The genomic and bioclimatic characterization of Ethiopian barley (*Hordeum vulgare* L.) unveils challenges and opportunities to adapt to a changing climate

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Abstract

The climate crisis is impacting agroecosystems of the global South, threatening the food security of millions of smallholder farmers. Understanding the effect of current and future climates on crop agrobiodiversity may guide breeding efforts and adaptation strategies to sustain the livelihoods of farmers cropping in challenging conditions. Here, we combine a genomic and climatic characterization of a large collection of traditional barley varieties from Ethiopia, key to food security in local smallholder farming systems. We employ data-driven approaches to characterize their local adaptation to current and future climates and identify barley genomic regions with potential for breeding for local adaptation. We used a sequencing approach to genotype at high-density 436 barley varieties, finding that their genetic diversity can be traced back to geography and environmental diversity in Ethiopia. We integrate this information in a genome-wide association study targeting phenology traits measured in common garden experiments as well as climatic features at sampling points of traditional varieties, describing 106 genomic loci associated with local adaptation. We then employ a machine learning approach to link barley genomic diversity with climate variation, estimating barley genomic offset in future climate scenarios. Our data show that the genomic characterization of traditional agrobiodiversity coupled

with climate modelling may contribute to the mitigation of the climate crisis effects on smallholder farming systems.

Introduction

Since the 1960s, the green revolution heralded by Norman Borlaug's work at CIMMITY enabled a marked increase in crop yields worldwide (Bailey-Serres, Parker, Ainsworth, Oldroyd, & Schroeder, 2019; Pingali, 2012). Thanks to a successful combination of genetic innovation, chemistry, and mechanization, the global cereal production has increased by 280 percent in the last 60 years (FAOSTAT, 2022) and supported the growth of the world population. The green revolution is also at the root the process of intensification of modern agriculture, where uncontrolled increased productivity per surface unit may lead to an increased use of inputs and therefore footprint of agricultural practices, a reduction of agrobiodiversity, and an impact on small-scale indigenous farming systems (Khoury et al., 2022). Indeed, conventional farming may provide higher yields but needs uniform management and external inputs including irrigation, fertilizers, and pesticides (Mondal et al., 2020). When optimal management conditions are not met, green revolution crop varieties can be outperformed by traditional varieties with local adaptation traits (Ricciardi, Mehrabi, Wittman, James, & Ramankutty, 2021). This is especially relevant in smallholder farming systems, which involve an estimated 570 million farms worldwide supporting the livelihoods of 2 billion people in highly diversified low-input cropping environments (Lowder, Skoet, & Raney, 2016). Here, low adoption rates are observed for modern improved varieties lacking adaptation to farming conditions as well as local culture (Acevedo et al., 2020), jeopardizing the impacts of breeders' efforts in the face of yield advantages which are not realized in the use environments (Mancini et al., 2017).

The adaptive capacity of subsistence-based agricultural practices is depending on the severity and speed of climate change, but context matters as well. In challenging farming systems, the climate crisis exposes smallholder farmers to severe fluctuations that thereby magnify the challenges they must face to avoid losses (Cohn et al., 2017). In these contexts with high vulnerability, high economic damages resulting in food insecurity are very likely (Coronese, Lamperti, Keller, Chiaromonte, & Roventini, 2019). In the wake of climate change, new

varieties that combine yield stability with local adaptation as well as appreciation by local users are paramount to achieve resilience and support food security (Simmonds, 1991). The Ethiopian cropping system is exemplative of this challenge. As a center of domestication and diversity of crops (Vavilov, 1951), Ethiopia still hosts highly diversified farming systems relying largely on smallholder farmers that maintain and cultivate thousands of landraces. This wealth of diversity is reflected by highly diversified landscapes, with 32 registered agroecological zones cultivated by approximately 80 million people (Bachewe & Taffesse, 2018). Previous studies on the Ethiopian landrace germplasm showed that the local agrobiodiversity is large but poorly represented in breeding, as in the case of durum wheat (Maccaferri et al., 2019) and barley (Milner et al., 2019). Barley (*Hordeum vulgare* L.) is the fifth most cultivated cereal in the country, grown by more than 4 million smallholder farmers on about one million hectares (Central Statistical Agency of Ethiopia, 2022; FAOSTAT, 2022). Ethiopian barley germplasm is markedly different from the international allele pool (Milner et al., 2019), and has potential for supporting breeding programs at local and international level (Jørgensen, 1992; Piffanelli et al., 2004), especially those targeting improved adaptation potential to enhance resilience to the climate crisis.

Until the recent past, barley has been cropped in Ethiopia in two seasons per year, the short rainy season *Belg* (February to April) and the main rainy season *Meher* (June to December). However, changing patterns of rainfall across the Horn of Africa makes it difficult to crop in two seasons (Wakjira et al., 2021). The Horn of Africa is among the most vulnerable regions in the continent where drastic changes in rain patterns are expected to have even more substantial impacts on food production in the future (Serdeczny et al., 2017). These projections are anticipated to coincide with low adaptive capacity as climate change intensifies stressors on small-scale agriculture (Morton, 2007). Today, breeding can operate in a big data dimension that connects genomics (Varshney et al., 2021), phenomics (Hickey, Chiurugwi, Mackay, & Powell, 2017), as well as climatic data and associated models describing current and projected climates (Yoder et al., 2014). When combining genomic information with remote sensing data and global descriptors of climatic conditions, it is possible to associate genetic diversity with environmental diversity at cultivation sites, identifying genomic loci associated with local

75 adaptation towards specific climates (Capblancq, Fitzpatrick, Bay, Exposito-Alonso, & Keller, 2020). Genomic
76 information can then be used to speed up the development of *climate-ready* varieties through the application of
77 classical or innovative approaches, including genomic selection (Scheben, Yuan, & Edwards, 2016) and
78 decentralized breeding (de Sousa et al., 2021).

79 In this study, we tap into the broad diversity of Ethiopian barley landraces to assess their genomic signatures for
80 uniqueness and adaptation to current and future climates. We use a data-driven approach combining genomics,
81 common garden experiments, and climate data analysis to describe the relation between barley diversity and
82 the landscape. We use a machine learning approach to model barley genetic composition across climate and
83 geography of Ethiopia; we use these approaches to look at projected climates and identify which area of current
84 barley cultivation is more likely to suffer the effects climate change. We integrate this information in a genome-
85 wide association study (GWAS) targeting phenology traits and current climate, identifying genomic loci
86 associated to adaptation. We discuss how transdisciplinary approaches combining quantitative genetics and
87 climate science may support barley improvement, unlocking the full potential of local landraces to foster a more
88 sustainable and resilient agriculture.

89 **Materials and Methods**

90 Plant material and DNA extraction

91 Plant materials used in this study were derived from the Ethiopian Biodiversity Institute (EBI) barley landrace
92 collection. Accessions were prioritized by completeness of passport data, and a core collection of 249 barley
93 landraces was selected to cover the entire geographical and agroecological range of barley cultivation in Ethiopia.
94 Landrace accessions were purified in an ear-to-row reproduction in the main season of 2016 at the experimental
95 station of Holeta, Ethiopia (9.065 N, 38.459 E). When different morphological types were present in an EBI
96 accession, this was split in as many accessions as types, resulting in 418 purified barley lines derived from
97 landrace accessions. Lines derived from landraces were sided by 40 improved lines, representing all main barley
98 improved lines released for cultivation in the country at the time of the assembly of the panel. Improved lines

99 were sourced from National and Regional agricultural research centers. Full description of the plant materials
100 used in this study is reported in Table S1. The full collection of 458 barley was germinated to extract genomic
101 DNA at the molecular biology laboratory of the EBI, Addis Abeba, Ethiopia. DNA was extracted from 3-5 seedlings
102 per line, pooled in equal quantity, with the GenElute Plant Genomic DNA Miniprep Kit (Sigma-Aldrich, St Louis,
103 MO) following the manufacturer's protocol. DNA was shipped to Italy and evaluated for quality and quantified
104 using a Microplate photometer (Thermo Scientific, Milford, MA) and agarose gel electrophoresis at the Scuola
105 Superiore Sant'Anna molecular laboratories.

106 Sequencing and bioinformatic analysis

107 Genotyping was performed at IGA Tech sequencing services (Udine, Italy) with a double digestion Restriction-
108 site Associated DNA sequencing (ddRAD-seq) approach (Peterson, Weber, Kay, Fisher, & Hoekstra, 2012).
109 Genomic libraries were prepared using *SphI* and *EcoRI* and sequenced on an Illumina HiSeq2500 instrument
110 (Illumina, San Diego, CA) with V4 chemistry in paired-end 125-bp mode. Raw reads were demultiplexed with
111 Stacks (Catchen, Hohenlohe, Bassham, Amores, & Cresko, 2013) and quality was assessed with FastQC tool (v
112 0.11.5). Reads of each sample were mapped against the *Hordeum vulgare* reference genome (MorexV3, DOI:
113 10.5447/ipk/2021/3) with BWA (Burrows-Weeler-Aligner v.0.7.12) using the MEM algorithm (Li, 2013). The
114 products of the alignment were subsequently indexed with PicardTools and SAMtools (Li et al., 2009). The
115 HaplotypeCaller algorithm, implemented in GATK and run in per-sample mode (McKenna et al., 2010), was used
116 for variant identification. Variant calling was completed with GenotypeVCFstool (Danecek et al., 2011) to derive
117 single nucleotide polymorphisms (SNPs). The resulting raw SNPs were filtered using GATK for the following
118 criteria: QUAL < 30; QD < 2.0; MQ < 40.0; AF < 0.01; DP < 580; *SNP clusters* (> 3 variants within 5 bp windows).

119 Genomic diversity

120 When not stated otherwise, all data analysis was performed in R (R Core Team, 2018). SNPs with minor allele
121 frequency (MAF) above 5% were used to calculate pairwise linkage disequilibrium (LD) with the r^2 metrics in
122 R/*Ldheatmap* (Shin, Blay, Mcneney, & Graham, 2006). LD decay was estimated on SNPs having MAF> 0.05, as

function of physical distance according to the Hill and Weir equation (Hill & Weir, 1988). A threshold of $r^2 = 0.3$ was used to estimate average LD decay for each chromosome. Genetic structure and diversity of the barley collection were studied using a set of SNP markers pruned by LD at a threshold of $r^2 = 0.5$, using PLINK (Chang et al., 2015) *indep-pairwise* function with a 150-variant window moving in 5-variant steps. A complete linkage agglomerative clustering, based on pairwise identity-by-state (IBS) distance, was run using PLINK with defaults. A pairwise dissimilarity neighbor joining (NJ) analysis was run in Tassel (Bradbury et al., 2007) to describe the phylogenetic relationship among lines. Genetic groupings of samples were detected with Discriminant Analysis of Principal Components (DAPC) (Jombart et al., 2010) using R/*adegenet* (Jombart, 2008). The diversity among samples was further described using Principal Component Analysis (PCA) and Admixture (Alexander & Lange, 2011).

Spatial and climatic characterization

GPS coordinates of landrace sampling locations, where available, were projected onto the map of Ethiopia using R/*raster* (Hijmans, 2015). Altitudes were derived at each site based on GPS coordinates, using the CGIAR SRTM database at 90 m resolution (Reuter, Nelson, & Jarvis, 2007). Agroecological zones (AEZ) used in this study are defined by the Ministry of Agriculture of Ethiopia (*Agro-Ecological zones of Ethiopia*, n.d.). The cultivation area of barley was defined by the union of all AEZ polygons in which at least two sampling sites of barley landraces were present. Significant associations between DAPC genetic clusters and administrative regions, subregions and AEZs were assessed using Pearson's Chi-squared test of independence.

Historical climate data for the study area was derived from the fifth generation of European Centre for Medium-Range Weather Forecasts (ECMWF) atmospheric reanalysis version (ERA5) data, released under the Copernicus Climate Change Service (Hersbach et al., 2020). The dataset covers over 30 years (1981-2010) at a spatial resolution of 0.25° x 0.25°. Climatological biases in temperature and precipitation across the East African region are reduced in ERA5 compared to the previous version of ERA-interim (Gleixner et al., 2020). Future climate projections were obtained from daily climate data extracted from a subset of 38 climate models among the

147 CMIP5 dataset at the horizon of 2050 and 2070 for two Representative Concentration Pathway (RCP): RCP4.5
148 and RCP8.5. We followed a recent study to select the representative CMIP5 GCM models, as the number of
149 genuinely independent ones in the CMIP5 archive is significantly less than the number of those submitted
150 (Sanderson, Knutti, & Caldwell, 2015). After reviewing previous works on model similarity (IPCC, 2019) and
151 quality metrics compared to historical observational data, we selected four relatively independent models:
152 CESM1-BGC, CMCC-CM, MIROC5, and MPI-ESM-MR, from which we prepared ensembles for future projected
153 climate. Climate extremes and small-scale variability are essential drivers in many climate change impact studies.
154 However, the spatial resolution achieved by the global models is still insufficient to identify the fine structure of
155 rainfall intensity correctly. Therefore, we employed a stochastic downscaling and bias technique, the Rainfall
156 Filtered Autoregressive Model (RainFARM), which has been extended for application to long climate simulations
157 (D'Onofrio, Palazzi, Von Hardenberg, Provenzale, & Calmanti, 2014; Rebora, Ferraris, von Hardenberg, &
158 Provenzale, 2006). To achieve optimal data spatial and temporal adjustment, we accessed data of 150 weather
159 station of the Ethiopian National Meteorology Agency (NMA), covering the entire barley cropping range.

160 Both historical and projected climate data were then derived only within the main barley growing season of
161 Ethiopia (June - December), the *Meher* (Gissila, Black, Grimes, & Slingo, 2004; Segele & Lamb, 2005). The resulting
162 historical and future climate data were used to derive 19 bioclimatic variables using R/*dismo* (Hijmans, Phillips,
163 Leathwick, & Elith, 2011). Bioclimatic variables are biological meaningful indicators, often used in species
164 distribution modelling; they represent seasonal trends and define seasonality and limiting climatic factors. Eleven
165 variables (from bio 1 to bio11) are derived from temperature data while the remaining eight are related to
166 precipitation (from bio12 to bio19). Collinearity among bioclimatic variables was then assessed with the
167 *ensemble.VIF*() function in R/*BiodiversityR* (Kindt & Coe, 2005). Only variables with a Variance Inflation Factor
168 (VIF) below 10 were retained for further analyses.

169 <u>Common garden-experiments and phenology data analysis</u>

170 The barley collection was characterized in common garden experiments at two locations in Ethiopia, Arsi Negele
171 (7° 21′ N, 38° 242′ E) and Holeta (9° 00' N, 38°30 E), during the *Meher* (June - December) of 2017 and the *Meher*
172 of 2018. Samples were arranged using alpha lattice design with two replications per site, in plots consisting of
173 four rows of 2.5 m in length and spaced 20 cm apart. Plots were fertilized with DAP and Urea as per the
174 recommended rate of applications for the two sites and agronomic management was uniformly applied to all
175 the genotypes. Two phenological traits were collected on full plots: days to 50% heading (DH) and days to 90%
176 maturity (DM). Grain filling period (GFP, days from heading to maturity) was derived from DM and DH. Best linear
177 unbiased predictions (BLUP) of measured traits were computed with R/ASReml (Gilmour, Gogel, Cullis, Welham,
178 & Thompson, 2014) using the general model in Eq. (1):

179

180 $$y_{ijkn} = \mu + g_i + l_k + y_m + gl_{ik} + gy_{im} + gly_{ikm} + e \qquad \text{Eq. (1)}$$

181

182 Where the observed phenotypic value is y_{ik}, μ is the overall mean of the population, g_i is the random effect for
183 the ith genotype *g*, l_k is the fixed effect for the kth location, y_m is the random effect for the mth year. Interaction
184 effects are considered for genotype, year, and location, and *e* is the error. For calculation of BLUPs within a single
185 location and/or year, the data was sub-set and analyzed with a reduced model in accordance with Eq. (1). Broad-
186 sense heritability (H^2) was derived from the variance component estimates deriving from Eq. (1) as follows:

187

188 $$H^2 = \frac{\sigma_g}{\left(\sigma_g + \frac{\sigma_{gl}}{n_{loc}} + \frac{\sigma_{gy}}{n_{year}} + \frac{\sigma_{gyl}}{n_{loc} * n_{year}} + \frac{\sigma_e}{n_{rep} * n_{loc} * n_{year}}\right)} \qquad \text{Eq. (2)}$$

189

190 In Eq. (2), σ_g is the variance component of genotypes,σ_{gl} is the genotype by location variance, σ_{gy} is the
191 genotype by year variance, σ_{gly} is the genotype by location by year variance, and σ_e is the error variance.

192 $n_{loc}, n_{year}, n_{rep}$ are the number of locations, years, and replications, respectively. For calculation of H^2 within
193 locations and years, Eq. (2) was simplified accordingly.

194 Estimation of Ethiopian barley genomic vulnerability to future climates

195 A Gradient Forest (GF) machine-learning regression tree-based algorithm was used to test which environmental
196 variables best explained barley genetic variation across its cultivation area in Ethiopia. The GF, implemented in
197 R/*gradientForest* (Ellis, Smith, & Pitcher, 2012), derives the importance, in terms of predictive power, of each
198 bioclimatic variable in the change of allele frequencies to predict genetic composition across the climatic
199 landscape. The GF was trained with environmental variables and with Moran's eigenvector map (MEM) variables
200 derived using the *dbmem*() function implemented in R /*adespatial* (S. Dray et al., 2012). MEMs are non-correlated
201 eigenvectors of a spatial weighting matrix derived from geographic coordinates at sampling locations (Stéphane
202 Dray, Legendre, & Peres-Neto, 2006; Griffith & Peres-Neto, 2006). A forest of 500 trees was built on each SNP as
203 response variable, using climatic variables and MEMs as predictors. The GF model was then used to predict and
204 measure the mismatch between the genetic composition under historical and future climate projections using
205 the method of Fitzpatrick and Keller (2015). Genomic offset of Ethiopian barley landraces was calculated as the
206 Euclidean distance between the allelic turnover under the historical and projected climate.

207 Genome-wide associations

208 A GWAS was run on climatic variables and phenotypic BLUPs using a Fixed and random model Circulating
209 Probability Unification (FarmCPU) (Liu, Huang, Fan, Buckler, & Zhang, 2016) implemented in R/rMVP (Yin et al.,
210 2021). FarmCPU was run with correction for kinship, and the first 10 genetic PCs as covariates to consider
211 population structure. Kinship was estimated using the VanRaden method (VanRaden, 2008). Both kinship and
212 genetic PCs were calculated using the set LD-based pruned markers. The GWA was run on a set of high-quality
213 SNP markers with MAF > 0.01. The thresholds to detect significant associations were set considering Bonferroni
214 correction with alpha=0.05 and the whole SNP set and a False Discovery Rate (FDR) at 5% for multiple testing
215 correction, computed with *R/qvalue* (Storey, Bass, Dabney, & Robinson, 2021).

216 The search for candidate genes was performed based on chromosome-specific LD as well as proximity to
217 significant associations. Barley gene annotations were derived from the latest version of the barley reference
218 genome (MorexV3, DOI: 10.5447/ipk/2021/3). Protein sequences of putative positional candidate genes were
219 then used as queries against Araport11 reference proteome (Cheng et al., 2017).

220

221 **Results**

222 Genomic diversity in the collection

223 The sequencing of the collection yielded over 1.25 billion raw sequences. After variant calling and quality check,
224 436 barley lines and 47,492 genotyped SNPs were retained. LD in the collection decayed on average within 9.52
225 Mb, with variation across the seven chromosomes (Figure S1, table S2). A smaller set of 2,064 SNP markers was
226 derived via LD-pruning to provide an unbiased representation of the diversity existing in the collection. Genetic
227 diversity analyses depicted a complex genetic structure that could be best summarized by eleven genetic clusters
228 (Figure S2, Figure S3), termed DAPC clusters 1-11. Improved barley varieties released for cultivation in Ethiopia
229 were markedly different from most local landraces and consistently fell in DAPC cluster 2 and cluster 11 (Fig. 1).
230 Landraces comprised all the other DAPC clusters and featured high genetic diversity; genetic structure was
231 however low, as reported by the low variance explained by the PC axes (Fig. 1 a). Barley landraces having GPS
232 coordinates at the sampling sites (n=383) span the entire geographical and AEZ range of barley cultivation in
233 Ethiopia, from 1350 m a.s.l. to more than 3,780 m a.s.l. (Figure s4). The relation between the DAPC genetic
234 clusters and the AEZs of origin of landraces showed that genetic groups are partially related to local cropping
235 conditions. Ethiopian farmers cultivate barley in mid-highlands in sub-moist, moist, sub-humid and humid
236 edaphic conditions, and DAPC clusters replaced one another across AEZs (Fig. 1 b). The DAPC cluster 8 and cluster
237 9 were mostly limited to sub-moist and sub-humid AEZs, respectively (Chi-square test p value < 0.05) (Figure S5).
238 The distribution of the DAPC clusters could also be traced back to administrative borders of Ethiopia, which
239 combine AEZs variation with historical and cultural diversity. DAPC cluster 8 was almost exclusively found in

240 Tigray (Chi-square test p value < 0.05) (Fig. 1 c), and specifically *Misrakawi* (Eastern Tigray) and *Debubawi*
241 (Southern Tigray) (Figure S5). DAPC cluster 10 and cluster 1 were mostly found in specific sub-regions of Amhara
242 (*Debub Wello*) and Oromia (*Bale*), while DAPC cluster 9 and 3 were mainly found in *Semen Omo* and *Gurage* in
243 the Southern Nations, Nationalities, and Peoples' Region (SNNP). Cluster 3, in lesser extent, was also present in
244 the sub-regions of *Hadiya* and *Keficho Shekicho* (Figure S6).

245 Climatic and phenological diversity in the collection

246 The climate ensemble modeling revealed an increased trend for temperature-related bioclimatic variables across
247 the Ethiopian barley cropping area at both scenarios and time horizons. Less variation was observed for
248 precipitation related variables; however, some areas showed a projected increase in rainfall during the wettest
249 months of cultivation of as much as 60% of the baseline (Figure S7). Temperature-related variables showed a
250 decreasing signal in the southern and northeastern part of Ethiopia during the driest months of the barley
251 growing season, especially under the most extreme RCP scenario (Figure S8).

252 To study the climatic diversity of the Ethiopian barley, a VIF approach was used to reduce multicollinearity of
253 bioclimatic variables, identifying a set of nine variables that were used to derive the climatic features. Among
254 the temperature-derived variables, bio2 (temperature range), bio3 (isothermality), bio4 (temperature
255 seasonality) and bio9 (mean temperature of the driest quarter) were retained. Among the variables related to
256 precipitation, bio12 (total precipitation), bio14 (precipitation of driest month), bio15 (precipitation coefficient of
257 variation), bio18 (precipitation of warmest quarter) and bio19 (precipitation of coldest quarter), all associated
258 with seasonality or limiting precipitation factors, were maintained.

259 The nine retained bioclimatic variables showed broad variation across the sampling area. When summarized by
260 a PCA, the first bioclimatic PC was positively correlated with temperature range (bio2) and seasonality (bio4) as
261 well as with precipitation seasonality (bio15) (Fig. 2 a) and explained 38.6 % of the climatic variance of the sites
262 of collection of barley landraces. PC2, positively associated with precipitation variables (bio12 and bio19),
263 accounted for 21.1 % of the bioclimatic variance, while PC3 explained 14.3 % of the variance, being negatively

264 correlated with the temperature of the driest quarter (bio9). Climatic PC variables could tell apart DAPC clusters
265 whose distribution pattern was associated with precipitation and temperature gradients (Fig. 2 b). DAPC cluster
266 9, mostly found in Tigray, is cultivated in warmer climates. DAPC cluster 5, not associated to any AEZ or
267 administrative region, and cluster 1 appeared to be cultivated in wetter and drier conditions, respectively, when
268 compared to the others. Some of the DAPC clusters, including cluster 2, seem to be cultivated in a broad
269 combination of climatic conditions (Fig. 2 b).

270 The phenological characterization of the collection, carried out at two sites during the main season of 2017 and
271 2018, showed extensive variation in length of the plant cycle measured as days to heading (DH), days to maturity
272 (DM), and grain filling period (GFP); BLUPs of these three traits are reported in Table S3). Landraces matured in
273 a span of more than 30 days (mean=65.7, SD=7.5), but improved varieties required a longer maturing time
274 (mean=72.8, SD=7.4). DH and DM had a strong genetic determination and were stable across locations and years,
275 as reported by high broad sense heritability (H^2_B), while GFP to a lesser extent (Table S4). Phenology matched
276 the genetic clustering observed in the collection. A PCA on phenology traits derived a PC1 highly correlated with
277 DH and DM, explaining about two-thirds of the variance, while PC2 separated genotypes by GFP (Fig. 2 c). DAPC
278 clusters are mostly ordered across PC1 and succeed one another in partially overlapping groupings. Several
279 landraces are earlier than improved varieties, most notably cluster 1, 5,8, 9 and 10 which mature well before all
280 the improved lines in the common garden experiment (Fig. 2 c).

281 <u>Outlook of barley cultivation in Ethiopia in a changed climate</u>

282 The current extent and distribution of Ethiopian barley genomic diversity may not be suited to future climate
283 scenarios. The GF analysis estimated the importance, in terms of predictive power, of the bioclimatic and spatial
284 variables in relation to the genomic variation observed across the cropping area. Overall, the allelic turnover was
285 best predicted by a bioclimatic indicator that describes variation of precipitation patterns (*i.e.* bio19), followed
286 by a number of MEM variables representing spatial structure in the collection, and bio 9 (mean temperature of
287 driest quarter) and bio12 (precipitation throughout the growing season) (Fig. 3 a). Predictors were used to

288 estimate climate-driven genomic variation across the landscape (Fig. 3 c and d). Among the 23,674 SNPs tested
289 as response variables, about 67% (n=15,869) were predicted by the model with $R^2 > 0$.

290 Based on the current landscape-genome relations modeled through GF, we predicted the genomic composition
291 at future RCP scenarios using projections derived from ensemble modeling climate data. We estimated barley
292 future genomic offset as the difference between observed and expected genetic variation for each of the tested
293 scenarios (Fig. 3 d). At all RCP-horizon combinations we observe high offset in the belt across the border that
294 separates the region Afar from Tigray and Amhara, as well as in the western part of SNNP (Figure S9). The western
295 part of Amhara and the region of Benishangul-Gumuz show medium offset (Fig. 3 d).

296 Genome-wide associations and genomic signatures of adaptation

297 A GWAS was used to capture the genetic mechanisms underlying phenology and adaptation of Ethiopian barley.
298 Twenty-four unique quantitative trait nucleotides (QTNs) were identified for DH and DM (Fig. 4 a and b) (Table
299 S5). QTNs explained up to the 11.7% and 3.9% of variance of DH and DM, respectively. Some of the associations
300 targeted well known flowering time genes in barley, but several others were unreported in literature. Among the
301 genes implicated in flowering time variation in barley, the allelic variation of *FRIGIDA* and *VRN-H1* underly
302 differences in phenology of Ethiopian barley. The same mapping approach was applied to the bioclimatic
303 variables derived from historical climate, identifying 83 unique QTNs, 17 of which were associated with the two
304 most important environmental predictors according to the GF model (bio19 and bio9) (Fig. 4 c and d) (Table S5).
305 We found that a QTN was shared among DH and bio9 (SNP chr4H-88623874), tagging *FRIGIDA* (Fig. 4 a and d).

306 **Discussion**

307 Our data shows that Ethiopian barley landraces are genetically different from most improved lines released for
308 cultivation in the country (Fig. 1 a). This means that their allele pool is poorly explored by modern breeding, a
309 finding in accordance with previous literature tapping into the world diversity of barley (Milner et al., 2019).
310 Indeed, local breeding made limited use of Ethiopian agrobiodiversity and national tend to rely on international

311 breeding materials rather than on traditional germplasm (Mengistu, Kidane, Fadda, & Pè, 2016). Still, some of
312 the improved varieties included in this study showed some degree of overlap with landraces, possibly due to
313 hybridizations by local breeding efforts or by mix-up at the field level, a feature not uncommon in material
314 sourced from genebank collections (Sansaloni et al., 2020). The low use of the local allele pool to breed improved
315 barley lines may leave behind variation relevant for adaptation to current and future climates.

316 Although high levels of admixture could be detected, as it is the case of other cereal landraces collections from
317 the horn of Africa (Westengen et al., 2014), we reported a compelling association between the genomic makeup
318 of landraces and Ethiopian AEZ and administrative regions (Fig. 1 b and c). Results show that the DAPC cluster 8
319 was almost limited to Tigray and to tepid sub-humid mid-highlands (SH3, Figure S4). This can be explained by
320 local adaptation processes as well as with historical factors. Ethiopian smallholder farming makes little use of
321 inputs, and largely depend on landraces that show adaptation to local environmental conditions.

322 The uniqueness of germplasm from Tigray was also reported on other crops, including teff (Woldeyohannes et
323 al., 2022) and wheat (Di Falco, Chavas, & Smale, 2006). Tigray is more limiting in terms of barley potential
324 production when compared to other regions of Ethiopia, and this aspect might have contributed to local selection
325 for unique barley lineages. Historical and socio-economic influences may also have played an import role in
326 shaping the distribution of the diversity on the landscape. Barley cultivation in the northern part of Ethiopia goes
327 back to the Aksumites, one of the earliest civilizations in Horn of Africa (Harrower et al., 2019). Recent
328 archeological evidence testifies and even earlier use of this crop in the region which corresponds to modern
329 Tigray (D'Andrea, Perry, Nixon-Darcus, Fahmy, & Attia, 2018). Modern Tigrayan communities use barley to
330 prepare *tihlo*, a typical dish based on barley which is not found in other parts of the country, and that may
331 contribute to the uniqueness of the barley from this region.

332 The diversity in maturing time variation that we found in Ethiopian barley also reflects the extraordinary range
333 of landscapes, farmers management practices and cultures. Phenology traits are quantitatively inherited (Table
334 S4), interact with environmental factors and are of pivotal importance to maximize yield potential in target fields;

335 well synchronized flowering and maturity time are necessary for achieving good harvest, especially in
336 environments exposed to harsh conditions like terminal drought and heat (Jung & Müller, 2009). Indeed, control
337 of phenology through breeding can reduce yield risks, for example achieving harvest earlier in the season.

338 Our climate projection analysis suggests that rain seasonality, as well as temperature, may change differently
339 across the Ethiopian landscape. A remarkable difference in total precipitation, expected to increase more than
340 60%, may realize in the southwestern part of the country, in particular in *Keficho Shekicho* (Figure S7). As for
341 temperature related variables, mean temperature of the driest quarter (bio9) showed a decreasing signal in the
342 southern a northeastern part of Ethiopia under RCP 8.5 at both horizons, while no change signal was observed
343 under RCP 4.5 (Figure S8). The ensemble approach used to generate projected climate showed comparable
344 trends when compared to the historical dataset, suggesting that the projected climate data used in this study
345 captured the ongoing climate trends across the region (Sanderson et al., 2015).

346 The combination of genomics, climatic data and common garden experiments was aimed at exploring the current
347 and future climatic adaptation of Ethiopian barley germplasm. GF predictive models can significantly improve
348 the ability to detect areas that are likely to be vulnerable (Rhoné et al., 2020); this approach represents a step
349 forward if compared to other methods based on species distribution modelling (de Sousa, van Zonneveld,
350 Holmgren, Kindt, & Ordoñez, 2019). The GF identified areas in which the extant landrace diversity of barley may
351 not be well adapted to future climate. This can be put in relation with seasonal shifts we expect during the *Meher*.
352 Under RCP8.5, the highest vulnerability for barley was predicted in northwestern SNNP (Fig. 3 d), in the
353 administrative zone of *Keficho Shekicho*, at the border with *Gambela*, already among the warmest areas of
354 Ethiopia (Degife, Zabel, & Mauser, 2021) and already marginal for barley production. Rather, the offset region
355 bordering Afar (Fig. 3 d) is found in an area with high production of barley, and in close vicinity of areas of unique
356 barley agrobiodiversity including Tigray, home of the cluster 8 described by this study (Fig. 1 c). The western part
357 of Amhara as well as the region of Benishangul-Gumuz show medium offset to future climate scenarios; however,
358 in this case, our dataset may not be representative, as the samples used in the analysis were collected in

359 neighboring zones yet with same agroecological features. These results show that climate change will impact
360 significant portions of the barley cropping areas in Ethiopia, especially those showing already hot and dry
361 features that are projected to worsen. These findings suggest that breeding should focus on those areas
362 exploiting local agrobiodiversity to enhance local adaptation of barley.

363 Candidate genes and molecular targets for breeding

364 Modern breeding approaches could counteract the predicted vulnerability tapping into traits for local adaptation
365 that are available in landraces. Our approach uncovered several QTNs associated with phenology and bioclimatic
366 diversity, including the two bioclimatic variables having higher predictive power towards the GF. Some of the
367 QTN tag genomic loci or genes already reported being associated with phenology and adaptation. A QTN at 527.9
368 Mb on Chr 5H, shared between DH and DM, is located 230 Kb downstream *VRN-H1* (Fu et al., 2005), homologous
369 to *APETALA1/ FRUITFUL* (*AP1/FUL*) of Arabidopsis. *VRN-H1* is a major player in flowering-time variation in barley,
370 and its effect is conserved across different genetic backgrounds (Milner et al., 2019) and environmental
371 conditions, with direct implications on yield (Francia et al., 2011; Tondelli et al., 2014). In cereals, transcription
372 of *VRN1* increases with exposure to low temperatures (Danyluk et al., 2003), so that *VRN1* may also be related
373 with recruitment of the floral-promoting potential of *AP1/FUL* genes to provide a low-temperature-induced
374 flowering switch.

375 The most significant QTN for DH was found on chr4H at 88.6 Mb (Fig. 4 a), also significantly associated with mean
376 temperature of driest quarter (bio9) (Fig. 4 d). This signal is located 185 Kb upstream of the gene model
377 *HORVU.MOREX.r3.4HG0348870*, homolog to *FRIGIDA*. This gene has been extensively studied in Arabidopsis
378 because of its role in flowering time variation (Noh & Amasino, 2003; Zhang & Jiménez-Gómez, 2020), having
379 direct implications in floral transition. Latitudinal variation in flowering times in Arabidopsis is modulated by
380 *FRIGIDA* (Stinchcombe et al., 2004), suggesting its key role in adaptation. DH and DM also share a significant SNP
381 on chr7H; the signal lies 270 Kb upstream *enolase* (*ENO*) (*HORVU.MOREX.r3.7HG0647190*) that encodes for a
382 protein homologous to Arabidopsis' ENO2 (AT2G36530), that acts as positive regulator of cold-responsive gene

383 transcription (Lee et al., 2002). In a recent work, Arabidopsis loss of function mutants for *ENO2* showed early
384 flowering phenotypes (Ma et al., 2021) that reinforce the relevance of this candidate gene.

385 On the same chromosome chr7H we observed an association for precipitation of the coldest quarter (bio19) at
386 401.4 Mb, about 600 Kb from the gene model *HORVU.MOREX.r3.7HG0701970.1*, encoding a
387 CALCIUM/CALMODULIN-REGULATED RECEPTOR-LIKE KINASE that shows high similarity with Arabidopsis CRLK1,
388 involved in cold sensing and tolerance (Yang, Chaudhuri, Yang, Du, & Poovaiah, 2010). The same bioclimatic
389 variable is associated with another signal on chr6H at 529.6 Mb. In this genomic region, 37Kb downstream the
390 SNP, lies a *3-ketoacyl-CoA synthase* (*HORVU.MOREX.r3.6HG0621140*). This gene has been reported as an
391 evolutionary conserved mechanism in barley and Arabidopsis for plant surfaces sensing of distantly related
392 powdery mildews and involved in related defense mechanism from these fungi. At 231.9 Mb on chr6H we
393 observe another signal of bio19 at about 606 Kb downstream *HORVU.MOREX.r3.6HG0582540*, which codes for
394 a putative disease resistance protein; notably, the same chromosomic region it is also tagged by the top
395 significant SNP associated with the temperature-related variable bio9. These finding may underlie patterns of
396 adaptation of Ethiopian barley landraces to pathogens, a feature well known and already exploited by breeding
397 (Jørgensen, 1992; Piffanelli et al., 2004), this time possibly in association with different rainfall regimes.

398 The GF results reinforce these findings. In several cases, loci associated to phenology and adaptive potential were
399 also those best predicted by the variation of the climatic indicators. The association of DM on chr 2 with DM at
400 506.2 Mb, is also characterized by high R^2 towards the GF model (> 99th percentile), meaning that its predictability
401 through bioclimatic variables and geographic features is highly consistent. This signal lies within the gene body
402 of *HORVU.MOREX.r3.2HG0172560*, encoding for a major facilitator superfamily transporter protein highly similar
403 to Arabidopsis' STP12 and STP10. This gene family is known to play a role in senescence, suggesting a possible
404 role in the dynamics of maturation in barley and more. In Arabidopsis, STPs are also implicated in response
405 mechanisms linked to a range of different environmental stressors like osmoregulation, salt tolerance,
406 dehydration response and, notably, low temperature response (Büttner, 2007).

407 **Conclusions**

408 Bridging genetic, climatic and phenological diversity under a genome-wide association framework allows the
409 identification of genomic loci with potential for future breeding efforts addressing local adaptation and climate
410 shifts. More studies are needed to further the characterization of genomic loci relevant for adaptation and
411 validation of candidate genes, yet our results show that relevant adaptation traits exist in Ethiopian landraces,
412 and that these genetic materials should be rapidly exploited by breeding to meet the needs of a changing climate.
413 Leveraging local genetic diversity, the result of local adaptation and farmers knowledge, it may be possible to
414 derive valuable options to foster new breeding models able to address smallholder farming system's needs as
415 well as put in place effective tailored strategies to protect farmer livelihoods and mitigate the effects climate
416 change.

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423 **Author contributions**

424 BF conducted data collection and data analysis with LC and MD. BF, YGK, and SA conducted field planning and
425 phenotyping. MM managed sequencing data and produced SNPs. JSA conducted climate analysis. SG analyzed
426 climatic and genomic data. MD, MEP, YGK and CF supervised the project. BF, LC, and MD drafted the manuscript.
427 LC produced figures. All authors read the final version and approved submission.

428 **Data availability**

429 Barley accessions are available upon request from the Ethiopian Biodiversity Institute (EBI,
430 http://www.ebi.gov.et/). Raw DNAsequencing reads are available on the Short Read Archive at NCBI
431 (https://www.ncbi.nlm.nih.gov/sra/), BioProject ID PRJNA841803; NCBI BioSample accessions from
432 SAMN28618042 to SAMN28618521.

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