

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 and threatening food security of millions of smallholder farmers. Understanding the potential for current and future climatic adaptation of local crop agrobiodiversity may guide breeding efforts and support resilience of agriculture. Here, we combine a genomic and climatic characterization of a large collection of traditional barley varieties from Ethiopia, a staple for local smallholder farmers cropping in challenging environments. We find that the genomic diversity of barley landraces can be partially traced back to geographic and environmental diversity of the landscape. We employ a machine learning approach to model Ethiopian barley adaptation to current climate and to identify areas where its existing diversity may not be well adapted in future climate scenarios. We use this information to identify optimal trajectories of assisted migration compensating to detrimental effects of climate change, finding that Ethiopian barley diversity bears opportunities for adaptation to the climate crisis. We then characterize phenology traits in the collection in two common garden experiments in Ethiopia, using genome-wide association approaches to identify genomic loci associated with timing of flowering and maturity of the spike. We combine this information with genotype–environment associations finding that loci involved in flowering time may also explain environmental adaptation. Our data show that integrated genomic, climatic, and phenotypic characterizations of agrobiodiversity may provide breeding with actionable information to improve local adaptation in smallholder farming systems.

KEY WORDS

adaptation genomics, agrobiodiversity, climate ready varieties, Ethiopia, landraces, smallholder farming

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1 | INTRODUCTION

The Green Revolution heralded by Norman Borlaug's work at CIMMYT in the 1960s enabled a remarkable increase in agricultural outputs worldwide (Bailey-Serres et al., 2019; Pingali, 2012). In fact, global cereal production has increased by 280% in the last 60 years (FAOSTAT, 2022), mostly thanks to a successful combination of genetic innovation, chemistry, and mechanization. In the chase for increased productivity per surface unit, however, the intensification of modern agriculture led to an increased footprint on global climate and ecosystems, and depletion of agrobiodiversity, impacting small-scale indigenous farming systems (Khoury et al., 2022). Intensive farming allows higher yields per surface unit, but requires uniform management and external inputs including irrigation, fertilizers, and pesticides to express its full potential (Mondal et al., 2020). When optimal conditions are not met, Green Revolution crop varieties may still be outperformed by traditional varieties with local adaptation (Mancini et al., 2017; Ricciardi et al., 2021). This is especially relevant in smallholder farming systems, which involve an estimated 570 million farms worldwide and support the livelihoods of 2 billion people in highly diversified low-input cropping environments (Lowder et al., 2016). In these cropping systems, low adoption rates are observed for modern improved varieties that lack adaptation to local farming conditions as well as to local cultural uses and end user tastes (Acevedo et al., 2020). Mismatches between breeding objectives and needs of local users may jeopardize the impacts of agricultural development efforts in a changing climate.

In contexts with high vulnerability to climate change, high economic damages become very likely and may result in food insecurity (Coronese et al., 2019). In low-input, challenging smallholder cropping environments, the climate crisis causes large environmental fluctuations that magnify the challenges that farmers must face to avoid losses (Cohn et al., 2017). 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 exemplary of this challenge. Ethiopia, a center of domestication and diversity of crops (Vavilov, 1951), still hosts highly diversified farming systems that largely rely on smallholder farmers actively maintaining thousands of landraces. This wealth of agrobiodiversity is reflected in Ethiopia's highly diversified landscape, with 32 registered agroecological zones (AEZs) cultivated by approximately 80 million people (Bachewe & Taffesse, 2018). Previous studies on Ethiopian crop landraces showed that the local agrobiodiversity is large but poorly represented in breeding, as in the case of durum wheat (Mengistu et al., 2016), teff (Woldeyohannes et al., 2022), 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 it has potential for supporting breeding programs at local and international levels (Jørgensen, 1992; Piffanelli

et al., 2004), especially those targeting improved adaptive potential to enhance resilience to the climate crisis.

Until recently, barley has been cropped in Ethiopia in two seasons per year, the short rainy season *Belg* (February–April) and the main rainy season *Meher* (June–December). However, changing patterns of rainfall across the Horn of Africa makes it now more difficult to crop in two seasons (Wakjira et al., 2021). The Horn of Africa is among the most climate vulnerable regions in the continent, and changes in rain patterns are expected to have substantial impacts on food production in the future (Serdaczny et al., 2017). Here, adverse climatic projections coincide with low adaptive capacity, with the result of increased stressors on small-scale agriculture (Morton, 2007). Today, breeding can operate in a big data dimension that connects genomics (Varshney et al., 2021), large-scale phenotyping (Hickey et al., 2017), and climate models describing current and projected climates (Yoder et al., 2014). 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 (Lasky et al., 2015), identifying genomic loci linked to adaptive responses to specific environments (Capblancq et al., 2020). Genomic information can then be used to speed up the development of *climate-ready* varieties through the application of molecular breeding (Lasky et al., 2015), genomic selection (Scheben et al., 2016), and decentralized breeding (de Sousa et al., 2021).

In this study, we tap into the broad diversity of Ethiopian barley landraces that is maintained by local farmers to assess their uniqueness and adaptation potential to current and future climates. We use a data-driven approach combining genomics, climate data analysis, and common garden experiments to describe the relation existing between Ethiopian barley diversity and the landscape in which is cultivated. We then model the barley genetic composition across the climate and geography of Ethiopia, identifying which areas of current barley cultivation are more vulnerable to climate change. We integrate this information in a genome-wide association study (GWAS) targeting phenology and adaptation traits, putting forward suggestions to breeding efforts targeting barley local adaptation.

2 | MATERIALS AND METHODS

2.1 | Plant material and DNA extraction

Plant materials used in this study were derived from the barley landrace collection at the Ethiopian Biodiversity Institute (EBI), the largest germplasm bank in Africa. We selected 249 barley landraces having near-complete passport information and covering the entire geographical and agroecological range of barley cultivation in Ethiopia. In Ethiopia, barley is cultivated as spring type. Therefore, all accessions in the EBI collection were either spring or facultative barley types. To account for potential heterogeneity of landraces stored at the EBI, accessions were propagated in a spike-to-row reproduction in the main season of 2015 at the experimental station of Holeta, Ethiopia (9.065 N, 38.459 E). When different morphological

types were present in an EBI landrace, the accession was split into as many different accessions as types, resulting in 418 barley lines derived from landrace accessions. The lines were again multiplied in the Belg season of 2016, prior to being molecularly and phenotypically characterized. The presence of different morphological types in each original EBI accession reflects the heterogeneity of Ethiopian landraces and the fact that farmers may cultivate more than one barley genotype in the same field.

The collection of 418 lines derived from landraces was sited by 40 improved lines, representing all main barley improved varieties released for cultivation in the country at the time of the assembly of the collection. Improved lines were sourced from National and Regional agricultural research centers. Full description of the plant materials used in this study is reported in **Table S1**. The entire collection of 458 genotypes was germinated to extract genomic DNA at the molecular biology laboratory of the EBI, Addis Ababa, Ethiopia. DNA was extracted from three to five seedlings per genotype, pooled in equal quantity, with the GenElute Plant Genomic DNA Miniprep Kit (Sigma-Aldrich) following the manufacturer's protocol. DNA was shipped to Italy and evaluated for quality and quantified using a Microplate photometer (Thermo Scientific, Milford, MA) and agarose gel electrophoresis at the Scuola Superiore Sant'Anna molecular laboratories.

2.2 | Sequencing and bioinformatic analysis

Genotyping was performed at IGA Tech sequencing services (Udine, Italy) with a double digestion restriction site-associated DNA sequencing (ddRAD-seq) approach (Peterson et al., 2012). Genomic libraries were prepared using *SphI* and *EcoRI* and sequenced on an Illumina HiSeq2500 instrument (Illumina) with V4 chemistry in paired-end 125-bp mode. Raw reads were demultiplexed using the process_radtags in Stacks v2.0 (Catchen et al., 2013) and quality was assessed with FastQC tool (v 0.11.5). Raw reads were filtered for quality with *erne-tool* from ERNE2 package (version 2.1.1, <http://erne.sourceforge.net/>; del Fabbro et al., 2013). Only bases with a Phred Score > 30 were retained and reads shorter than 50 nt were discarded. Trimmed reads of each sample were mapped against the *H. vulgare* reference genome (MorexV3, <https://doi.org/10.5447/1pk/2021/3>; Mascher et al., 2021) with BWA-MEM algorithm (Burrows–Weeler aligner v.0.7.12; Li, 2013). The HaplotypeCaller algorithm, implemented in GATK and run in per-sample mode, was used for variant identification (Poplin et al., 2018). Variant genotyping was completed with GATK GenotypeGVCFstool (Danecek et al., 2011) to derive raw single nucleotide polymorphisms (SNPs). To restrict the analysis to a trustable dataset of putative variants, the resulting raw SNPs were hard-filtered at site level using GATK VariantFiltration tool, removing positions with low site-variant confidence (QUAL < 30), low coverage across all samples (DP < 580), and allele frequency lower than 1% (AF < 0.01). Positions with low variant quality were normalized by allele depth for each variant (QD < 2.0); after this step, they were also filtered out to avoid the inflation of confidence

caused by deep coverage. The mapping quality of each variant site over all reads was requested to be high (MQ > 40.0). If at least three variants fell in a window of 5 bp (using options --cluster-size 3 and --cluster-window-size 5), such variants were also removed. The final set of SNPs used for downstream analyses was restricted to makers with minor allele frequency (MAF) > 0.05 and individuals and SNP markers with missingness > 0.2 were removed.

2.3 | Genotypic diversity

When not stated otherwise, data analysis was performed in R (R Core Team, 2022). Quality-filtered SNPs were used to calculate pairwise linkage disequilibrium (LD) using the r^2 metrics in R/Ldheatmap (Shin et al., 2006). LD decay was estimated as function of physical distance according to the Hill and Weir equation (Hill & Weir, 1988). A threshold of $r^2 = .3$ was considered null LD and used to derive average LD decay distance 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 $r^2 = .5$, using PLINK (Chang et al., 2015) *indep-pairwise* function with a 150-variant window moving in five-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 genotypes. Genetic groupings of samples were identified with discriminant analysis of principal components (DAPC; Jombart et al., 2010) using R/adegenet (Jombart, 2008). The diversity among samples was further described with principal component analysis (PCA) and admixture (Alexander & Lange, 2011).

2.4 | Spatial and climatic characterization of the collection

GPS coordinates of sampling locations of EBI landraces, where available, were projected onto the map of Ethiopia using R/raster (Hijmans & van Etten, 2016). Due to the process of purification of the original EBI accessions, different genotypes in the collection may share the same GPS sampling location. Altitudes were derived at each site based on GPS coordinates, using the CGIAR SRTM database at 90m resolution (Reuter et al., 2007). AEZs were derived from the definition given by the Ministry of Agriculture of Ethiopia (Ministry of Agriculture (MoA) – National Resources Management & REgulatory Department, 1998). 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. Associations between DAPC genetic clusters and Ethiopian administrative regions, sub-regions, and AEZs were assessed using Pearson's chi-squared test of independence. Historical climate data for the study area were 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. The dataset covers over 30 years (1981–2010) at a spatial resolution of $0.25^\circ \times 0.25^\circ$. 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 CMIP5 dataset at the horizon of 2050 and 2070 for two representative concentration pathway (RCP): RCP4.5 and RCP8.5. The number of independent models in the CMIP5 archive is significantly less than the number of those submitted (Sanderson et al., 2015). After reviewing previous works on model similarity (IPCC, 2019) and 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. To improve the spatial resolution of the data and identify the fine structure of rainfall intensity, we employed a stochastic downscaling and bias technique, the Rainfall Filtered Autoregressive Model (RainFARM), which has been extended for application to long-term climate simulations (D'Onofrio et al., 2014; Rebora et al., 2006). To achieve optimal 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 derived only within the main barley-growing season of Ethiopia, the Meher (June–December; Gissila et al., 2004; Segele & Lamb, 2005). The resulting historical and future climate data were used to derive 19 bioclimatic variables using R/dismo (Hijmans et al., 2017). Bioclimatic variables are biologically meaningful indicators, often used in species distribution modeling; they represent seasonal trends and define seasonality and limiting climatic factors. The first 11 bioclimatic variables refer to temperature measures, such as mean temperature (bio1), temperature range (bio7), and monthly and quarterly temperatures (bio5, bio6, bio8–bio11). Bioclimatic variables bio12–bio19 refer to rainfall, including total amount (bio12), coefficient of variation (bio15), and monthly and quarterly amounts (bio13, bio14, bio16–bio19). In this research, bioclimatic variables are derived from data specific to the Meher and should be interpreted accordingly (Table S2). Collinearity among bioclimatic variables was assessed with the `ensemble.VIF()` function in R/BiodiversityR (Kindt & Coe, 2005); only variables with a variance inflation factor below 10 were retained for further analyses.

2.5 | Common garden experiments and phenology data analysis

The barley collection was characterized in common garden experiments at two locations in Ethiopia: Arsi Negele ($7^\circ 21' N$, $38^\circ 242' E$) and Holeta ($9^\circ 00' N$, $38^\circ 30' E$), during the Meher (June–December) of 2016 and the Meher of 2017. 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

both sites: 150 and 100 kg/ha, respectively, corresponding to 69 kg/ha of P and 73 kg/ha of N; agronomic management was uniformly applied to all the trials. 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 et al., 2014) using the general model in Equation (1):

$$y_{ikm} = \mu + g_i + l_k + y_m + gl_{ik} + gy_{im} + gly_{ikm} + e, \quad (1)$$

where the observed phenotypic value is y_{ikm} , μ is the overall mean of the population, g_i is the random effect for the i th genotype, l_k is the fixed effect for the k th location, y_m is the random effect for the m th year. Interaction effects are considered for genotype, year, and location, and e is the error. For the calculation of BLUPs within a single location and/or year, the data were subset and analyzed with a reduced model in accordance with Equation (1). Broad-sense heritability (H^2) was derived from the variance component estimates deriving from Equation (1) as follows:

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

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

The genotypes in the collection were also characterized for lateral florets fertility, a classic trait of barley genetics, commonly referred to as row type, ascribing each genotype to one of the following categories: (a) two-rowed, (b) six-rowed, and (c) irregular. In the two-rowed genotypes, each node of the inflorescence stem bears a spikelet triplet, where only the central is fertile. When no suppression of lateral spikelet development occurs, all spikelets flower, resulting in six-rowed types; intermediate types, commonly referred to as “irregular,” were also considered. The genotypes were also categorized as hulled or hull-less types according to the presence of the hulls.

2.6 | Identification of drivers of barley differentiation on the landscape

We used partial redundancy analysis (pRDA) to identify the drivers of barley landrace differentiation across Ethiopia. In the pRDA, we used the set of LD-pruned SNP ($r^2 = .5$) as response variables while environment, geography, and genetic structure as explanatory variables. We then estimated the proportion of genetic variance explained by any set of explanatory variables once the influence of other sets of variables was removed in a stepwise fashion

(Capblancq & Forester, 2021). The environment was represented by noncollinear bioclimatic variables derived at the sampling points. Geography was represented by latitude and longitude of the accessions; genetic structure by the first three axes of the genetic PCA conducted with the same set of LD-pruned markers. We then used pRDA to look for genotype–environment associations, employing a model controlling for genetic structure (first three genetic PCs) and the nine noncollinear bioclimatic indicators as explanatory variables. To define associated loci and to look for genomic signatures of adaptation, we employed the multivariate method implemented by Capblancq et al. (2018): Adaptive loci were identified based on their position along a Mahalanobis distance distribution calculated among each marker and the center of the RDA space using the first two axes; the distances were then corrected for the inflation factor to derive *p*-values using a chi-squared distribution with two degrees of freedom. A Bonferroni threshold with a nominal *p* value of 5% was used to identify outliers. The analysis was carried out using R/vegan (Oksanen et al., 2022) and outliers were detected with the R function *rdadapt()* and following the filtering, imputation and interpretation procedure developed by Capblancq and Forester (2021).

2.7 | Estimation of barley vulnerability to future climates

A gradient forest (GF) machine-learning regression tree-based algorithm was used to test which environmental variables best explained barley genetic variation across its cultivation area in Ethiopia. To improve the representativeness of the analysis and reduce bias due to under-sampling of allelic diversity, the GF analysis was limited to the area deriving from the union of AEZs in which at least 10 barley accessions were collected. The GF, implemented in R/gradientForest (Ellis et al., 2012), derives the importance, in terms of predictive power, of each bioclimatic variable in the change of alleles to predict genetic composition across the climatic landscape. The GF was trained with environmental variables and with Moran's Eigenvector Maps (MEM) derived using the *dbmem()* function, implemented in R/adespatial (Dray et al., 2012). MEMs are noncorrelated eigenvectors of the pairwise spatial weighting matrix of the geographic coordinates among samples (Dray et al., 2006; Griffith & Peres-Neto, 2006). A forest of 500 trees was built on each SNP as response variable, using the set of noncollinear bioclimatic variables and MEMs as predictors. The GF model was then used to predict and measure the mismatch between the genetic composition under historical and future climate projections using the method of Fitzpatrick and Keller (Fitzpatrick & Keller, 2015). Genomic offset of Ethiopian barley landraces was calculated as the Euclidean distance (ED) between the allelic turnover under the historical and projected climate. To understand the areas which are more likely to hold useful barley genetic diversity and that can compensate future predicted maladaptation, that is, genomic offset, we modeled future assisted migration scenarios using a method developed by Rhoné et al. (2020) and implemented in R/dbSCAN (Hahsler & Piekenbrock, 2022). For all the

tested RCP–horizon combinations, we defined the most vulnerable areas clustering pixels with genomic offset values above the 95th percentile of the distribution, constraining the minimum number of vulnerable pixels used to generate a cluster to 16. The pixel with the highest vulnerability for each cluster was retained, and migration was restricted to a geographic distance of 500 km. Migration load was defined combining the migration distance with the compensation of genomic offset as a measure of ED. Low migration loads indicate an assisted migration of genotypes that may adapt well to the projected conditions.

2.8 | Genome-wide associations

A GWAS was run on bioclimatic variables and phenotypic BLUPs using a Fixed and random model Circulating Probability Unification (FarmCPU; Liu et al., 2016) implemented in R/rMVP (Yin et al., 2021). FarmCPU is a method developed to overcome limitations of general linear models (GLM) and mixed linear models (MLM) in dealing with population structure, resulting in higher statistical power (Liu et al., 2016). FarmCPU was run with correction for kinship, using the VanRaden method (Van Raden, 2008). SNP data imputation was performed natively by the program. Genetic structure in the panel was also corrected using from 2 to 10 genetic PCs. For each trait, the most appropriate number of PCs was derived checking model fit on QQ-plots. Both kinship and genetic PCs were calculated using the set of LD-based pruned markers. The GWAS was run on a set of high-quality SNP markers with MAF >0.05. Associations were defined significant when they surpassed the stringent threshold of a Bonferroni correction with $\alpha = .05$ or the less stringent threshold of false discovery rate (FDR) at 5% computed with R/qvalue (Storey et al., 2021). For each of the tested traits, we estimated the proportion of phenotypic variance explained by each significant SNP (Teslovich et al., 2010) after FDR correction for multiple testing. The search for positional candidate genes was performed based on chromosome-specific LD windows, calculated using a threshold of $r^2 = .3$ (see Section 2.3), as well as proximity to significant associations. Barley gene annotations were derived from the latest version of the barley reference genome (MorexV3, <https://doi.org/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).

3 | RESULTS

3.1 | Uniqueness and diversity of Ethiopian barley landraces

The sequencing of the barley collection yielded over 1.25 billion raw sequences; after variant calling and quality filtering, 436 barley lines and 23,674 genotyped SNPs with MAF >0.05 and overall missingness of 3.38% were retained. LD in the collection decayed on average

within 9.52 Mb, with variation across the seven barley chromosomes (**Figure S1**; **Table S3**). A smaller set of 2064 SNP markers was derived via LD-pruning to provide an unbiased representation of the diversity existing in the collection. Genetic diversity analyses reported a complex genetic structure that could be best summarized by 11 genetic clusters (**Figures S2** and **S3**), 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 grouped in all the other DAPC clusters featured high genetic diversity and admixture (**Figure S3**).

Barley genotypes having GPS coordinates ($n = 383$) at the sampling sites ($n = 249$) span the entire geographic and agroecological range of barley cultivation in Ethiopia, from 1350 m.a.s.l. to more than 3780 m.a.s.l. (**Figure S4**). The relation between the DAPC genetic clusters and the AEZs of origin of landraces suggests that the

distribution of barley genetic groups is related to local cropping conditions. Ethiopian farmers cultivate barley in mid-highlands in submoist (SM2–SM4), moist (M2–M5), subhumid (SH2–SH6), and humid (H3 and H4) edaphic conditions, and DAPC clusters replace one another across AEZs (**Figure 1b**). DAPC clusters 8 and 9 are mostly limited to submoist and subhumid AEZs, respectively (chi-squared test p value $< .05$; **Figure S5**). The distribution of the DAPC clusters could also be traced back to administrative borders of Ethiopia (**Figure S4**), which combine AEZs variation with historical and cultural diversity. DAPC cluster 8 was almost exclusively found in Tigray (chi-squared test p value $< .05$; **Figure 1c**), and specifically Misrakawi (Eastern Tigray) and Debubawi (Southern Tigray; **Figure S6**). DAPC cluster 10 and cluster 1 were mostly found in specific subregions of Amhara (Debub Wello) and Oromia (Bale), while DAPC clusters 9 and 3 were mainly found in Semen Omo and Gurage

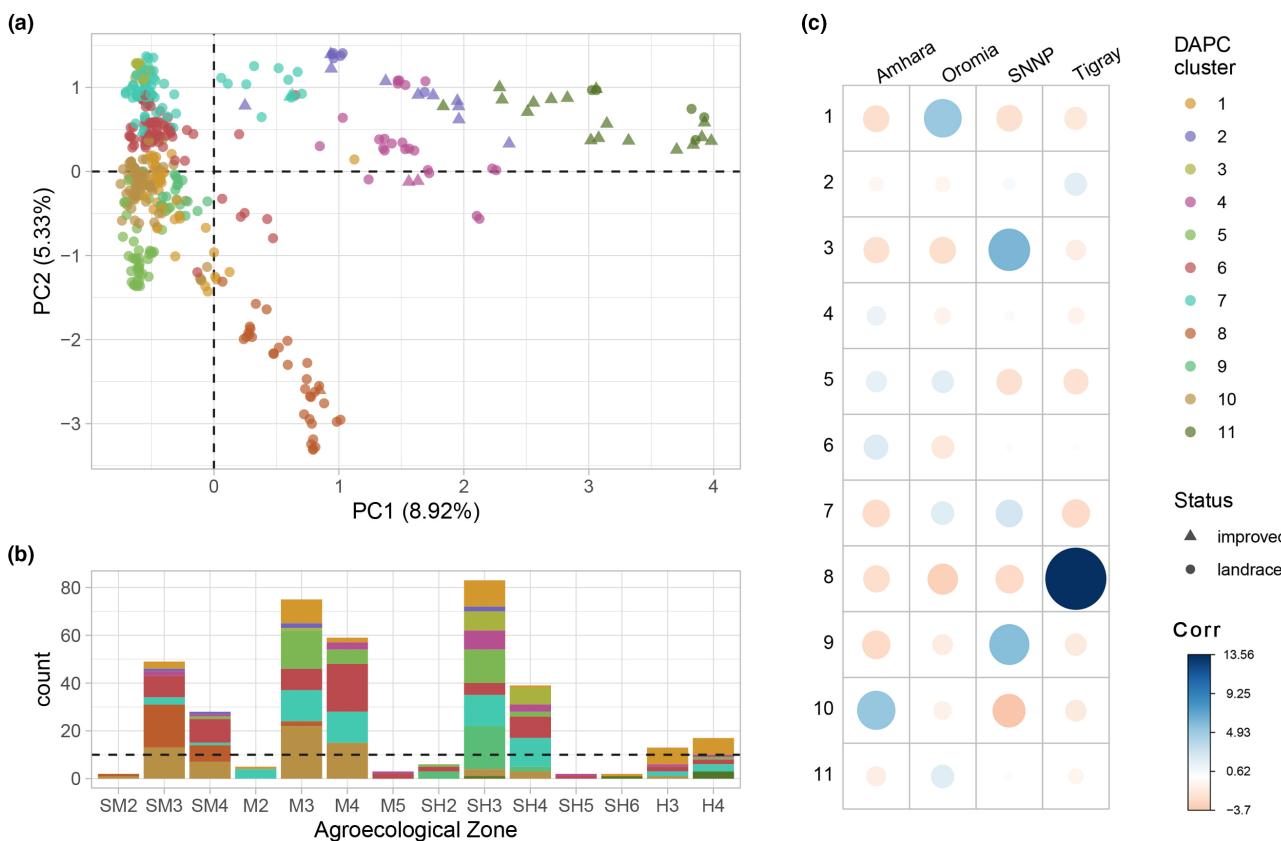


FIGURE 1 Genomic diversity of the Ethiopian barley collection ($n = 436$) based on linkage disequilibrium-pruned single nucleotide polymorphism markers. (a) First two axes of the principal component analysis on molecular data, with individual genotypes colored according to the cluster assignation from the discriminant analysis of principal components (DAPC). Landraces and improved varieties are reported with circles and triangles, respectively. Colors and shapes according to legend to the right. Axes report the relative proportion of explained genetic variance (%). (b) Genetic cluster composition across Ethiopian agroecological zones (AEZs), with colors coded as in panel "a." On the y-axis, count of genotypes derived from landraces ($n = 383$), grouped by AEZs. The horizontal dotted line indicates a threshold of 10 hits later used for the Gradient Forest analysis. 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-squared 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 subhumid lowlands; SH3, tepid subhumid mid-highlands; SH4, cool subhumid mid-highlands; SH5, cold subhumid sub-auro-alpine to afro-alpine; SH6, very cold subhumid sub-auro to afro-alpine; SM2, warm submoist lowlands; SM3, tepid submoist mid-highlands; SM4, cool submoist mid-highlands. PC, principal component; SNNP, Southern Nations, Nationalities, and Peoples' Region.

in the Southern Nations, Nationalities, and Peoples' Region (SNNP). Cluster 3, in lesser extent, was also present in the subregions of Hadiya and Keficho Shekicho, in SNNP (Figure S6). Barley diversity can also be traced back to spike types. The first three genetic PCs separated two-row from six-row types, while intermediate forms (referred to as "Irregular"), not commonly found as improved material, were genetically closer to six-row types (Figure S7a). Hull-less barley types were scarcely represented in the collection ($n = 9$) and all belonged to genetic cluster 4 (Figure S7b).

3.2 | Climatic drivers of barley differentiation

We used nine nonredundant bioclimatic variables to characterize the climatic features of the barley cultivation landscape: bio2, bio3, bio4, and bio9 related to temperature variation while bio12, bio14, bio15, bio18, and bio19 describing precipitation patterns throughout the cropping season (Table S2). 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 8, mostly found in Tigray, is cultivated in warmer climates. The DAPC cluster 5, that could not be associated with any AEZ or administrative region, and the DAPC cluster 1 are cultivated in wetter and drier conditions than the other clusters, respectively. Some of the DAPC clusters, including cluster 2, seem to be cultivated in a broad range of climatic conditions (Figure 2b). Improved materials used in this study also fall in this cluster (Figure 1). Although these varieties are not georeferenced, and hence they cannot be reconnected to specific combinations

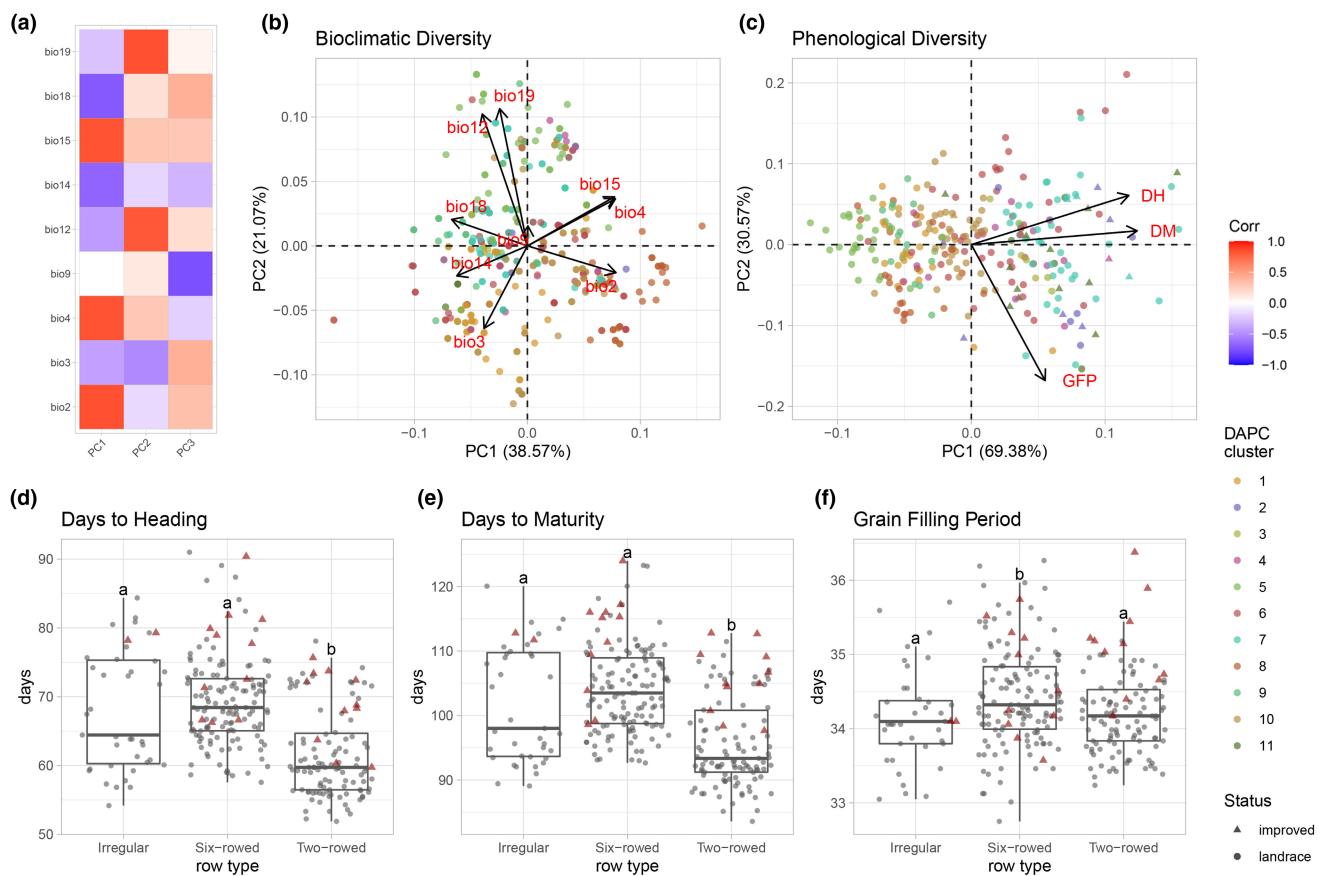


FIGURE 2 Bioclimatic and phenological diversity in the barley collection. (a) Correlation between historical bioclimatic variables and derived PCs, colored according to legend. (b, c) Principal component analysis of bioclimatic diversity of 383 georeferenced barley landraces and phenotypic diversity of the whole collection; in (b) the axes report the proportion of explained bioclimatic variance (%), while in (c), the axes report the proportion of phenotypic variance explained (%). 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) BLUPs distribution by row type of days to heading (DH), days to maturity (DM), and grain-filling period (GFP). Landraces are represented by gray dots while improved material by red triangles. Letters represent differences between row-type groups as tested by pairwise Wilcoxon rank sum tests ($p \leq .05$). PC, principal component.

of bioclimatic features, it is likely that they also belong to broad adaptation genetic types.

The pRDA-based variance partitioning revealed that, overall, climate, geography, and genetic structure could explain 22% of the total genetic variance across Ethiopian barley landraces (Table 1). The sole effect of genetic structure accounted for almost half (48%) of the explained variation. The effect of climate, with control on both neutral genetic structure and geography, was significant and explained as much as 22% of the genotypic variation, while geographical coordinates were responsible for 6% of the explainable variance, supporting the hypothesis of associations between climatic gradients and distribution of barley landrace diversity (Table 1). We observed that a quarter of the explainable variation could not be directly related to either climate, geography, or structure (Table 1).

3.3 | Phenological diversity in the collection

The collection was characterized for its phenology traits at two locations in Ethiopia, showing extensive variation in the length of the plant cycle measured as days to heading (DH, mean = 66.28, SD = 7.73), days to maturity (DM, mean = 100.65, SD 8.18), and grain-filling period (GFP; Table S4). Landraces matured in a span of about 40 days, but improved varieties required a longer maturation time (Figure 2e). DH and DM had a strong genetic determination and were stable across locations and years, as reported by high broad sense heritability (H_B^2). The GFP, derived from DH and DM, was overall heritable to a lesser extent (Table S5). This phenotype likely captures the portion of phenological variance that is most affected by environmental factors. Indeed, within experiment, GFP measures were highly heritable (Table S5). 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). The distribution of phenology in the collection reflected the genetic clustering. DAPC clusters are mostly ordered across PC1 and succeed one another in partially overlapping groupings. Several landraces are earlier than improved varieties, most notably clusters

1, 5, 8, 9, and 10 which matured well before all the improved lines in the common garden experiment (Figure 2c). Row type was also clearly associated with phenology. Six-rowed and irregular row types showed late DH and DM (Figure 2d,e); however, irregular spike types behaved as two-rowed ones in terms of GFP, while six-row types showed longest period (pairwise Wilcoxon rank sum tests, $p \leq .05$) and growth cycle overall (Figure 2f).

3.4 | Outlook of barley cultivation in Ethiopia in a changed climate

For what concerns future climatic conditions of the Ethiopian barley cropping area, the climate models' ensemble reported an increasing trend for temperature-related bioclimatic variables at all emission scenarios and at all time horizons (Figure S8). Projections also indicate an increase in rainfall during the wettest months of cultivation of as much as 60% of the baseline in specific areas of the country, although the direction of change appears to be less consistent at the country level (Figure S8). In the southern and north-eastern part of Ethiopia, the temperature is projected to increase to a lesser degree, especially during the driest months of the barley growing season, even under the most extreme RCP scenario (Figure S9).

The current extent and distribution of Ethiopian barley genomic diversity may not be suited to future climate scenarios. The GF analysis estimated the importance, in terms of predictive power, of the tested bioclimatic variables and MEMs (describing spatial structure) in relation to the genomic variation observed across the cropping area. Overall, the allelic turnover was best predicted by the bioclimatic indicator that describes the variation of precipitation patterns (i.e., bio19), followed by a number of MEM variables representing spatial structure in the collection, bio9 (mean temperature of driest quarter) and bio12 (precipitation throughout the growing season; Figure 3a). Predictors were then used to estimate climate-driven genomic variation across the landscape (Figure 3c,d). Among the 2064 SNPs tested as response variables, about 63% ($n = 1309$, $R^2 > 0$) were predicted by the model.

Based on the current landscape-genome relations modeled through GF, we predicted the genomic composition at future

TABLE 1 Effect of climate, geography, and genetic structure on the observed genetic variation of 383 Ethiopian barley landraces decomposed using partial redundancy analysis (pRDA). The proportion of explainable variance represents the total constrained variation explained by the full model; the term inertia refers to variance

pRDA model	Inertia	R^2	adj R^2	$p(>F)$	Proportion of explainable variance	Proportion of total variance
Full model: G~clim. + geog. + struct.	247.1	.22	.19	.001***	1.00	.22
Pure climate: G~clim. (geog. + struct)	54.7	.05	.03	.001***	.22	.05
Pure structure: G~struct. (clim. + geog.)	118.1	.11	.10	.001***	.48	.11
Pure geography: G~geog. (clim. + struct.)	13.6	.01	.01	.001***	.06	.01
Confounded climate/structure/geography	60.8				.25	.05
Total unexplained	860.5					.78
Total inertia	1107.6					1.00

*** $p \leq .001$.

RCP–horizon combinations using projections derived from ensemble modeling climate data. We estimated barley future genomic offset as the difference between observed and expected genetic variation for each of the tested scenarios (Figure 3d). At all RCP–horizon combinations, we observe high offset in eastern Tigray (Figure S10), the highest in the region of Benishangul-Gumuz extending to the bordering territories of Oromia (Figure 3d). We estimated the best assisted migration trajectories as measures of compensation to genomic offset in each emission scenario and time horizon. We found a minimum of 26 vulnerable areas (RCP 4.5, 2050) and a maximum of 38 (RCP 8.5, 2070). In all cases, we found potential compensating mechanisms by migration of current allelic diversity from areas within a radius of 500 km. In the region of Tigray, where offset is predicted to be higher in southern and hotter areas, assisted migration may be realized with germplasm already growing relatively nearby (Figure S11). The vulnerable area in Benishangul-Gumuz may be compensated by migration trajectories moving toward the south within the same region or from bordering territories of Oromia (Figure S11). The average geographical distance of assisted migration, considering all the tested RCP–horizon combinations, was 61 km, with a maximum value of 283 km.

3.5 | Genome-wide associations and genomic signatures of adaptation

A GWAS was used to describe the genetic mechanisms underlying phenology and adaptation in the collection. Nineteen unique quantitative trait nucleotides (QTNs) were identified for DH and DM after FDR correction for multiple testing (Figure 4a,b; Table S6) while no association was observed for GFP (Figure S12). Five QTN loci were shared among DH and DM (Table S6), and overall DH showed the highest number of signals ($n = 14$). QTNS explained from 3% to 14.6% of phenotypic variance for phenology, with the association found for DH on chromosome 5H at 527.9 Mb being the most important. Several of the associations, including the latter, targeted well-known flowering time loci in barley, while some others were unreported in literature. Among the loci implicated in flowering time variation in barley and captured in the collection are VRN-H1 and FRIGIDA (Figure 4a). The same mapping approach was employed on the noncollinear bioclimatic variables derived from historical climate at the sampling points. GWAS on bio12 and bio14 was run using the first two genetic PCs as covariates in the model to minimize inflation in the *p* value distributions (Figure S12; Table S6). The other associations were identified using the first 10 PCs (Table S6). We identified 63 unique QTNS (FDR 0.05) underlying associations between genetic constitution of the panel and the climatic variation, with the highest number of signals on chromosome 7H ($n = 17$) and 2H ($n = 13$). The QTNS associated with the tested bioclimatic indicators explained a variance ranging from 2 to 10.6% (Table S6). We regressed the set of LD-pruned SNP markers against the same bioclimatic variables using pRDA with control on genetic structure and found that loci associated with environmental variation may

also play a role in phenology. Among the six adaptive loci identified through pRDA, we found associations in the vicinity of FRIGIDA and PHOTOPERIOD-H1 (Table S7).

4 | DISCUSSION

4.1 | Diversity and adaptation of Ethiopian barley

We found that Ethiopian barley landraces are genetically distinct from most improved lines released for cultivation in the country (Figure 1a). This shows that the local allele pool is poorly exploited by modern breeding, either nationally or internationally. Previous literature reported the uniqueness of Ethiopian barley in the broader frame of the global diversity of barley, suggesting that high potential for improvement exists untapped in local agrobiodiversity (Milner et al., 2019). National and international breeding made limited use of Ethiopian agrobiodiversity also in wheat (Mengistu et al., 2016) and teff (Woldeyohannes et al., 2022), which has enormous allelic diversity and potential for local adaptation. Some of the barley improved varieties included in this study showed genetic similarity with landraces (Figure 1a), possibly due to hybridizations resulting from local breeding efforts or by mix-up at the field level, a feature not uncommon in material sourced from genebank collections (Sansaloni et al., 2020). This large, local barley allele pool may hold variation relevant for adaptation to current and future climates.

Ethiopian smallholder farming makes little use of inputs, and largely depends on landraces that have adaptation to local environmental conditions. Notwithstanding relatively high levels of admixture between genetic clusters (Figure S3), a common feature of landrace collections from the horn of Africa (Westengen et al., 2014), we could identify suggestive associations between the genomic makeup of landraces and the Ethiopian AEZs and administrative regions where they are cultivated (Figure 1b,c). Some of the local barley genetic clusters may be related to adaptation to local pedoclimatic conditions and cultural uses. We found that the DAPC cluster 8 was very specific to the Tigray region and to tepid subhumid mid-highlands (SH3, Figure S4). The uniqueness of germplasm from Tigray was already reported on other crops, including teff (Woldeyohannes et al., 2022) and wheat (Di Falco et al., 2007). When compared to other regions of Ethiopia, Tigray is more limiting in terms of potential for barley production, and this aspect might have contributed to local selection for unique allelic combinations. Historical and socio-economic influences may also have played an important role in shaping the distribution of barley diversity. Barley cultivation in the northern part of Ethiopia goes back to the Aksumites, one of the earliest civilizations in Horn of Africa (Harrower et al., 2019). Recent archeological evidence testifies an even earlier use of this crop in the region which corresponds to modern Tigray (D'Andrea et al., 2018). Modern Tigrayan communities use barley to prepare *tihlo*, a typical dish based on barley which is not found in other parts of the country, and that may also have contributed to the selection for specific barley traits in this region.

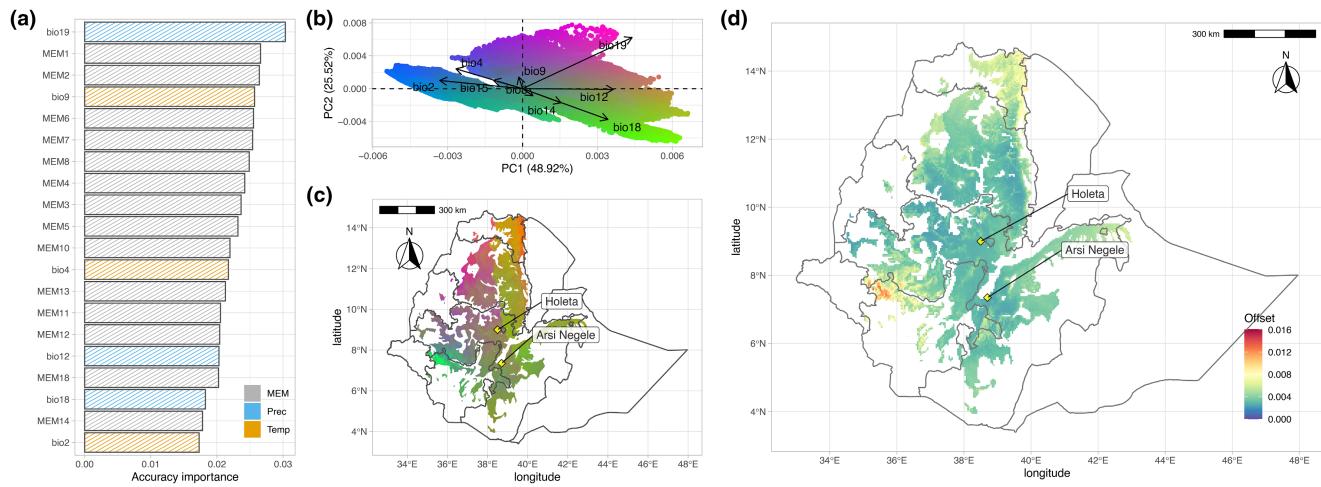


FIGURE 3 Bioclimatic and spatial diversity explains genomic variation in Ethiopian barley landraces and highlights genomic offset in future climate scenarios. (a) Ranked accuracy importance, in terms of predictive power, of the top 20 bioclimatic and spatial variables, based on gradient forest (GF) analysis. (b) Biplot of the biological space, represented by principal components of the transformed grid; the first three principal components were transformed into a defined RGB color palette where red is defined by values of PC1 + PC2, green by negative values of PC2, and blue by PC3 + PC2 – PC1. This visualization allows to display different adaptive environments across the cropping area (“c”), where similar colors represent similar alleles at climate-responsive loci ($R^2 > 0$); in the biplot, axes report the portion of bioclimatic variance (%) explained by the PCs of the transformed grid. (c) GF-transformed bioclimatic variables across the cropping area of barley (agroecological zone [AEZ] > 10 sampling locations). Colors based on the biplot of the biological space in “b.” (d) Genomic offset across AEZs having at least 10 sampling points based on representative concentration pathway 8.5 ensemble climate projections at the horizon of 2070. The color scale indicates the magnitude of the mismatch between current and projected climate-driven turnover of alleles. Common garden experiment locations are shown with yellow diamonds in panels “c” and “d.” Map lines delineate study areas and do not necessarily depict accepted national boundaries. MEM, Moran's Eigenvector Map; PC, principal component.

4.2 | Ethiopian barley cultivation in a changing climate

Barley is among the most broadly adapted cereal species currently cultivated, and it is grown in a wide range of environments. Results of our characterization showed broad environmental variation at the sampling points and subsequent analyses revealed that a relevant fraction of the genetic diversity of the Ethiopian landraces can be traced back to climatic variation (Table 1). This diversity is also reflected by the maturing time variation that we have found in our collection, testifying the extraordinary range of landscapes, farmers management practices, and cultures that contributed shaping barley diversity in Ethiopia. Phenology traits are quantitatively inherited (Table S5), interact with environmental factors, and are of pivotal importance to maximize yield potential. Well-synchronized flowering and maturity are necessary for achieving good harvest in environments exposed to harsh conditions where terminal drought and heat may negatively affect harvest (Jung & Müller, 2009). Manipulation of phenology through breeding can reduce yield risks, for example, achieving harvest earlier in the season.

Our climate projection analysis suggests that rain seasonality, as well as temperature, may change differently across the Ethiopian landscape. A remarkable difference in total precipitation, expected to increase more than 60%, may realize in the southwestern part of the country, in particular in Keficho Shekicho (Figure S8). As for temperature-related variables, mean temperature of the driest quarter (bio9) is projected to decrease in the southern and northeastern

parts of Ethiopia under RCP 8.5, while no change is projected under RCP 4.5 (Figure S9). The ensemble approach used to generate future climates showed comparable trends when compared to the historical dataset, suggesting that the projected climate data used in this study captured the ongoing climate trends across the region (Sanderson et al., 2015).

We combined this information with genomics and common garden experiments to explore the current and future climatic adaptation of Ethiopian barley germplasm. Genome-based GF predictive models, an ideal evolution of species distribution modeling (Stephenson et al., 2021), can significantly improve the ability to detect areas that are likely to be vulnerable (Aguirre-Liguori et al., 2019; Rhoné et al., 2020). In our case, the GF identified areas in which the extant barley landrace diversity may not be well adapted to future climate. This can be put in relation to seasonal shifts that are projected for the Meher. Under RCP8.5, the highest vulnerability for barley was predicted in northwestern SNNP (Figure 3d), in the administrative zone of Keficho Shekicho, at the border with Gambela, already among the warmest areas of Ethiopia (Degife et al., 2021) and at the margins of the barley production area. According to our model, another area with high projected offset will be eastern Tigray (Figure 3d), where current production of barley is high and relies on unique barley agrobiodiversity (DAPC cluster 8 described by this study, Figure 1c). These results show that climate change may impact significant portions of the barley cropping areas in Ethiopia, especially those that are already relatively hot and dry and projected to worsen. These findings suggest that barley breeding should concentrate on those

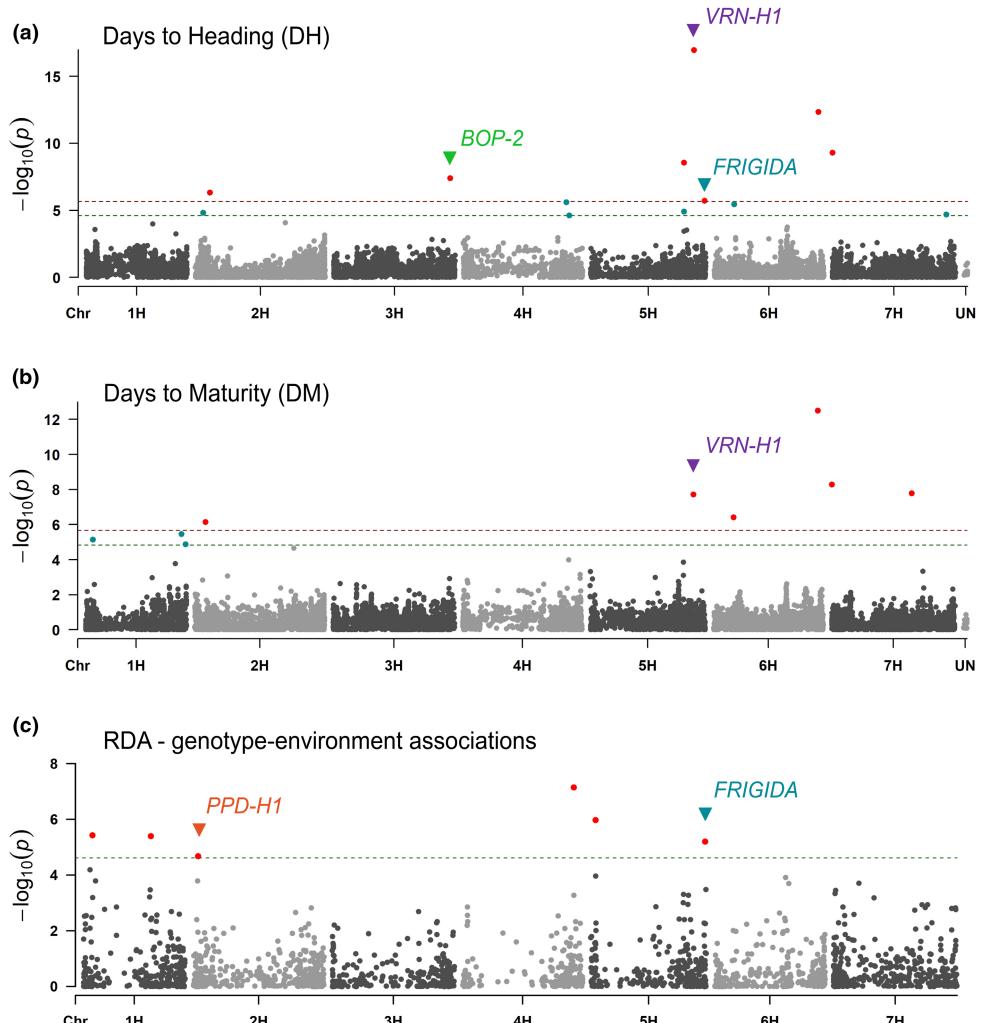


FIGURE 4 Genome-wide association study using SNP with $MAF > 0.05$ ($n = 23,674$) for: (a) days to heading and (b) days to maturity. The horizontal dashed lines indicate genome-wide significance thresholds: The dark red line refers to Bonferroni correction based on $\alpha = .05$ ($-\log_{10}(p) = 5.675$) while the green line is based on false discovery rate with $q\text{-value} > .05$, specific for each trait. (c) Genotype–environment association using redundancy analysis on the linkage disequilibrium-pruned SNP markers ($n = 2064$). The horizontal dashed dark red line indicates a Bonferroni thresholds based on $\alpha = .05$ ($-\log_{10}(p) = 4.616$). In each plot, the x-axis reports the physical position of SNPs on the barley genome, the y-axis reports the level of the statistical association. Each dot represents an SNP marker. Violet, light-blue, orange, and green arrowheads mark the position of the loci involved in flowering time variation VRN-H1, FRIGIDA, PPD-H1, and BOP-2, respectively. MAF, minor allele frequency; SNP, single nucleotide polymorphism.

areas exploiting local agrobiodiversity to enhance local adaptation of barley.

Building upon the actual distribution of barley landrace diversity, we tested possible replacement strategies at different RCP–horizon combinations. We observed that most migration distances are estimated to be relatively short (<100 km), even if for some of the tested scenarios, the compensation may be not complete (Figure S11). The evidence arising from these results suggests that Ethiopian smallholder farmers maintain agrobiodiversity that may contribute to climatic adaptation. Even if this diversity may not suffice to fully compensate projected vulnerability, it represents a fundamental resource for future compensation via migration and for breeding strategies targeting vulnerable areas in Ethiopia.

4.3 | Candidate genes and molecular targets for breeding

Modern breeding approaches may counteract predicted vulnerability of crop species by tapping into traits for local adaptation that are currently available in landraces. The characterization of our collection uncovered several QTNs associated with barley phenology and potential adaptation to bioclimatic diversity. Some of the QTNs tag well-known genomic loci with a high likelihood of being associated with phenology and adaptation. A QTN at 527.9 Mb on Chr 5H, shared between DH and DM, is located 230 kb downstream VRN-H1 (Fu et al., 2005), homologous to *APETALA1* (AP1) of *arabidopsis*. VRN-H1 is a major player in flowering time variation in barley, and its effect is conserved across

different genetic backgrounds (Milner et al., 2019) and environmental conditions, with direct implications on yield (Francia et al., 2011; Tondelli et al., 2014). Genetic analyses of a barley global collection suggest that its variation correlates with flowering time change in spring-sown barleys (Milner et al., 2019). Another QTN for DH appears on chromosome 3H, 163kb upstream a copy of *BLADE ON PETIOLE-2* (BOP-2); according to the Araport11 database, the ortholog of this gene in arabidopsis is involved in the control of floral meristem fate and determinacy in a pathway targeting AP1 among others. Indeed, BOP-2 proteins are redundantly required for expression of both AP1 and LEAFY. In barley, this gene is also responsible for tillering and leaf patterning (Cul4; Tavakol et al., 2015).

Among the significant QTNs, a signal on chr5H at 581.1 Mb (Figure 4a) lays 34kb upstream of the gene model encoding for a copy of *FRI*. This gene has been extensively studied in arabidopsis revealing a role not only in floral transition (Noh & Amasino, 2003; Zhang & Jiménez-Gómez, 2020) but also towards adaptation in response to temperature change (Stinchcombe et al., 2004). Its variation has been reported to enhance adaptation in arabidopsis through a complex pleiotropic mechanism (Lovell et al., 2013). Results of the pRDA genotype–environment associations give us additional information to reinforce this finding: we observe the same signal on chr5H at 581.1 Mb observed in the GWAS for DH, associated with the same copy of *FRI*. Among other significant adaptive loci, the signal on chromosome 2H lays in the vicinity of the known flowering time barley gene *PPD-H1* (929 kb downstream). More studies are needed to further the characterization of genomic loci relevant for adaptation and the validation of candidate genes; however, our results show that allelic variation for flowering time loci is available in Ethiopian germplasm. Association analysis identified loci in the close vicinity of *PPD-H1* and a copy of *FRI*, which may have unique haplotypic diversity in local germplasm. This information, if leveraged by local and international breeding, could expand the toolbox of barley breeding to address local adaptation to climate and user needs.

5 | CONCLUSIONS

Our results show that transdisciplinary approaches combining quantitative genetics and climate science may unlock the potential of local landraces to foster a more sustainable and resilient agriculture. Bridging genetic, climatic, and phenological diversity in untapped plant genetic resources allows the identification of allelic combinations and genomic loci with potential for breeding for local adaptation and mitigation of climate shifts. Relevant adaptation traits exist in Ethiopian landraces, and these genetic materials could rapidly be exploited by breeding using molecular tools. By leveraging their local genetic diversity, which is the result of adaptation to local cropping conditions and end users' needs, breeding may put in place tailored strategies to protect farmer livelihoods and mitigate the effects of the climate crisis at the level of local communities.

AUTHOR CONTRIBUTIONS

Basazen Fantahun Lakew conducted data collection and data analysis with Leonardo Caproni and Matteo Dell'Acqua. Basazen Fantahun Lakew and Seyoum Asefie Kassaw conducted phenotyping. Mara Miculan managed sequencing data and produced SNPs. Jemal Seid Ahmed conducted climate analysis. Simona Grazioli analyzed climatic and genomic data. Matteo Dell'Acqua, Mario Enrico Pè, and Carlo Fadda supervised the project. Leonardo Caproni, Basazen Fantahun Lakew, and Matteo Dell'Acqua drafted the manuscript. Leonardo Caproni produced figures. All authors read the final version and approved submission.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Barley accessions are available upon request from the Ethiopian Biodiversity Institute (EBI, <http://www.ebi.gov.et/>). Raw DNA sequencing reads are available on the Short Read Archive at NCBI (<https://www.ncbi.nlm.nih.gov/sra/>), BioProject ID PRJNA841803; NCBI BioSample accessions from SAMN28618042 to SAMN28618521. Scripts and additional raw data used for this study can be found on https://github.com/mdeLLh2o/ETH_barley and at <https://doi.org/10.5281/zenodo.7436265>.

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REFERENCES

- Acevedo, M., Pixley, K., Zinyengere, N., Meng, S., Tufan, H., Cichy, K., Bizikova, L., Isaacs, K., Ghezzi-Kopel, K., & Porciello, J. (2020). A scoping review of adoption of climate-resilient crops by small-scale producers in low- and middle-income countries. *Nature Plants*, 6(10), 1231–1241. <https://doi.org/10.1038/s41477-020-00783-z>
- Aguirre-Liguori, J. A., Ramírez-Barahona, S., Tiffin, P., & Eguiarte, L. E. (2019). Climate change is predicted to disrupt patterns of local adaptation in wild and cultivated maize. *Proceedings of the Royal Society B*, 286(1906), 20190486. <https://doi.org/10.1098/RSPB.2019.0486>
- Alexander, D. H., & Lange, K. (2011). Enhancements to the ADMIXTURE algorithm for individual ancestry estimation. *BMC Bioinformatics*, 12(1), 246. <https://doi.org/10.1186/1471-2105-12-246>
- Bachewe, F. N., & Taffesse, A. S. (2018). Supply response of smallholder households in Ethiopia. In *The economics of teff: Exploring Ethiopia's biggest cash crop* (pp. 181–204). International Food Policy Research Institute (IFPRI). https://doi.org/10.2499/9780896292833_08
- Bailey-Serres, J., Parker, J. E., Ainsworth, E. A., Oldroyd, G. E. D., & Schroeder, J. I. (2019). Genetic strategies for improving crop yields. *Nature*, 575(7781), 109–118. <https://doi.org/10.1038/s41586-019-1679-0>
- Bradbury, P. J., Zhang, Z., Kroon, D. E., Casstevens, T. M., Ramdoss, Y., & Buckler, E. S. (2007). TASSEL: Software for association mapping of complex traits in diverse samples. *Bioinformatics*, 23(19), 2633–2635. <https://doi.org/10.1093/bioinformatics/btm308>
- Capblancq, T., Fitzpatrick, M. C., Bay, R. A., Exposito-Alonso, M., & Keller, S. R. (2020). Genomic prediction of (mal)adaptation across current and future climatic landscapes. *Annual Review of Ecology, Evolution, and Systematics*, 51(1), 245–269. <https://doi.org/10.1146/annurev-ecolsys-020720-042553>
- Capblancq, T., & Forester, B. R. (2021). Redundancy analysis: A Swiss Army Knife for landscape genomics. *Methods in Ecology and Evolution*, 12(12), 2298–2309. <https://doi.org/10.1111/2041-210X.13722>
- Capblancq, T., Luu, K., Blum, M. G. B., & Bazin, E. (2018). Evaluation of redundancy analysis to identify signatures of local adaptation. *Molecular Ecology Resources*, 18(6), 1223–1233. <https://doi.org/10.1111/1755-0998.12906>
- Catchen, J., Hohenlohe, P. A., Bassham, S., Amores, A., & Cresko, W. A. (2013). Stacks: An analysis tool set for population genomics. *Molecular Ecology*, 22(11), 3124–3140. <https://doi.org/10.1111/mec.12354>
- Central Statistical Agency of Ethiopia. (2022). *CountrySTAT Ethiopia*. <http://ethiopia.countrystat.org/search-and-visualize-data/en/>
- Chang, C. C., Chow, C. C., Tellier, L. C., Vattikuti, S., Purcell, S. M., & Lee, J. J. (2015). Second-generation PLINK: Rising to the challenge of larger and richer datasets. *GigaScience*, 4(1), 7. <https://doi.org/10.1186/s13742-015-0047-8>
- Cheng, C.-Y., Krishnakumar, V., Chan, A. P., Thibaud-Nissen, F., Schobel, S., & Town, C. D. (2017). Araport11: A complete reannotation of the *Arabidopsis thaliana* reference genome. *The Plant Journal: For Cell and Molecular Biology*, 89(4), 789–804. <https://doi.org/10.1111/tpj.13415>
- Cohn, A. S., Newton, P., Gil, J. D. B., Kuhl, L., Samberg, L., Ricciardi, V., Manly, J. R., & Northrop, S. (2017). Smallholder agriculture and climate change. *Annual Review of Environment and Resources*, 42, 347–375. <https://doi.org/10.1146/Annurev-Environ-102016-060946>
- Coronese, M., Lamperti, F., Keller, K., Chiaromonte, F., & Roventini, A. (2019). Evidence for sharp increase in the economic damages of extreme natural disasters. *Proceedings of the National Academy of Sciences of the United States of America*, 116(43), 21450–21455. https://doi.org/10.1073/PNAS.1907826116/SUPPL_FILE/PNAS.1907826116.SAPP.PDF
- D'Andrea, A. C., Perry, L., Nixon-Darcus, L., Fahmy, A. G., & Attia, E. A. E. (2018). A pre-Aksumite culinary practice at the Mezber site, northern Ethiopia. In *Plants and people in the African past* (pp. 453–478). Springer International Publishing. https://doi.org/10.1007/978-3-319-89839-1_20
- Danecek, P., Auton, A., Abecasis, G., Albers, C. A., Banks, E., DePristo, M. A., Handsaker, R. E., Lunter, G., Marth, G. T., Sherry, S. T., McVean, G., & Durbin, R. (2011). The variant call format and VCFtools. *Bioinformatics*, 27(15), 2156–2158. <https://doi.org/10.1093/bioinformatics/btr330>
- de Sousa, K., van Etten, J., Poland, J., Fadda, C., Jannink, J.-L., Kidane, Y. G., Fantahun, B., Mengistu, D. K., Pè, M. E., Solberg, S. O., & Dell'Acqua, M. (2021). Data-driven decentralized breeding increases prediction accuracy in a challenging crop production environment. *Communications Biology*, 4, 944. <https://doi.org/10.1038/s42003-021-02463-w>
- Degife, A. W., Zabel, F., & Mauser, W. (2021). Climate change impacts on potential maize yields in Gambella region, Ethiopia. *Regional Environmental Change*, 21(2). <https://doi.org/10.1007/s10113-021-01773-3>
- del Fabbro, C., Scalabrin, S., Morgante, M., & Giorgi, F. M. (2013). An extensive evaluation of read trimming effects on Illumina NGS data analysis. *PLoS One*, 8(12), e85024. <https://doi.org/10.1371/JOURNALAL.PONE.0085024>
- Di Falco, S., Chavas, J.-P., & Smale, M. (2007). Farmer management of production risk on degraded lands: The role of wheat variety diversity in the Tigray region, Ethiopia. *Agricultural Economics*, 36(2), 147–156.
- D'Onofrio, D., Palazzi, E., Von Hardenberg, J., Provenzale, A., & Calmant, S. (2014). Stochastic rainfall downscaling of climate models. *Journal of Hydrometeorology*, 15(2), 830–843. <https://doi.org/10.1175/JHM-D-13-096.1>
- Dray, S., Legendre, P., & Peres-Neto, P. R. (2006). Spatial modelling: A comprehensive framework for principal coordinate analysis of neighbour matrices (PCNM). *Ecological Modelling*, 196(3–4), 483–493. <https://doi.org/10.1016/J.ECOLMODEL.2006.02.015>
- Dray, S., Pélissier, R., Couteron, P., Fortin, M.-J., Legendre, P., Peres-Neto, P. R., Bellier, E., Bivand, R., Blanchet, F. G., De Cáceres, M., Dufour, A.-B., Heegaard, E., Jombart, T., Munoz, F., Oksanen, J., Thioulouse, J., & Wagner, H. H. (2012). Community ecology in the age of multivariate multiscale spatial analysis. *Ecological Monographs*, 82(3), 257–275. <https://doi.org/10.1890/11-1183.1>
- Ellis, N., Smith, S. J., & Pitcher, C. R. (2012). Gradient forests: Calculating importance gradients on physical predictors. *Ecology*, 93(1), 156–168. <https://doi.org/10.1890/11-0252.1>
- FAOSTAT. (2022). *FAOSTAT database collections*. Food and Agriculture Organization of the United Nations.
- Fitzpatrick, M. C., & Keller, S. R. (2015). Ecological genomics meets community-level modelling of biodiversity: Mapping the genomic landscape of current and future environmental adaptation. *Ecology Letters*, 18(1), 1–16. <https://doi.org/10.1111/ele.12376>
- Francia, E., Tondelli, A., Rizza, F., Badeck, F. W., Li Destri Nicosia, O., Akar, T., Grando, S., Al-Yassin, A., Benbelkacem, A., Thomas, W. T. B., van Eeuwijk, F., Romagosa, I., Stanca, A. M., & Pecchioni, N. (2011). Determinants of barley grain yield in a wide range of Mediterranean environments. *Field Crops Research*, 120(1), 169–178. <https://doi.org/10.1016/j.fcr.2010.09.010>
- Fu, D., Szucs, P., Yan, L., Helguera, M., Skinner, J. S., von Zitzewitz, J., Hayes, P. M., & Dubcovsky, J. (2005). Large deletions within the first intron in VRN-1 are associated with spring growth habit in barley and wheat. *Molecular Genetics and Genomics*, 273, 54–65. <https://doi.org/10.1007/s00438-004-1095-4>
- Gilmour, A. R., Gogel, B. J., Cullis, B. R., Welham, S. J., & Thompson, R. (2014). *ASReml user guide release 4.1 functional specification*. VSN International Ltd. www.vsni.co.uk

- Gissila, T., Black, E., Grimes, D. I. F., & Slingo, J. M. (2004). Seasonal forecasting of the Ethiopian summer rains. *International Journal of Climatology*, 24(11), 1345–1358. <https://doi.org/10.1002/joc.1078>
- Gleixner, S., Demissie, T., & Diro, G. T. (2020). Did ERA5 improve temperature and precipitation reanalysis over East Africa? *Atmosphere*, 11, 996. <https://doi.org/10.3390/ATMOS11090996>
- Griffith, D. A., & Peres-Neto, P. R. (2006). Spatial modeling in ecology: The flexibility of eigenfunction spatial analyses. *Ecology*, 87(10), 2603–2613. [https://doi.org/10.1890/0012-9658\(2006\)87\[2603:smietf\]2.0.co;2](https://doi.org/10.1890/0012-9658(2006)87[2603:smietf]2.0.co;2)
- Hahsler, M., & Piekenbrock, M. (2022). *Density-based spatial clustering of applications with noise (DBSCAN) and related algorithms* (R package version 1.1-10). <https://cran.r-project.org/package=dbscan>
- Harrower, M. J., Dumitru, I. A., Perlingieri, C., Nathan, S., Zerue, K., Lamont, J. L., Bausi, A., Swerida, J. L., Bongers, J. L., Woldekiros, H. S., Poolman, L. A., Pohl, C. M., Brandt, S. A., & Peterson, E. A. (2019). Beta Samati: Discovery and excavation of an Aksumite town. *Antiquity*, 93(372), 1534–1552. <https://doi.org/10.15184/aqy.2019.84>
- Hickey, J. M., Chiurugwi, T., Mackay, I., & Powell, W. (2017). Genomic prediction unifies animal and plant breeding programs to form platforms for biological discovery. *Nature Genetics*, 49(9), 1297–1303. <https://doi.org/10.1038/ng.3920>
- Hijmans, R. J., & van Etten, J. (2016). *Raster: Geographic data analysis and modeling* (R package version 3.4-5).
- Hijmans, R. J., Phillips, S., Leathwick, J., Elith, J., & Hijmans, M. R. J. (2017). Package 'dismo'. *Circles*, 9(1), 1–68.
- Hill, W. G., & Weir, B. S. (1988). Variances and covariances of squared linkage disequilibria in finite populations. *Theoretical Population Biology*, 33(1), 54–78. [https://doi.org/10.1016/0040-5809\(88\)90004-4](https://doi.org/10.1016/0040-5809(88)90004-4)
- IPCC. (2019). Climate change and land: an IPCC special report on climate change, desertification, land degradation, sustainable land management, food security, and greenhouse gas fluxes in terrestrial ecosystems.
- Jombart, T. (2008). adegenet: A R package for the multivariate analysis of genetic markers. *Bioinformatics*, 24(11), 1403–1405. <https://doi.org/10.1093/bioinformatics/btn129>
- Jombart, T., Devillard, S., Balloux, F., Falush, D., Stephens, M., Pritchard, J., Pritchard, J., Stephens, M., Donnelly, P., Corander, J., Waldmann, P., Sillanpaa, M., Tang, J., Hanage, W., Fraser, C., Corander, J., Lee, C., Abdo, A., Huang, C., ... Nei, M. (2010). Discriminant analysis of principal components: A new method for the analysis of genetically structured populations. *BMC Genetics*, 11(1), 94. <https://doi.org/10.1186/1471-2156-11-94>
- Jørgensen, I. H. (1992). Discovery, characterization and exploitation of Mlo powdery mildew resistance in barley. *Euphytica*, 63(1–2), 141–152. <https://doi.org/10.1007/BF00023919>
- Jung, C., & Müller, A. E. (2009). Flowering time control and applications in plant breeding. *Trends in Plant Science*, 14(10), 563–573. <https://doi.org/10.1016/j.tplants.2009.07.005>
- Khoury, C. K., Brush, S., Costich, D. E., Curry, H. A., Haan, S., Engels, J. M. M., Guarino, L., Hoban, S., Mercer, K. L., Miller, A. J., Nabhan, G. P., Perales, H. R., Richards, C., Riggins, C., & Thormann, I. (2022). Crop genetic erosion: Understanding and responding to loss of crop diversity. *New Phytologist*, 233(1), 84–118. <https://doi.org/10.1111/nph.17733>
- Kindt, R., & Coe, R. (2005). *Tree diversity analysis: A manual and software for common statistical methods for ecological and biodiversity studies*. World Agroforestry Centre.
- Lasky, J. R., Upadhyaya, H. D., Ramu, P., Deshpande, S., Hash, C. T., Bonnette, J., Juenger, T. E., Hyma, K., Acharya, C., Mitchell, S. E., Buckler, E. S., Brenton, Z., Kresovich, S., & Morris, G. P. (2015). Genome-environment associations in sorghum landraces predict adaptive traits. *Science Advances*, 1(6), 1–14. <https://doi.org/10.1126/sciadv.1400218>
- Li, H. (2013). Aligning sequence reads, clone sequences and assembly contigs with BWA-MEM. *arXiv preprint arXiv:1303.3997*.
- Liu, X., Huang, M., Fan, B., Buckler, E. S., & Zhang, Z. (2016). Iterative usage of fixed and random effect models for powerful and efficient genome-wide association studies. *PLoS Genetics*, 12(2), e1005767. <https://doi.org/10.1371/journal.pgen.1005767>
- Lovell, J. T., Juenger, T. E., Michaels, S. D., Lasky, J. R., Platt, A., Richards, J. H., Yu, X., Easlon, H. M., Sen, S., & McKay, J. K. (2013). Pleiotropy of FRIGIDA enhances the potential for multivariate adaptation. *Proceedings of the Royal Society B: Biological Sciences*, 280(1763), 20131043. <https://doi.org/10.1098/rspb.2013.1043>
- Lowder, S. K., Skoet, J., & Raney, T. (2016). The number, size, and distribution of farms, smallholder farms, and family farms worldwide. *World Development*, 87, 16–29. <https://doi.org/10.1016/J.WORLDDEV.2015.10.041>
- Mancini, C., Kidane, Y. G., Mengistu, D. K., Pè, M. E., Fadda, C., & Dell'Acqua, M. (2017). Joining smallholder farmers' traditional knowledge with metric traits to select better varieties of Ethiopian wheat. *Scientific Reports*, 7(1), 9120. <https://doi.org/10.1038/s41598-017-07628-4>
- Mascher, M., Wicker, T., Jenkins, J., Plott, C., Lux, T., Koh, C. S., Ens, J., Gundlach, H., Boston, L. B., Tulipová, Z., Holden, S., Hernández-Pinzón, I., Scholz, U., Mayer, K. F. X., Spannagl, M., Pozniak, C. J., Sharpe, A. G., Simková, H., Moscou, M. J., ... Stein, N. (2021). Long-read sequence assembly: A technical evaluation in barley. *The Plant Cell*, 33(6), 1888–1906. <https://doi.org/10.1093/PLCELL/KOAB077>
- Mengistu, D. K., Kidane, Y. G., Catellani, M., Frascarioli, E., Fadda, C., Pè, M. E., & Dell'Acqua, M. (2016). High-density molecular characterization and association mapping in Ethiopian durum wheat landraces reveals high diversity and potential for wheat breeding. *Plant Biotechnology Journal*, 14(9), 1800–1812. <https://doi.org/10.1111/PBI.12538>
- Milner, S. G., Jost, M., Taketa, S., Mazón, E. R., Himmelbach, A., Oppermann, M., Weise, S., Knüpffer, H., Basterrechea, M., König, P., Schüler, D., Sharma, R., Pasam, R. K., Rutten, T., Guo, G., Xu, D., Zhang, J., Herren, G., Müller, T., ... Stein, N. (2019). Genebank genomics highlights the diversity of a global barley collection. *Nature Genetics*, 51(2), 319–326. <https://doi.org/10.1038/s41588-018-0266-x>
- Ministry of Agriculture (MoA) – National Resources Management & Regulatory Department. (1998). *Agro-Ecological Zones of Ethiopia*. <http://publication.eiar.gov.et:8080/xmlui/bitstream/handle/123456789/2517/AGRO-ECOLOGICALZONES%20OF%20ETHIOPIA.pdfABBYYY.pdf?sequence=1&isAllowed=y>
- Mondal, S., Dutta, S., Crespo-Herrera, L., Huerta-Espino, J., Braun, H. J., & Singh, R. P. (2020). Fifty years of semi-dwarf spring wheat breeding at CIMMYT: Grain yield progress in optimum, drought and heat stress environments. *Field Crops Research*, 250, 107757. <https://doi.org/10.1016/J.FCR.2020.107757>
- Morton, J. F. (2007). The impact of climate change on smallholder and subsistence agriculture. *Proceedings of the National Academy of Sciences of the United States of America*, 104(50), 19680–19685. <https://doi.org/10.1073/pnas.0701855104>
- Noh, Y.-S., & Amasino, R. M. (2003). PIE1, an ISWI family gene, is required for FLC activation and floral repression in *Arabidopsis*. *The Plant Cell*, 15, 1671–1682. <https://doi.org/10.1105/tpc.012161>
- Oksanen, J., Simpson, G. L., Blanchet, F. G., Kindt, R., Legendre, G., Minchin, P. R., O'Hara, R. B., Solymos, P., Stevens, M. H. M., Szoecs, E., Wagner, H., Barbour, M., Bedward, M., Bolker, B., Borcard, D., Carvalho, G., Chirico, M., de Caceres, M., Durand, S., ... Weedon, J. (2022). *vegan: Community ecology package* (R package version 2.6-2). <https://CRAN.R-project.org/package=vegan>
- Peterson, B. K., Weber, J. N., Kay, E. H., Fisher, H. S., & Hoekstra, H. E. (2012). Double digest RADseq: An inexpensive method for de novo SNP discovery and genotyping in model and non-model

- species. *PLoS One*, 7(5), e37135. <https://doi.org/10.1371/journal.pone.0037135>
- Piffanelli, P., Ramsay, L., Waugh, R., Benabdelmouna, A., D'Hont, A., Hollricher, K., Jørgensen, J. H., Schulze-Lefert, P., & Panstruga, R. (2004). A barley cultivation-associated polymorphism conveys resistance to powdery mildew. *Nature*, 430(7002), 887–891. <https://doi.org/10.1038/nature02781>
- Pingali, P. L. (2012). Green revolution: Impacts, limits, and the path ahead. *Proceedings of the National Academy of Sciences of the United States of America*, 109(31), 12302–12308. <https://doi.org/10.1073/pnas.0912953109>
- Poplin, R., Ruano-Rubio, V., DePristo, M. A., Fennell, T. J., Carneiro, M. O., van der Auwera, G. A., Kling, D. E., Gauthier, L. D., Levy-Moonshine, A., Roazen, D., Shakir, K., Thibault, J., Chandran, S., Whelan, C., Lek, M., Gabriel, S., Daly, M. J., Neale, B., MacArthur, D. G., & Banks, E. (2018). Scaling accurate genetic variant discovery to tens of thousands of samples. *BioRxiv*, 201178. <https://doi.org/10.1101/201178>
- R Core Team. (2022). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. <https://www.r-project.org/>
- Rebora, N., Ferraris, L., von Hardenberg, J., & Provenzale, A. (2006). RainFARM: Rainfall downscaling by a filtered autoregressive model. *Journal of Hydrometeorology*, 7(4), 724–738. <https://doi.org/10.1175/JHM517.1>
- Reuter, H. I., Nelson, A., & Jarvis, A. (2007). An evaluation of void-filling interpolation methods for SRTM data. *International Journal of Geographical Information Science*, 21(9), 983–1008. <https://doi.org/10.1080/13658810601169899>
- Rhoné, B., Defrance, D., Berthouly-Salazar, C., Mariac, C., Cubry, P., Couderc, M., Dequincey, A., Assoumanne, A., Kane, N. A., Sultan, B., Barnaud, A., & Vigouroux, Y. (2020). Pearl millet genomic vulnerability to climate change in West Africa highlights the need for regional collaboration. *Nature Communications*, 11(1). <https://doi.org/10.1038/s41467-020-19066-4>
- Ricciardi, V., Mehrabi, Z., Wittman, H., James, D., & Ramankutty, N. (2021). Higher yields and more biodiversity on smaller farms. *Nature Sustainability*, 4(7), 651–657. <https://doi.org/10.1038/s41893-021-00699-2>
- Sanderson, B. M., Knutti, R., & Caldwell, P. (2015). A representative democracy to reduce interdependency in a multimodel ensemble. *Journal of Climate*, 28(13), 5171–5194. <https://doi.org/10.1175/JCLI-D-14-00362.1>
- Sansaloni, C., Franco, J., Santos, B., Percival-Alwyn, L., Singh, S., Petroli, C., Campos, J., Dreher, K., Payne, T., Marshall, D., Kilian, B., Milne, I., Raubach, S., Shaw, P., Stephen, G., Carling, J., Pierre, C. S., Burgueño, J., Crosa, J., ... Pixley, K. (2020). Diversity analysis of 80,000 wheat accessions reveals consequences and opportunities of selection footprints. *Nature Communications*, 11(1), 4572. <https://doi.org/10.1038/s41467-020-18404-w>
- Scheben, A., Yuan, Y., & Edwards, D. (2016). Advances in genomics for adapting crops to climate change. *Current Plant Biology*, 6, 2–10. <https://doi.org/10.1016/J.CPB.2016.09.001>
- Segele, Z. T., & Lamb, P. J. (2005). Characterization and variability of Kiremt rainy season over Ethiopia. *Meteorology and Atmospheric Physics*, 89(1–4), 153–180. <https://doi.org/10.1007/s00703-005-0127-x>
- Serdeczny, O., Adams, S., Baarsch, F., Coumou, D., Robinson, A., Hare, W., Schaeffer, M., Perrette, M., & Reinhardt, J. (2017). Climate change impacts in Sub-Saharan Africa: From physical changes to their social repercussions. *Regional Environmental Change*, 17(6), 1585–1600. <https://doi.org/10.1007/s10113-015-0910-2>
- Shin, J.-H., Blay, S., Mcneney, B., & Graham, J. (2006). LDheatmap: An R function for graphical display of pairwise linkage disequilibria between single nucleotide polymorphisms. *Journal of Statistical Software*, 16, 1–9. <https://doi.org/10.18637/jss.v000.i00>
- Simmonds, N. W. (1991). Selection for local adaptation in a plant breeding programme. *Theoretical and Applied Genetics*, 82(3), 363–367. <https://doi.org/10.1007/BF02190624>
- Stephenson, F., Leathwick, J. R., Geange, S., Moilanen, A., Pitcher, C. R., & Lundquist, C. J. (2021). Species composition and turnover models provide robust approximations of biodiversity in marine conservation planning. *Ocean and Coastal Management*, 212(July), 105855. <https://doi.org/10.1016/j.ocecoaman.2021.105855>
- Stinchcombe, J. R., Weinig, C., Ungerer, M., Olsen, K. M., Mays, C., Halldorsdottir, S. S., Purugganan, M. D., & Schmitt, J. (2004). A latitudinal cline in flowering time in *Arabidopsis thaliana* modulated by the flowering time gene FRIGIDA. *Proceedings of the National Academy of Sciences of the United States of America*, 101(13), 4712–4717. <https://doi.org/10.1073/pnas.0306401101>
- Storey, J., Bass, A. J., Dabney, A., & Robinson, D. (2021). Q-value estimation for false discovery rate control (R package version 2.24.0).
- Tavakol, E., Okagaki, R., Verderio, G., Vahid, S. J., Hussien, A., Bilgic, H., Scanlon, M. J., Todt, N. R., Close, T. J., Druka, A., Waugh, R., Steuernagel, B., Ariyadasa, R., Himmelbach, A., Stein, N., Muehlbauer, G. J., & Rossini, L. (2015). The barley Uniculme4 gene encodes a BLADE-ON-PETIOLE-like protein that controls Tillering and leaf patterning. *Plant Physiology*, 168(1), 164–174. <https://doi.org/10.1104/PP.114.252882>
- Teslovich, T. M., Musunuru, K., Smith, A. v., Edmondson, A. C., Stylianou, I. M., Koseki, M., Pirruccello, J. P., Ripatti, S., Chasman, D. I., Willer, C. J., Johansen, C. T., Fouchier, S. W., Isaacs, A., Peloso, G. M., Barbalic, M., Ricketts, S. L., Bis, J. C., Aulchenko, Y. S., Thorleifsson, G., ... Kathiresan, S. (2010). Biological, clinical and population relevance of 95 loci for blood lipids. *Nature*, 466(7307), 707–713. <https://doi.org/10.1038/nature09270>
- Tondelli, A., Francia, E., Visioni, A., Comadran, J., Mastrangelo, A. M., Akar, T., Al-Yassin, A., Ceccarelli, S., Grando, S., Benbelkacem, A., van Eeuwijk, F. A., Thomas, W. T. B., Stanca, A. M., Romagosa, I., & Pecchioni, N. (2014). QTLs for barley yield adaptation to Mediterranean environments in the "Nure" × "Tremois" biparental population. *Euphytica*, 197(1), 73–86. <https://doi.org/10.1007/s10681-013-1053-5>
- Van Raden, P. M. (2008). Efficient methods to compute genomic predictions. *Journal of Dairy Science*, 91(11), 4414–4423. <https://doi.org/10.3168/JDS.2007-0980>
- Varshney, R. K., Bohra, A., Yu, J., Graner, A., Zhang, Q., & Sorrells, M. E. (2021). Designing future crops: Genomics-assisted breeding comes of age. *Trends in Plant Science*, 26(6), 631–649. <https://doi.org/10.1016/j.tplants.2021.03.010>
- Vavilov, N. I. (1951). The origin, variation, immunity and breeding of cultivated plants translated from Russian by K. Starr Chester. *Chronica Botanica*, 13(1/6), 364.
- Wakjira, M. T., Peleg, N., Anghileri, D., Molnar, D., Alamirew, T., Six, J., & Molnar, P. (2021). Rainfall seasonality and timing: Implications for cereal crop production in Ethiopia. *Agricultural and Forest Meteorology*, 310, 108633. <https://doi.org/10.1016/J.AGRFORMAT.2021.108633>
- Westengen, O. T., Okongo, M. A., Oniek, L., Berg, T., Upadhyaya, H., Birkeland, S., Khalsa, S. D. K., Ring, K. H., Stenseth, N. C., & Brysting, A. K. (2014). Ethnolinguistic structuring of sorghum genetic diversity in Africa and the role of local seed systems. *Proceedings of the National Academy of Sciences of the United States of America*, 111(39), 14100–14105. <https://doi.org/10.1073/pnas.1401646111>
- Woldeyohannes, A. B., Iohannes, S. D., Miculan, M., Caproni, L., Ahmed, J. S., de Sousa, K., Desta, E. A., Fadda, C., Pè, M. E., & Dell'Acqua, M. (2022). Data-driven, participatory characterization of farmer varieties discloses teff breeding potential under current and future climates. *eLife*, 11, e80009. <https://doi.org/10.7554/ELIFE.80009>
- Yin, L., Zhang, H., Tang, Z., Xu, J., Yin, D., Zhang, Z., Yuan, X., Zhu, M., Zhao, S., Li, X., & Liu, X. (2021). rMVP: A memory-efficient, visualization-enhanced, and parallel-accelerated tool for genome-wide

- association study. *Genomics, Proteomics & Bioinformatics*, 19, 619–628. <https://doi.org/10.1016/J.GPB.2020.10.007>
- Yoder, J. B., Stanton-Geddes, J., Zhou, P., Briskine, R., Young, N. D., & Tiffin, P. (2014). Genomic signature of adaptation to climate in *Medicago truncatula*. *Genetics*, 196(4), 1263–1275. <https://doi.org/10.1534/genetics.113.159319>
- Zhang, L., & Jiménez-Gómez, J. M. (2020). Functional analysis of FRIGIDA using naturally occurring variation in *Arabidopsis thaliana*. *The Plant Journal*, 103(1), 154–165. <https://doi.org/10.1111/tpj.14716>

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