Genomic and bioclimatic diversity of Ethiopian barley (*Hordeum vulgare* L.) landraces reveals vulnerability to climate change

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

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

87 **Materials and Methods**

88 Plant material and DNA extraction

89 Plant materials used in this study were derived from the Ethiopian Biodiversity Institute (EBI) barley landrace
90 collection. Accessions were prioritized by completeness of passport data, and a core collection of 249 barley
91 landraces was selected to cover the entire geographical and agroecological range of barley cultivation in Ethiopia.
92 Landrace accessions were purified in an ear-to-row reproduction in the main season of 2016 at the experimental
93 station of Holeta, Ethiopia (9.065 N, 38.459 E). When different morphological types were present in an EBI
94 accession, this was split in as many accessions as types, resulting in 418 purified barley lines derived from
95 landrace accessions. Lines derived from landraces were sided by 40 improved lines, representing all main barley
96 improved lines released for cultivation in the country at the time of the assembly of the panel. Improved lines
97 were sourced from National and Regional agricultural research centers. Full description of the plant materials
98 used in this study is reported in Supplementary Table 1. The full collection of 458 barley was germinated to
99 extract genomic DNA at the molecular biology laboratory of the EBI, Addis Abeba, Ethiopia. DNA was extracted
100 from 3-5 seedlings per line, pooled in equal quantity, with the GenElute Plant Genomic DNA Miniprep Kit (Sigma-
101 Aldrich, St Louis, MO) following the manufacturer's protocol. DNA was shipped to Italy and evaluated for quality
102 and quantified using a Microplate photometer (Thermo Scientific, Milford, MA) and agarose gel electrophoresis
103 at the Scuola Superiore Sant'Anna molecular laboratories.

104 Sequencing and bioinformatic analysis

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

117 Genomic diversity

118 When not stated otherwise, all data analysis was performed in R (R Core Team, 2018). SNPs with minor allele
119 frequency (MAF) above 5% were used to calculate pairwise linkage disequilibrium (LD) with the r^2 metrics in
120 R/*Ldheatmap* (Shin, Blay, Mcneney, & Graham, 2006). LD decay was estimated on SNPs having MAF> 0.05, as
121 function of physical distance according to the Hill and Weir equation (Hill & Weir, 1988). A threshold of $r^2 = 0.3$
122 was used to estimate average LD decay for each chromosome. Genetic structure and diversity of the barley
123 collection were studied using a set of SNP markers pruned by LD at a threshold of $r^2 = 0.5$, using PLINK (Chang et
124 al., 2015) *indep-pairwise* function with a 150-variant window moving in 5-variant steps. A complete linkage
125 agglomerative clustering, based on pairwise identity-by-state (IBS) distance, was run using PLINK with defaults.
126 A pairwise dissimilarity neighbor joining (NJ) analysis was run in Tassel (Bradbury et al., 2007) to describe the
127 phylogenetic relationship among lines. Genetic groupings of samples were detected with Discriminant Analysis
128 of Principal Components (DAPC) (Jombart et al., 2010) using R/*adegenet* (Jombart, 2008). The diversity among
129 samples was further described using Principal Component Analysis (PCA) and Admixture (Alexander & Lange,
130 2011).

131 Spatial and climatic characterization

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

139 Historical climate data for the study area was derived from the fifth generation of European Centre for Medium-
140 Range Weather Forecasts (ECMWF) atmospheric reanalysis version (ERA5) data, released under the Copernicus
141 Climate Change Service (Hersbach et al., 2020). The dataset covers over 30 years (1981-2010) at a spatial
142 resolution of 0.25° x 0.25°. Climatological biases in temperature and precipitation across the East African region
143 are reduced in ERA5 compared to the previous version of ERA-interim (Gleixner et al., 2020). Future climate
144 projections were obtained from daily climate data extracted from a subset of 38 climate models among the
145 CMIP5 dataset at the horizon of 2050 and 2070 for two Representative Concentration Pathway (RCP): RCP4.5
146 and RCP8.5. We followed a recent study to select the representative CMIP5 GCM models, as the number of
147 genuinely independent ones in the CMIP5 archive is significantly less than the number of those submitted
148 (Sanderson, Knutti, & Caldwell, 2015). After reviewing previous works on model similarity (IPCC, 2019) and
149 quality metrics compared to historical observational data, we selected four relatively independent models:

CESM1-BGC, CMCC-CM, MIROC5, and MPI-ESM-MR, from which we prepared ensembles for future projected climate. Climate extremes and small-scale variability are essential drivers in many climate change impact studies. However, the spatial resolution achieved by the global models is still insufficient to identify the fine structure of rainfall intensity correctly. Therefore, we employed a stochastic downscaling and bias technique, the Rainfall Filtered Autoregressive Model (RainFARM), which has been extended for application to long climate simulations (D'Onofrio, Palazzi, Von Hardenberg, Provenzale, & Calmanti, 2014; Rebora, Ferraris, von Hardenberg, & Provenzale, 2006). To achieve optimal data spatial and temporal adjustment, we accessed data of 150 weather station of the Ethiopian National Meteorology Agency (NMA), covering the entire barley cropping range.

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

Common garden-experiments and phenology data analysis

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

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

180 Where the observed phenotypic value is y_{ik}, μ is the overall mean of the population, g_i is the random effect for
181 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
182 effects are considered for genotype, year, and location, and e is the error. For calculation of BLUPs within a single
183 location and/or year, the data was sub-set and analyzed with a reduced model in accordance with Eq. (1). Broad-
184 sense heritability (H^2) was derived from the variance component estimates deriving from Eq. (1) as follows:

185

186 $$H^2 = \frac{\sigma_g}{\left(\sigma_g + \frac{\sigma_{gl}}{n_{loc}} + \frac{\sigma_{gy}}{n_{year}} + \frac{\sigma_{gyl}}{n_{loc} * n_{year}} + \frac{\sigma_e}{n_{rep} * n_{loc} * n_{year}}\right)} \quad \text{Eq. (2)}$$

187

188 In Eq. (2), σ_g is the variance component of genotypes,σ_{gl} is the genotype by location variance, σ_{gy} is the
189 genotype by year variance, σ_{gly} is the genotype by location by year variance, and σ_e is the error variance.
190 $n_{loc}, n_{year}, n_{rep}$ are the number of locations, years, and replications, respectively. For calculation of H^2 within
191 locations and years, Eq. (2) was simplified accordingly.

192 Estimation of Ethiopian barley genomic vulnerability to future climates

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

205 Genome-wide associations

206 A GWAS was run on climatic variables and phenotypic BLUPs using a Fixed and random model Circulating
207 Probability Unification (FarmCPU) (Liu, Huang, Fan, Buckler, & Zhang, 2016) implemented in R/rMVP (Yin et al.,
208 2021). FarmCPU was run with correction for kinship, and the first 10 genetic PCs as covariates to consider

population structure. Kinship was estimated using the VanRaden method (VanRaden, 2008). Both kinship and genetic PCs were calculated using the set LD-based pruned markers. The GWA was run on a set of high-quality SNP markers with MAF > 0.01. The thresholds to detect significant associations were set considering Bonferroni correction with alpha=0.05 and the whole SNP set and a False Discovery Rate (FDR) at 5% for multiple testing correction, computed with *R/qvalue* (Storey, Bass, Dabney, & Robinson, 2021).

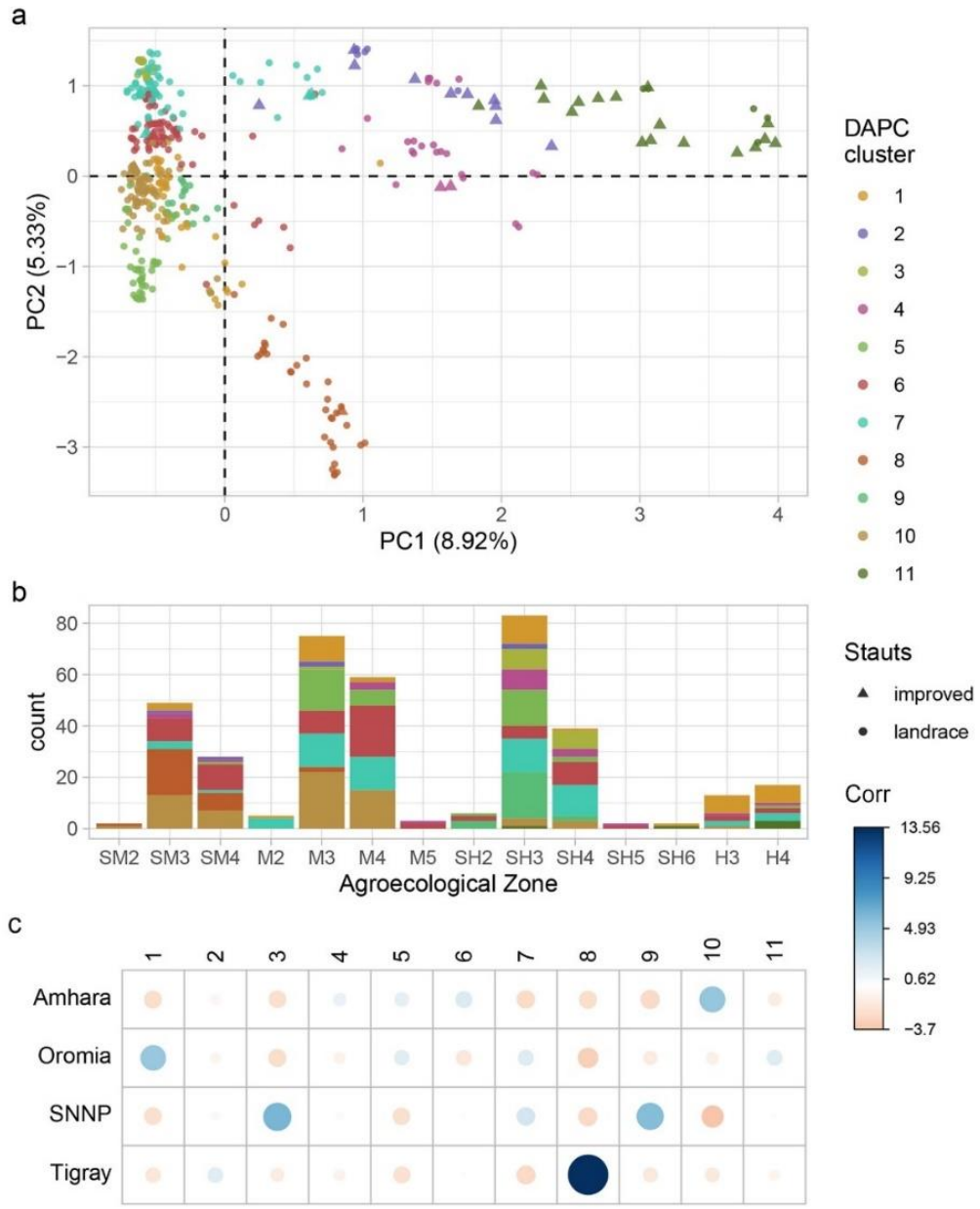
The search for candidate genes was performed based on chromosome-specific LD as well as proximity to significant associations. Barley gene annotations were derived from the latest version of the barley reference genome (MorexV3, DOI: 10.5447/ipk/2021/3). Protein sequences of putative positional candidate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

Results

Genomic diversity in the collection

The sequencing of the collection yielded over 1.25 billion raw sequences. After variant calling and quality check, 436 barley lines and 47,492 genotyped SNPs were retained. LD in the collection decayed on average within 9.52 Mb, with variation across the seven chromosomes (Supplementary Figure 1, Supplementary table 2). A smaller set of 2,064 SNP markers was derived via LD-pruning to provide an unbiased representation of the diversity existing in the collection. Genetic diversity analyses depicted a complex genetic structure that could be best summarized by eleven genetic clusters (Supplementary Figure 2, Supplementary Figure 3), termed DAPC clusters 1-11. Improved barley varieties released for cultivation in Ethiopia were markedly different from most local landraces and consistently fell in DAPC cluster 2 and cluster 11 (Figure 1). Landraces comprised all the other DAPC clusters and featured high genetic diversity; genetic structure was however low, as reported by the low variance explained by the PC axes (Fig. 1a). Barley landraces having GPS coordinates at the sampling sites (n=383) span the entire geographical and AEZ range of barley cultivation in Ethiopia, from 1350 m a.s.l. to more than 3,780 m a.s.l. (Supplementary Figure 4). The relation between the DAPC genetic clusters and the AEZs of origin of landraces showed that genetic groups are partially related to local cropping conditions. Ethiopian farmers cultivate barley in mid-highlands in sub-moist, moist, sub-humid and humid edaphic conditions, and DAPC clusters replaced one another across AEZs (Figure 1b). The DAPC cluster 8 and cluster 9 were mostly limited to sub-moist and sub-humid AEZs, respectively (Chi-square test p value < 0.05) (Supplementary Figure 5). The distribution of the DAPC clusters could also be traced back to administrative borders of Ethiopia, which combine AEZs variation with historical and cultural diversity. DAPC cluster 8 was almost exclusively found in Tigray (Chi-square test p value < 0.05) (Figure 1c), and specifically *Misrakawi* (Eastern Tigray) and *Debubawi* (Southern Tigray) (Supplementary figure 5). DAPC cluster 10 and cluster 1 were mostly found in specific sub-regions of

241 Amhara (*Debub Wello*) and Oromia (*Bale*), while DAPC cluster 9 and 3 were mainly found in *Semen Omo* and
242 *Gurage* in the Southern Nations, Nationalities, and Peoples' Region (SNNP). Cluster 3, in lesser extent, was also
243 present in the sub-regions of *Hadiya* and *Keficho Shekicho* (Supplementary figure 6).



244

245 **Figure 1.** Genomic diversity of the barley collection based on LD-pruned SNP markers. **a)** First two axes of the Principal
246 Component Analysis (PCA) on molecular data, with individual genotypes colored according to the cluster assignation from
247 the Discriminant Analysis of Principal Components (DAPC). Landraces and improved varieties are reported with circles and
248 triangles, respectively. Colors and shapes according to legend to the right. **b)** Genetic cluster composition across Ethiopian
249 AEZs, with colors coded as in panel 'a'. On the y axis, count of genotypes with a specific DAPC cluster assignation by AEZ (x-
250 axis). AEZ codes are given below. **c)** Residual plot for the Pearson's Chi-squared test of independence between genetic

clusters and Ethiopian Regions (*p*-value < 2.2e-16). The size of circles indicates the relative contribution of each combination to the Chi-square score, with colors according to legend. AEZ codes: H3, tepid humid mid-highlands; H4, cool humid mid-highlands; M2, warm moist lowlands; M3, tepid moist mid-highlands; M4, cool moist mid-highlands; SH2, warm sub-humid lowlands; SH3, tepid sub-humid mid-highlands; SH4, cool sub-humid mid-highlands; SH5, Cold sub-humid sub-afro-alpine to afro-alpine;SH6 Very cold sub-humid sub-afro to afro- alpine; SM2, warm sub-moist lowlands; SM3, tepid sub-moist mid-highlands; SM4, cool sub-moist mid-highlands; ZNR, zone not relevant (no hits).

Climatic and phenologic diversity in the collection

The climate ensemble modeling revealed an increased trend for temperature-related bioclimatic variables across the Ethiopian barley cropping area at both scenarios and time horizons. Less variation was observed for precipitation related variables; however, some areas showed a projected increase in rainfall during the wettest months of cultivation of as much as 60% of the baseline (Supplementary figure 7). Temperature-related variables showed a decreasing signal in the southern and northeastern part of Ethiopia during the driest months of the barley growing season, especially under the most extreme RCP scenario (Supplementary figure 8).

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

The nine retained bioclimatic variables showed broad variation across the sampling area. When summarized by a PCA, the first bioclimatic PC was positively correlated with temperature range (bio2) and seasonality (bio4) as well as with precipitation seasonality (bio15) (Figure 2a) and explained 38.6 % of the climatic variance of the sites of collection of barley landraces. PC2, positively associated with precipitation variables (bio12 and bio19), accounted for 21.1 % of the bioclimatic variance, while PC3 explained 14.3 % of the variance, being negatively correlated with the temperature of the driest quarter (bio9). Climatic PC variables could tell apart DAPC clusters whose distribution pattern was associated with precipitation and temperature gradients (Figure 2b). DAPC cluster 9, mostly found in Tigray, is cultivated in warmer climates. DAPC cluster 5, not associated to any AEZ or administrative region, and cluster 1 appeared to be cultivated in wetter and drier conditions, respectively, when compared to the others. Some of the DAPC clusters, including cluster 2, seem to be cultivated in a broad combination of climatic conditions (Figure 2b).

The phenologic characterization of the collection, carried out at two sites during the main season of 2017 and 2018, showed extensive variation in length of the plant cycle measured as days to heading (DH), days to maturity (DM), and grain filling period (GFP). Landraces matured in a span of more than 30 days (mean=65.7, SD=7.5), but improved varieties required a longer maturing time (mean=72.8, SD=7.4). DH and DM had a strong genetic determination and were stable across locations and years, as reported by high broad sense heritability (H^2_B), while GFP to a lesser extent (Supplementary Table 3). Phenology matched the genetic clustering observed in the collection. A PCA on phenology traits derived a PC1 highly correlated with DH and DM, explaining about two-thirds of the variance, while PC2 separated genotypes by GFP (Figure 2c). DAPC clusters are mostly ordered across PC1 and succeed one another in partially overlapping groupings. Several landraces are earlier than improved varieties, most notably cluster 1, 5,8, 9 and 10 which mature well before all the improved lines in the common garden experiment (Figure 2c).

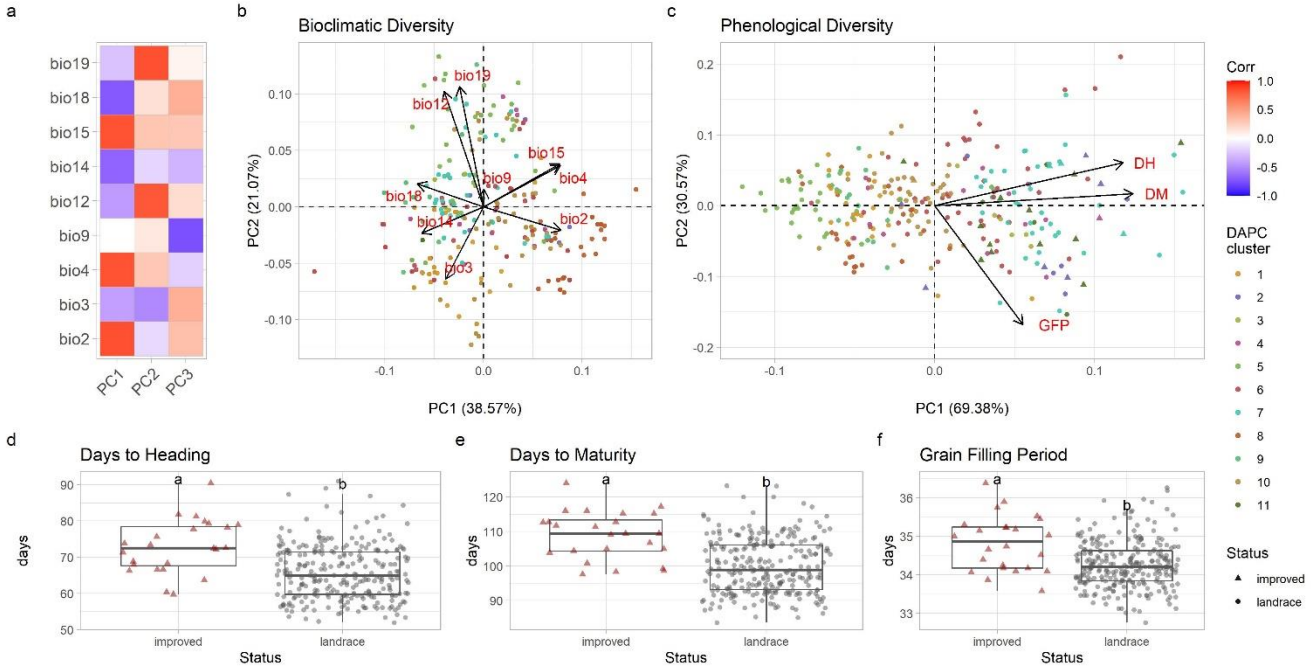


Figure 2. Bioclimatic and Phenological diversity in the barley collection. **a)** Correlation between historical bioclimatic variables and derived PCs, colored according to legend. **b-c)** Principal Component Analysis (PCA) of bioclimatic diversity of 383 georeferenced barley landraces and phenotypic diversity of the whole collection. Dots and triangles are colored according to DAPC clusters as in legend, where dots indicate landraces and triangles indicate improved materials; vectors represent the scale, verse, and direction of drivers of differentiation. **d-f)** BLUP distribution by biological status of Days to Heading (DH), Days to Maturity (DM) and Grain Filling Period (GFP). Landraces are represented by grey dots while improved material by red triangles. Differences between improved materials and landraces were tested by non-parametric Wilcoxon Rank Sum test ($p \leq 0.05$).

305 Outlook of barley cultivation in Ethiopia in a changed climate

306 The current extent and distribution of Ethiopian barley genomic diversity may not be suited to future climate
307 scenarios. The GF analysis estimated the importance, in terms of predictive power, of the bioclimatic and spatial
308 variables in relation to the genomic variation observed across the cropping area. Overall, the allelic turnover was
309 best predicted by a bioclimatic indicator that describes variation of precipitation patterns (*i.e.* bio19), followed
310 by a number of MEM variables representing spatial structure in the collection, and bio 9 (mean temperature of
311 driest quarter) and bio12 (precipitation throughout the growing season) (Figure 3a). Predictors were used to
312 estimate climate-driven genomic variation across the landscape (Figure 3c, d). Among the 23,674 SNPs tested as
313 response variables, about 67% (n=15,869) were predicted by the model with $R^2 > 0$.

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

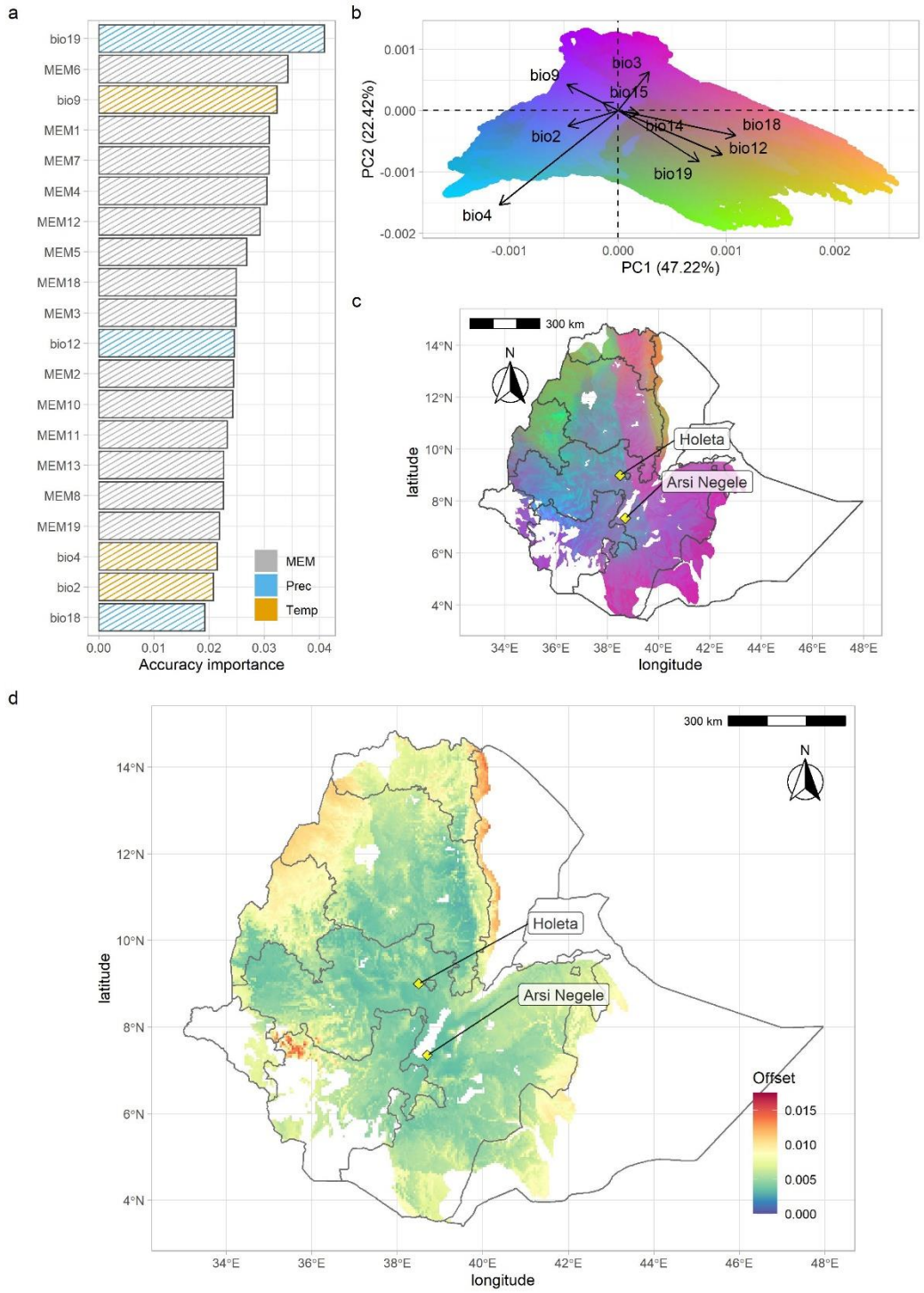


Figure 3. Bioclimatic and spatial diversity explain genomic variation in Ethiopian barley landraces and highlight genomic offset in future climate scenarios. **a)** Ranked accuracy importance, in terms of predictive power, of the top 20 bioclimatic and spatial variables, based on Gradient Forest (GF) analysis. **b)** Biplot of the biological space, represented by Principal Components of the transformed grid with an RGB color palette relative to its first three dimensions. **c)** GF-transformed bioclimatic variables across the cropping area of barley. Colors based on bioclimatic-genetic space in 'b'. **d)** Genomic offset across the barley cropping area based on RCP 8.5 ensemble climate projections at the horizon of 2070. The color scale

327 indicates the magnitude of the mismatch between current and projected climate-driven turnover in allele frequencies.
328 Common garden experiment locations are shown with yellow diamonds in panels 'c' and 'd'.

329

330 Genome-wide associations and genomic signatures of adaptation

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

341

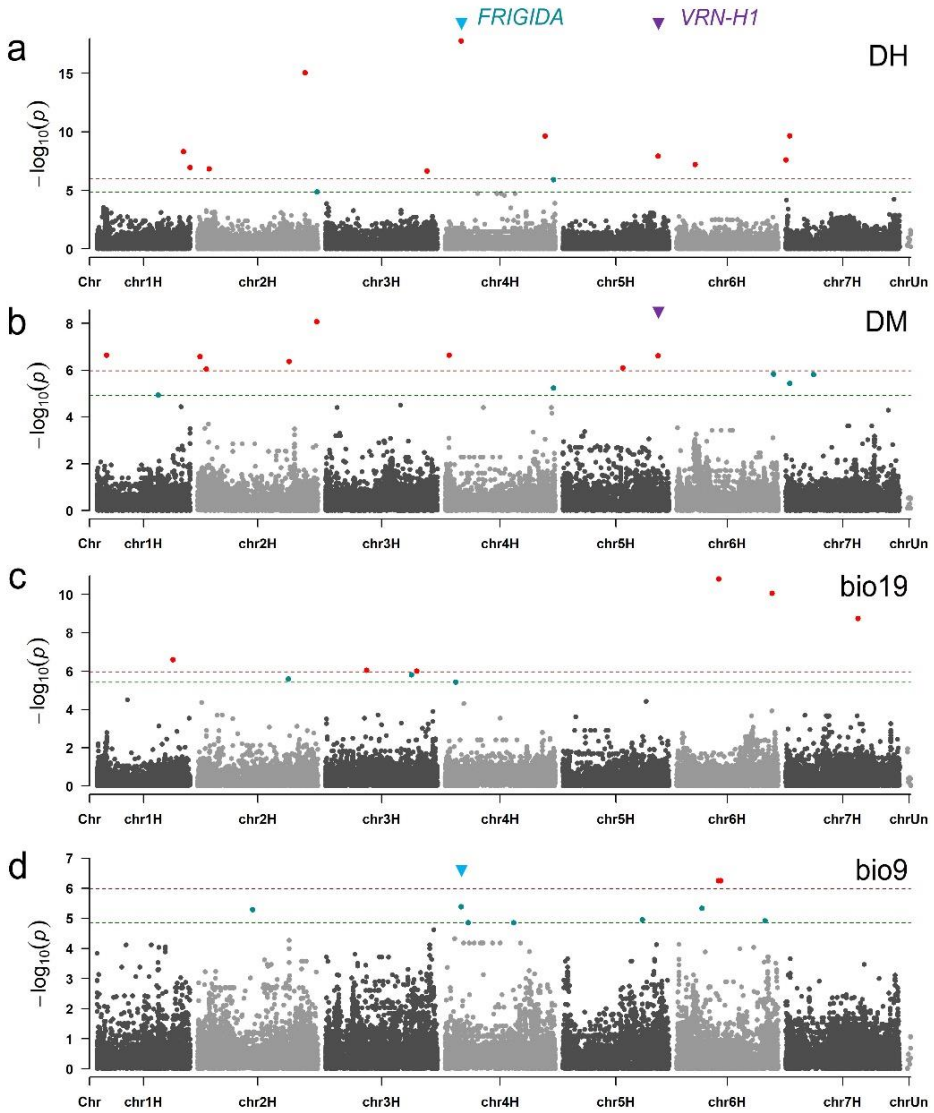


Figure 4. Genome wide association (GWA) study for selected phenology and bioclimatic traits: **a)** days to heading (DH), **b)** days to maturity (DM), **c)** precipitation of coldest quarter (bio19) and **d)** mean temperature of driest quarter (bio9). In each plot, the x axis reports the position on the barley genome, the y axis reports the strength of the statistical association. Each do represent a SNP marker. The horizontal dashed lines indicate genome-wide significance thresholds: the dark-red line refers to Bonferroni correction based on α = 0.05 (-log10 (*p*)= 5.978) while the green line is based on False Discovery Rate (FDR) with q-value > 0.05, specific for each trait. Light-blue and violet arrowheads mark, FRIGIDA and VRN-H1 the position of the major flowering time genes *FRIGIDA* and *VRN-H1*, respectively.

Discussion

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

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

361 Although high levels of admixture could be detected, as it is the case of other cereal landraces collections from
362 the horn of Africa (Westengen et al., 2014), we reported a compelling association between the genomic makeup
363 of landraces and Ethiopian AEZ and administrative regions (Figure 1b and c). Results show that the DAPC cluster
364 8 was almost limited to Tigray and to tepid sub-humid mid-highlands (SH3, Supplementary Figure 4). This can be
365 explained by local adaptation processes as well as with historical factors. Ethiopian smallholder farming makes
366 little use of inputs, and largely depend on landraces that show adaptation to local environmental conditions.

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

377 The diversity in maturing time variation that we found in Ethiopian barley also reflects the extraordinary range
378 of landscapes, farmers management practices and cultures. Phenology traits are quantitatively inherited
379 (supplementary table 3), interact with environmental factors and are of pivotal importance to maximize yield
380 potential in target fields; well synchronized flowering and maturity time are necessary for achieving good
381 harvest, especially in environments exposed to harsh conditions like terminal drought and heat (Jung & Müller,
382 2009). Indeed, control of phenology through breeding can reduce yield risks, for example achieving harvest
383 earlier in the season.

384 Our climate projection analysis suggests that rain seasonality, as well as temperature, may change differently
385 across the Ethiopian landscape. A remarkable difference in total precipitation, expected to increase more than
386 60%, may realize in the southwestern part of the country, in particular in *Keficho Shekicho* (Supplementary figure

387 7). As for temperature related variables, mean temperature of the driest quarter (bio9) showed a decreasing
388 signal in the southern a northeastern part of Ethiopia under RCP 8.5 at both horizons, while no change signal was
389 observed under RCP 4.5 (Supplementary figure 8). The ensemble approach used to generate projected climate
390 showed comparable trends when compared to the historical dataset, suggesting that the projected climate data
391 used in this study captured the ongoing climate trends across the region (Sanderson et al., 2015).

392 The combination of genomics, climatic data and common garden experiments was aimed at exploring the current
393 and future climatic adaptation of Ethiopian barley germplasm. GF predictive models can significantly improve
394 the ability to detect areas that are likely to be vulnerable (Rhoné et al., 2020); this approach represents a step
395 forward if compared to other methods based on species distribution modelling (de Sousa, van Zonneveld,
396 Holmgren, Kindt, & Ordoñez, 2019). The GF identified areas in which the extant landrace diversity of barley may
397 not be well adapted to future climate. This can be put in relation with seasonal shifts we expect during the *Meher*.
398 Under RCP8.5, the highest vulnerability for barley was predicted in northwestern SNNP (Figure 3d), in the
399 administrative zone of *Keficho Shekicho*, at the border with *Gambela*, already among the warmest areas of
400 Ethiopia (Degife, Zabel, & Mauser, 2021) and already marginal for barley production. Rather, the offset region
401 bordering Afar (Figure 3d) is found in an area with high production of barley, and in close vicinity of areas of
402 unique barley agrobiodiversity including Tigray, home of the cluster 8 described by this study (Fig. 1c). The
403 western part of Amhara as well as the region of Benishangul-Gumuz show medium offset to future climate
404 scenarios; however, in this case, our dataset may not be representative, as the samples used in the analysis were
405 collected in neighboring zones yet with same agroecological features. These results show that climate change
406 will impact significant portions of the barley cropping areas in Ethiopia, especially those showing already hot and
407 dry features that are projected to worsen. These findings suggest that breeding should focus on those areas
408 exploiting local agrobiodiversity to enhance local adaptation of barley.

409 <u>Candidate genes and molecular targets for breeding</u>

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

419 with recruitment of the floral-promoting potential of *AP1/FUL* genes to provide a low-temperature-induced
420 flowering switch.

421 The most significant QTN for DH was found on chr4H at 88.6 Mb (Figure 4a), also significantly associated with
422 mean temperature of driest quarter (bio9) (Figure 4d). This signal is located 185 Kb upstream of the gene model
423 *HORVU.MOREX.r3.4HG0348870*, homolog to *FRIGIDA*. This gene has been extensively studied in Arabidopsis
424 because of its role in flowering time variation (Noh & Amasino, 2003; Zhang & Jiménez-Gómez, 2020), having
425 direct implications in floral transition. Latitudinal variation in flowering times in Arabidopsis is modulated by
426 *FRIGIDA* (Stinchcombe et al., 2004), suggesting its key role in adaptation. DH and DM also share a significant SNP
427 on chr7H; the signal lies 270 Kb upstream *enolase* (*ENO*) (*HORVU.MOREX.r3.7HG0647190*) that encodes for a
428 protein homologous to Arabidopsis' ENO2 (AT2G36530), that acts as positive regulator of cold-responsive gene
429 transcription (Lee et al., 2002). In a recent work, Arabidopsis loss of function mutants for *ENO2* showed early
430 flowering phenotypes (Ma et al., 2021) that reinforce the relevance of this candidate gene.

431 On the same chromosome chr7H we observed an association for precipitation of the coldest quarter (bio19) at
432 401.4 Mb, about 600 Kb from the gene model *HORVU.MOREX.r3.7HG0701970.1*, encoding a
433 CALCIUM/CALMODULIN-REGULATED RECEPTOR-LIKE KINASE that shows high similarity with Arabidopsis CRLK1,
434 involved in cold sensing and tolerance (Yang, Chaudhuri, Yang, Du, & Poovaiah, 2010). The same bioclimatic
435 variable is associated with another signal on chr6H at 529.6 Mb. In this genomic region, 37Kb downstream the
436 SNP, lies a *3-ketoacyl-CoA synthase* (*HORVU.MOREX.r3.6HG0621140*). This gene has been reported as an
437 evolutionary conserved mechanism in barley and Arabidopsis for plant surfaces sensing of distantly related
438 powdery mildews and involved in related defense mechanism from these fungi. At 231.9 Mb on chr6H we
439 observe another signal of bio19 at about 606 Kb downstream *HORVU.MOREX.r3.6HG0582540*, which codes for
440 a putative disease resistance protein; notably, the same chromosomic region it is also tagged by the top
441 significant SNP associated with the temperature-related variable bio9. These finding may underlie patterns of
442 adaptation of Ethiopian barley landraces to pathogens, a feature well known and already exploited by breeding
443 (Jørgensen, 1992; Piffanelli et al., 2004), this time possibly in association with different rainfall regimes.

444 The GF results reinforce these findings. In several cases, loci associated to phenology and adaptive potential were
445 also those best predicted by the variation of the climatic indicators. The association of DM on chr 2 with DM at
446 506.2 Mb, is also characterized by high R^2 towards the GF model (> 99th percentile), meaning that its predictability
447 through bioclimatic variables and geographic features is highly consistent. This signal lies within the gene body
448 of *HORVU.MOREX.r3.2HG0172560*, encoding for a major facilitator superfamily transporter protein highly similar
449 to Arabidopsis' STP12 and STP10. This gene family is known to play a role in senescence, suggesting a possible
450 role in the dynamics of maturation in barley and more. In Arabidopsis, STPs are also implicated in response

451 mechanisms linked to a range of different environmental stressors like osmoregulation, salt tolerance,
452 dehydration response and, notably, low temperature response (Büttner, 2007).

453 **Conclusions**

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

463

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468

469 **Author contributions**

470 BF conducted data collection and data analysis with LC and MD. BF and SA conducted phenotyping. MM managed
471 sequencing data and produced SNPs. JSA conducted climate analysis. SG analyzed climatic and genomic data.
472 MD, MEP and CF supervised the project. BF, LC, and MD drafted the manuscript. LC produced figures. All authors
473 read the final version and approved submission.

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