) to the need of "geolocated" accessions in order to model and predict (mal)adaptation due to climatic conditions. Genomic prediction of collection site climatic variables (environment of origin) could be a solution, but its contribution to prediction accuracy remains to be explored (Li et al., 2025).

To conclude, our study is the first to apply GP using the HPG approach to characterize the *per se* performance of maize landraces across multiple environments. HPG-GP approach paves the way for low cost characterization of landraces, that are conserved either *ex situ* in genebank or *in situ* by farmers, for various complex traits as phenology, performance, quality traits, tolerance to abiotic stress. This is also the first study to show that GO and Hs can provide valuable, complementary information for predicting maize landrace performance opening an avenue for their integration in GP model for characterizing heterogeneous genetic resources. This integrative approach combining GO with GP could be very useful for pre-breeding activities by identifying a subset of landraces suited for cultivation in specific environments (present or future) based on both an adaptation criterion (GO) and an agronomic performance criterion (GP-GO model). GO predictions highlighted that landraces coming from other geographic area may be pre-adapted to future conditions in regions highly disturbed by climate change, supporting the need of international collaboration to adapt crops to a changing climate. Integrating GO and Hs into the GP models was most useful for improving GP accuracy for the most challenging prediction scenario (predict a new accession in a new environment) and the most challenging trait (low heritability and high G×E). In the end, our GP-GO model also predicted stability of landraces in fluctuating environments which is relevant considering that climatic change will increase climatic instability in the future (Heino et al., 2023).

257 ## Material and Methods

258 ### Plant material

259 Accessions from a panel of 626 European maize landraces (hereafter called "EVA Panel")
260 from nine European genebanks, previously assembled and described in Balconi, Galaretto et
261 al. (2024). Landrace selection were made by each genebank primarily to represent national
262 diversity in geographical origin and variability in morphological and agronomic traits, in-
263 cluding tolerance to biotic and abiotic stresses. Based on DNA pool genotyping, Balconi,
264 Galaretto et al. (2024) identified nine main genetic groups using Admixture (Alexander et al.,
265 2009): Popcorn (K1), SE-Spanish (K2), SC-Italian (K3), Northern Flint (K4, NF), N-Italian (K5),
266 Portuguese (K6), Galician (K7), Corn Belt Dent (K8, CBD) and Pyrenean (K9) (**Table S1**). Note
267 that the interpretation of K8 as the "Corn Belt Dent" genetic group in Balconi, Galaretto et
268 al., (2024) is based on the quantitative assignment of European landraces to the American
269 "Corn Belt Dent" group using the structuration analysis of 156 landraces from America and
270 Europe (Arca et al., 2023).

271 We retrieved geolocation for 483 landraces based on their collection sites described in
272 passport data from EURISCO Catalog (Kotni et al., 2023). Using these coordinates, we re-
273 trieved climatic variables from climatic databases (see section "climatic characterization" in
274 Methods). Finally, a subset of 470 landraces with no missing climatic data was used to mod-
275 el adaptation using gradient forest (GF) (Ellis et al., 2012; see section "genomic offset" in
276 Methods).

277 ### Genotyping and diversity analysis

278 The landraces from the EVA panel were genotyped with the 50K Illumina Infinium HD array
279 (Ganal et al., 2011) and allelic frequency was obtained for 35,878 SNPs, following a DNA
280 pool approach proposed by Arca et al. (2021) and analyzed by Balconi et al. (2024) for struc-
281 ture analysis. Markers without missing data and minor allelic frequency higher than 0.05
282 were retained. Out of the 31,950 SNPs, after filtering, a subset of 23,412 SNPs with low as-
283 certainment bias was used to estimate gene diversity within each landrace (within-

284 population gene diversity, Hs) and genetic relatedness (kinship) between landraces.

285 We retrieved the Hs estimation made by Balconi, Galaretto et al. (2024) following Nei (1973).
286 We estimated the Kinship matrix (K) using allelic frequencies according to Cericola et al.
287 (2018), as:

$$K = \frac{MM'}{\sigma_G^2}$$

288 where M is the centered allelic frequency matrix, M' is transposed matrix of M and σ_G^2 is the
289 sum of expected variances across SNPs, defined by Ashraf et al. (2014), as:

$$\sigma_G^2 = \frac{1}{n}\sum_{j=1}^{m} \hat{p}_j\left(1 - \hat{p}_j\right)$$

290 where $\hat{p}_j$ is the allelic frequency of jth SNP at the whole panel level, m is the total number of
291 SNPs and n is the ploidy number which is equal to 2 for maize.

292 **Analysis of agronomic traits evaluated across EVA field trial Network**

293 The European Evaluation Network (EVA Network) was established to evaluate a large num-
294 ber of maize landraces in field experiments under a sparse testing design (not all landraces
295 were evaluated in all experiments). Targeted traits involved phenology, agro-morphological
296 characters and tolerance to biotic and abiotic stress. A total of 64 experiments were carried
297 out between 2021 and 2024 across Europe where *per se* value of 588 landraces were evalu-
298 ated along 5 commercial hybrid checks. Experiments were conducted by genebanks, re-
299 search institutes and private partners under the framework of the EVA Network led by the
300 European Cooperative Program for Plant Genetic Resources (ECPGR -
301 https://www.ecpgr.org/eva/eva-networks/maize).

302 We used a subset of 397 landraces evaluated for grain yield, complete collection site climat-
303 ic information and within-population gene diversity above 0.05 (see next section in Meth-
304 ods) to evaluate the ability of genomic prediction (GP) to predict landraces traits across 25
305 different environments (**Table S1**). All landraces had been evaluated for plant height (PH),

grain yield (GY) and days from sowing to male flowering. We estimated the thermal time for male flowering (MF) as growing degree units (GDU) accumulated from sowing to when 50% of the plants have shed pollen, using Tb = 6°C as in Rebourg et al., (2001). Plant height (PH) was recorded as the average of measurements taken from 10 competitive plants per plot. For each plant, PH was measured in centimeters as the distance from ground level to the base of the tassel.

We determined GY as the weight of shelled grain from all harvested ears per plot, adjusted to 10% grain moisture and expressed in t/ha. The 25 environments involved 6 locations: Belgrade (Serbia), Coimbra (Portugal), Avenches (Switzerland), Pontevedra (Spain), Suceava (Romania) and Zagreb (Croatia), four years (2021, 2022, 2023, and 2024), and different evaluation conditions: standard (*n* = 19), early sowing (*n* = 2), inoculation with the fungus *Fusarium verticilloides* (*n* = 2), and artificial infestation with the pest *Sesamia. nonagrioides* (*n* = 2) (**Table S6)**. The number of entries and experimental design varied across the network (**Table S5 and Table S6)**. Landraces were evaluated on average in 2.8 environments, with five landraces evaluated in a maximum of 12 environments (Table S5). The number of landraces per environment varied from 17 to 165, with an average of 45 (Table S6).

We corrected field plot values for spatial and design effects in each environment, as by Roth et al. (2022), using the mixed model of the form:

$$Y_{grc} = \mu + G_g + R_r + C_c + \varepsilon_{grc}$$

$$G \sim N(0, I\sigma_G^2)$$

$$R \sim N(0, I\sigma_R^2)$$

$$C \sim N(0, I\sigma_C^2)$$

$$\varepsilon \sim N(0, I\sigma_\varepsilon^2)$$

$$G \perp R \perp C \perp \varepsilon$$

where Y_{grc} is the plot value of genotype *g* (landrace or check) measured at row *r* and column *c* and σ_G^2, σ_R^2, $\sigma_C^2$and σ_ε^2 are genotypic, row, column and error variances components,

respectively. All effects were considered random and independent (⊥). Heritability for each trait in each environment was estimated as $\frac{\sigma_G^2}{(\sigma_G^2+\sigma_\varepsilon^2/n_{rep})}$, with the number of replications (n_{rep}) varying between 1 and 3 (**Table S5**). We estimated corrected field values ($\tilde{Y}_{grc}$) by removing the spatial and design effects from the plot values. Then, we computed adjusted means within environment ($\bar{Y}_{ge}$) as the mean of the corrected field values. Finally, we estimated least square means (*lsmeans)* across environments for each landrace ($\overline{Y}_{g.}$) with the model:

$$\overline{Y}_{ge} = \mu + \tau_g + \tau_e + \varepsilon$$

where τ_g and τ_e are the fixed effects of genotype *g* and environment *e*, ε is the random error. The *lsmeans* for each genotype *g* was estimated as $\overline{Y}_{g.} = \mu + \tau_g$.

Climatic characterization

To characterize climatic conditions in which landraces were collected, we used original collection site coordinates to retrieve past climatic information from WorldClim2.1 (Fick & Hijmans, 2017). WorldClim2.1 provides 55 climatic variables, including monthly averages of maximum temperature (*tmax*), minimum temperature (*tmin*), precipitation accumulation (*prec*) and 19 bioclimatic variables (*bio1* to *bio19*) for the period 1970-2000 (see **Table S2** for definitions). We used R packages *raster* (Hijmans, 2010) and *terra* (Hijmans, 2020) to extract climatic and bioclimatic variables for the 483 collection site coordinates available. After removing sites with missing values, a total of 470 landrace collection sites (**Table S1**) and 55 climatic variables were retained for further analyses. Summary statistics for each climatic variable are provided in **Table S2**.

In order to characterize climatic conditions at environments (field experiments) of the EVA Network we used NASA Power (Sparks, 2018) to retrieve daily information on temperature and precipitation. To enable comparison of these climatic conditions with those at landrace collection sites, we compiled temperature and precipitation data on a monthly basis and used *biovars* function of *dismo* R package (Hijmans et al., 2010) to obtain the same bioclimatic variables than WorldClim2.1. Summary statistics for climatic data of EVA Network are

352 also provided in **Table S2**.

353 **Genomic offset estimation using gradient forest**

354 Genomic offset (GO) is a metric of maladaptation based on the prediction of disruption of
355 (assumed) optimal gene-environment relationship (Fitzpatrick & Keller, 2015). In order to
356 estimate GO between the climatic conditions experienced at landrace collection sites and
357 the environments included in the EVA Network, we first modeled the change in allelic fre-
358 quencies across climatic gradients using the R package *gradientForest* (Ellis et al., 2012).
359 Gradient forest (GF) is a Random Forest-based algorithm that was designed to model the
360 response of biodiversity to environmental gradients. Fitzpatrick & Keller (2015) proposed
361 using genomic data instead of species count to model the response of a set of loci to envi-
362 ronmental gradients. This GF model is used to predict optimal allelic frequencies in a given
363 environment, based on environmental variables for current, past or future climates. GO then
364 measures maladaptation as the shift between the allelic frequencies of each population and
365 those predicted by the model for each environment. To select loci involved in adaptation,
366 we first adjusted a GF model including all 55 climatic variables and 35,878 SNPs, using R
367 functions from "geneticOffsetR" (Fitzpatrick et al., 2021), which allowed to fit GF models for
368 a large number of SNPs and recover only GF model goodness-of-fit (R^2) for each marker.
369 Then, empirical *p-values* were calculated by determining the rank of the R^2 value for each
370 SNP, within a distribution of intergenic SNPs (Fitzpatrick et al., 2021). For this, we used the
371 set of 2,500 unlinked SNPs previously selected in Arca et al. (2023). 243 outlier adaptive *loci*
372 were retained (p-value < 0.01) and then used in a second GF model to select the most im-
373 portant among the 55 climatic variables WorldClim2.1. We used GF variable importance
374 ranking based on their efficiency for predicting allelic frequency variations, to select the 15
375 top variables (importance >0.6, **Table S3**). In the end, we fitted a third GF model using these
376 15 selected climatic variables and these 243 outlier SNPs. This model served two main pur-
377 poses: first, to analyze the spatial variation in predicted genetic compositions and second, to
378 predict landrace GO for climatic conditions of each EVA Network field experiment.

379 To achieve this first objective, we used cumulative importance curves derived from GF. The-

380 se curves represent transformations of the environmental data that are shaped by genomic
381 patterns. They illustrate both the rate and magnitude of allele frequency shifts along each
382 environmental gradient, including any threshold responses. By rescaling the environmental
383 data into common units of genetic turnover, these functions provide a more accurate repre-
384 sentation of genetic composition patterns than raw, untransformed environmental data. To
385 draw a geographical map of the impact of environmental gradient on genomic change
386 (turnover map), we first performed a PCA analysis based on GF-transformed climatic varia-
387 bles from each WorlClim2.1 grid across Europe (2.5 arc minutes resolution ~ 4.5km x 4.5 km
388 at the Equator). We created a multivariate color scale, by assigning Red, Green and Blue to
389 the first three most important PCA axes and applied the resulting color to each grid of the
390 map. The turnover map colors represent patterns of genetic composition, where change in
391 color (turnover region) represent a shift in adaptive allelic frequencies. To investigate the
392 climatic variability of the landrace collection sites and compare them with the environments
393 explored in the EVA network, we projected each collection site and experiment on the dif-
394 ferent PCA axis, using GF-transformed climatic variables. To facilitate visualization, we re-
395 moved admixed landraces (assignment to genetic groups <0.6).

396 Finally, we used the resulting multidimensional rescaled environmental spaces to quantify
397 genetic differences, measured as genomic offset (GO). This was calculated using the Euclid-
398 ean distance (using the *dist* function of R package *stat* (R Core Team, 2024)) between the
399 population's original environment and the EVA Network field experiments, following the
400 approach described by (Fitzpatrick et al., 2021). High values of GO indicate large differences
401 between optimal and landrace genetic composition, which is expected to lead to a loss of
402 fitness.

403 **Variance decomposition of genomic offset and within-population gene diversity ef-**
404 **fects on traits**

405 To investigate the relationship between GO values across the EVA Network environments
406 and landrace traits, we fitted linear regressions between GO and the within environment
407 adjusted means ($\bar{Y}_{ge}$) for MF, PH and GY. Similarly, we investigated the relationship between

Hs and *lsmeans* ($\overline{Y}_{g.}$) for each landrace across the EVA Network

To quantify the amount of variation explained by GO and Hs, we performed variance decomposition by adjusting different models to the complete data set of corrected field values ($\tilde{Y}_{grc}$). A total of 4 models were adjusted using the *sommer* R package (Covarrubias-Pazaran, 2016) as follows:

$$\overline{Y} = 1\mu + Z_G u_G + X_E \beta_E + Z_{GE} u_{GE} + \varepsilon \qquad \text{(M1)}$$

$$\overline{Y} = 1\mu + Z_G u_G + X_E \beta_E + Z_{GE} u_{GE} + X_{GO} \beta_{GO} + \varepsilon \qquad \text{(M2)}$$

$$\overline{Y} = 1\mu + Z_G u_G + X_E \beta_E + Z_{GE} u_{GE} + X_{Hs} \beta_{Hs} + \varepsilon \qquad \text{(M3)}$$

$$\overline{Y} = 1\mu + Z_G u_G + X_E \beta_E + Z_{GE} u_{GE} + X_{Hs} \beta_{Hs} + X_{GO} \beta_{GO} + \varepsilon \qquad \text{(M4)}$$

$$u_G \sim N(0, K\sigma_G^2), u_{GE} \sim N(0, \mathrm{I}_E \otimes K\sigma_{GE}^2), \varepsilon \sim N(0, I\sigma_\varepsilon^2)$$

where $\overline{Y}$ is the vector of phenotypes, 1 is a vector of ones, μ is the intercept, X_E is the incidence matrix for the environment fixed effects, β_E is the vector of environment fixed effects, u_G is the vector of main random genetic effects for landraces, u_{GE} is the vector of random effects for genotype-environment interactions, ε is the vector of random errors, Z_g is the genotypic incidence matrix of size, K in the kinship matrix, Z_{GE} is the genotype-environment interaction incidence matrix, I_E is the identity matrix, X_{GO} is the vector of GO estimates for the corresponding landrace and environment, β_{GO} is the GO fixed effect, X_{Hs} is the vector of within-population gene diversity, β_{Hs} is the within-population gene diversity fixed effect, $\otimes$ is the Kronecker product and σ_G^2, σ_{GE}^2, and σ_ε^2 are the unknown genotypic, genotype-environment interaction and error variances, respectively.

Genomic Prediction

We evaluated the performance of the 4 models for genomic prediction under three different prediction scenarios represented by previously used cross validation (CV) schemes (Burgueño et al., 2012b; Jarquín et al., 2017)(Figure S11):

433 • **CV2** (prediction under sparse testing): five-fold cross validation where genotype-
434 environment combinations were randomly divided in 5 and at each round four folds
435 (80%) were used for training and the remaining fold (20%) is used for validation
436 • **CV1** (prediction of new genotypes): five-fold cross validation where genotypes were
437 randomly divided in 5 and, at each round, four folds (80%) were used for training and
438 the remaining fold (20%) is used for validation
439 • **CV00** (prediction of new genotypes in new environments): at each fold training sets
440 were built using information of all environments, except one that was used for valida-
441 tion. In addition, the data for the genotypes present in the validation set were re-
442 moved across environment in the training set. Therefore, neither the environment
443 nor the genotypes to be predicted were observed in the training set.
444 For CV2 and CV1, we repeated random sampling for the five folds 100 times. For CV00, we
445 divided the three biggest environments in more than one-fold to avoid bias related to envi-
446 ronment size. As a result, CV00 included 34 different folds of similar size.

447 We computed predictive ability (PA) for each fold as the correlation between observed and
448 predicted values, as well as mean and standard deviation of PA. Finally, the gain in PA (%)
449 was computed as the relative PA using M1 as the reference.

450 **Genomic offset application to future climatic scenarios**

451 To investigate the prediction of adaptation or maladaptation of landraces to future climates,
452 we used the GF model to perform GO predictions for future climatic scenarios. We retrieved
453 downscaled CMIP6 2.5-min resolution climatic predictions for two Shared Socio-economic
454 Pathways (SSP126 and SSP585) and two time periods (2041-2060 and 2081-2100) from
455 WorldClim2.1 (https://www.worldclim.org/data/cmip6/cmip6climate.html). We computed
456 GO individually for each of the 13 Global Climatic Models (GCMs, **Table S4**) to then obtain
457 the mean landrace GO for each future scenario (SSP-time period combination). We used
458 mean landrace GO for each scenario to visualize GO landscape and evolution by mapping
459 GO to each 2.5-min grid in the map, using the *ggplot2* R package (Wickham et al., 2007). To
460 provide representative examples, we selected 4 landraces from different geographic regions

and genetic groups and represented GO at two periods in the future (2041-2060 and 2081-2100) using these different scenarios of global warming (SSP126 and SSP585).

We then used the GO values to screen among the landraces for putatively best adapted ones (GO <0.03). We focused on two relevant maize production regions of Europe: NE-Romania and SW-France. Among landraces with low GO, we selected landraces from different regions as diversity source, considering performance and stability for grain yield derived from GP M4 (GO+Hs). We assessed yield using the genotypic best linear unbiased predictor ($BLUP_G$), Hs effect and GO effect, while yield stability was assessed using the standard deviation of G×E BLUPs ($SD_{BLUPGxE}$). Before incorporating $SD_{BLUPGxE}$ as a stability indicator, we studied the relationship of $SD_{BLUPGxE}$ with Hs, $BLUP_G$, and observed standard deviation G×E (SD_{GxE}), to discard possible spurious relationships. We computed observed $SD_{G\times E}$ as the standard deviation of observed GxE effect in each environment: $\bar{Y}_{ge} - \mu - \tau_g - \tau_e = \varepsilon$. Then, we selected one landrace for each target region considering predictions of yield and stability, and used the GO effect retrieved from M4 to generate yield variation map across Europe linked to GO.

Finally, we assessed the consequences of climate change on landrace performance under the most pessimistic scenario (SSP585 – 2081-2100). We computed the differences between past and future GO across Europe and we used the GO effect to transform GO difference into yield losses/gains.

Author Contributions

Conceptualization: AOG, SDN, AC, BG, LM

Methodology: AOG, SDN, LM, MP, AC, BG

Investigation: DMa, CV, CBau, RM, AB, PR, CBal, PMM, HS, AMB, DMu, BSC, AS, VA, SG

Formal analysis: AOG, SDN, AC, LM, MPVisualization: AOG, MP, SDN, AC, LM, MP

Supervision: SDN, AC, LM, BG

Writing original draft: AOG, SDN

Writing review & editing: AOG, SDN, AC, LM, RM, CBal, AB, PR, HS, VA, SG

Project administration: SG

Funding acquisition: SG, SDN

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Data Availability

Information on accessions and environmental data are all available in supplementary materials. All data required for statistical analysis (Genetic structuration, Genotyping, Phenotyping and Environmental data) are also available in dataverse https://entrepot.recherche.data.gouv.fr/ with following name "EVA Maize genotyping and phenotypic dataset" (https://doi.org/10.57745/TNAURQ) and with a private link for peer-reviewing (https://entrepot.recherche.data.gouv.fr/privateurl.xhtml?token=5ad9e67e-1772-4980-ac4e-28475cd4f4f7). Raw phenotyping data are available on request and will be made available in the EURISCO catalogue (www.ecpgr.org/eurisco). Seeds from each accession can be supplied on request by the different European genebanks (holding institute) listed in the accession list (Table S1), in accordance with the FAO Standard Material Transfer Agreement.

Declaration

All authors declare that they have no competing of interest. Dr. Alexandre Strigens is employed by the company DSP—Delley Semences et Plantes SA, Switzerland. All authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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