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Adaptive potential of *Coffea canephora* from Uganda in response to climate change

Sinara Oliveira de Aquino[1,2] | Catherine Kiwuka[3,4] | Rémi Tournebize[1] | Clément Gain[5,6] | Pierre Marraccini[1] | Cédric Mariac[1] | Kévin Bethune[1] | Marie Couderc[1] | Philippe Cubry[1] | Alan C. Andrade[7] | Maud Lepelley[8] | Olivier Darracq[8] | Dominique Crouzillat[8] | Niels Anten[4] | Pascal Musoli[3] | Yves Vigouroux[1] | Alexandre de Kochko[1] | Stéphanie Manel[9] | Olivier François[5,6] | Valérie Poncet[1]

[1]DIADE, Univ Montpellier, CIRAD, IRD, Montpellier, France

[2]Federal University of Lavras, Lavras, Brazil

[3]NARO, Kampala, Uganda

[4]Centre for Crop Systems Analysis, Wageningen University, Wageningen, Netherlands

[5]U. Grenoble-Alpes, TIMC-IMAG, CNRS, UMR 5525, Grenoble, France

[6]LJK, Inria, Grenoble, France

[7]EMBRAPA Coffee-INOVACAFE, Lavras, Brazil

[8]NESTLE Research, Tours, France

[9]CEFE, Univ Montpellier, CNRS, EPHE-PSL University, IRD, Montpellier, France

Correspondence
Valérie Poncet, DIADE, Univ Montpellier, CIRAD, IRD, Montpellier, France.
Email: valerie.poncet@ird.fr

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Abstract

Understanding vulnerabilities of plant populations to climate change could help preserve their biodiversity and reveal new elite parents for future breeding programmes. To this end, landscape genomics is a useful approach for assessing putative adaptations to future climatic conditions, especially in long-lived species such as trees. We conducted a population genomics study of 207 *Coffea canephora* trees from seven forests along different climate gradients in Uganda. For this, we sequenced 323 candidate genes involved in key metabolic and defence pathways in coffee. Seventy-one single nucleotide polymorphisms (SNPs) were found to be significantly associated with bioclimatic variables, and were thereby considered as putatively adaptive loci. These SNPs were linked to key candidate genes, including transcription factors, like *DREB*-like and *MYB* family genes controlling plant responses to abiotic stresses, as well as other genes of organoleptic interest, such as the *DXMT* gene involved in caffeine biosynthesis and a putative pest repellent. These climate-associated genetic markers were used to compute genetic offsets, predicting population responses to future climatic conditions based on local climate change forecasts. Using these measures of maladaptation to future conditions, substantial levels of genetic differentiation between present and future diversity were estimated for all populations and scenarios considered. The populations from the forests Zoka and Budongo, in the northernmost zone of Uganda, appeared to have the lowest genetic offsets under all predicted climate change patterns, while populations from Kalangala and Mabira, in the Lake Victoria region, exhibited the highest genetic offsets. The potential of these findings in terms of ex situ conservation strategies are discussed.

KEYWORDS
candidate genes, climate change, environmental association, landscape genomics, target capture, wild coffee

1 | INTRODUCTION

Long-term projections indicate that by 2100, atmospheric CO_2 concentrations could reach ~1000 ppm, alongside a predicted global temperature increase of up to 4.8°C (IPCC, 2014). This climate change pattern could be associated with an increase in the frequency and severity of extreme events, including heat waves, floods and prolonged drought episodes (IPCC, 2013, 2014). The tropics are particularly vulnerable to climate change since extreme climatic conditions are predicted to first occur in these regions, and since many tropical plant species are relatively vulnerable to even minor climate changes (Mora et al., 2013). As they also host a major share of species diversity on Earth, climate change will probably have an acute impact in the tropics.

To avoid local extinction, plants (i) can broaden their range to colonize more suitable habitats, (ii) adjust to novel conditions through phenotypic plasticity, or (iii) adapt to the new environmental conditions through genetic changes (Aitken et al., 2008; Merilä & Hendry, 2014; Nicotra et al., 2010). Regarding the latter option and given the current pace of climate change, local adaptation through genetic changes would strongly depend on existent genetic variation. Identification of selection signals along the genome is an effective way to pinpoint the genetic architecture of local adaptation (Barrett & Schluter, 2008; Manel et al., 2016). Associated genetic markers could then be useful for predicting population responses to future climatic conditions (Capblancq et al., 2020; Rellstab et al., 2016).

Substantial numbers of molecular markers (e.g., single nucleotide polymorphisms, SNPs) spanning the genome are needed for adaptive evolution studies (Fuentes-Pardo & Ruzzante, 2017; Miao et al., 2017). These markers can often be identified by whole genome sequencing (WGS) approaches (Kumar et al., 2012), yet they can be obtained by sequencing specific genomic regions like candidate genes (CG) (Cronn et al., 2012). This type of target sequencing after enrichment by capture can facilitate studies across hundreds of samples, while being cost- and time efficient (Hale et al., 2020; Mariac et al., 2014, 2022). This approach has been used in an array of plant species such as maize (Fu et al., 2010), eucalyptus (Dasgupta et al., 2015) and pine (Neves et al., 2013). As the proteins encoded by these CGs are involved in major metabolic pathways or stress response, for example, they would have a higher likelihood of being under selection than other genomic regions, especially if their function relates to selective pressure that vary across the studied areas (Luikart et al., 2003; Nielsen, 2005).

Genotype–environment association (GEA) analysis approaches provide a powerful way to identify adaptive genetic variation shaped by environmental factors (Joost et al., 2007; Li et al., 2017). Such methods have enabled identification of SNPs related to local adaptation to drought in sugar pine (Vangestel et al., 2016), soybean (Leamy et al., 2016) and sugar beet (Manel et al., 2018). While several GEA methods have been proposed, not all have proven effective due to their failure to take population structure and other factors into account (De Mita et al., 2013; Holderegger et al., 2010; Lotterhos & Whitlock, 2015; Manel & Holderegger, 2013; Manel et al., 2010; Sork et al., 2013). To account for hidden confounders, Frichot et al. (2013) developed latent factor mixed models (LFMMs) that evaluate environment-genotype associations while estimating the effects of hidden factors representing background residual levels of population structure. These authors applied LFMM to loblolly pines and showed that several proteins involved in photosynthesis or abiotic stress were significantly associated with climatic gradients. More recently, landscape genomic approaches have also been used to assess the vulnerability of populations to future climate change (Jordan et al., 2017; Razgour et al., 2019; Rellstab et al., 2016; Ruegg et al., 2018). More specifically, by looking at the difference between optimal genetic composition in current and future conditions, one can estimate a genetic offset (Fitzpatrick & Keller, 2015; Rellstab et al., 2021), representing the lag that a population would have to overcome in order to track the local fitness optimum.

Climate change is predicted to have marked negative impacts on *Coffea* species, particularly because the pace of change could be too fast and drastic for species to be able to migrate or adapt via new mutations (Bunn et al., 2015; Bunn et al., 2015; Davis et al., 2012, 2019; Moat et al., 2017, 2019; Ovalle-Rivera et al., 2015). Adaptive strategies to mitigate these effects largely depend on how the species responds to climate variability and on the availability of genetic resources within wild populations that could be tapped to enhance drought- and heat-tolerance.

Within the *Coffea* genus, *Coffea canephora*, also known as Robusta, is a diploid ($2n = 2\times = 22$) species (Davis et al., 2011) and the male parental species of allotetraploid *Coffea arabica* (Lashermes et al., 1999). As *C. canephora* is also strictly allogamous, this species consists of polymorphic populations of highly heterozygous individuals. *Coffea canephora* is distributed throughout a wide range of African lowland tropical rain forests from Guinea to Uganda and Central African Republic to Angola (Davis et al., 2006). High diversity prevails within the species for many agronomic traits, such as pest and disease resistance and abiotic stress tolerance (Leroy et al., 1993; Montagnon et al., 1992). Regarding the genetic structure of wild African *C. canephora*, a marked separation between accessions from Upper-Lower Guinean (West Africa) and Congolese (Central Africa) regions has been described, with further subdivision into eight well-defined genetic groups, that is, four in the Guinean region and four in the Congolese region (Cubry et al., 2013; Gomez et al., 2009; Merot-L'Anthoene et al., 2019; Musoli et al., 2009) (Figure S1A). The Ugandan group is organized in well-structured wild populations (Kiwuka et al., 2021) presenting a wide range of phenotypic variations regarding tree morphology, agronomic traits, green bean physical and biochemical characteristics (Aluka, 2013; Berthaud & Charrier, 1988; Kiwuka, 2020).

Physiological studies on the relationship between drought tolerance and gene expression have led to the identification of more than 80 CGs in both *C. canephora* (Marraccini et al., 2011, 2012; Vieira et al., 2013; Vinecky et al., 2012) and *C. arabica* (Freire et al., 2013; Mofatto et al., 2016). Additional genes that are assumed to play a key role in plant responses to abiotic stress have also been identified (Marraccini, 2020), such as those involved in the ABA

biosynthetic pathway (Costa, 2014; Cotta, 2017; Simkin et al., 2008), cell protection and detoxification (Hinniger et al., 2006; Santos & Mazzafera, 2012; Thioune et al., 2017, 2020), and aquaporins biosynthesis (Miniussi et al., 2015; Santos & Mazzafera, 2013). Other genes are involved in carotenoid/phenylpropanoid (Lepelley et al., 2012; Simkin et al., 2010), caffeine (Denoeud et al., 2014) and sugar (Geromel et al., 2006; Privat et al., 2008) biosynthetic pathways, or they encode transcription factors (Alves, 2015; Alves et al., 2017, 2018; Thioune et al., 2017, 2020; Torres et al., 2019).

In this study, we applied a landscape genomic approach to assess potential signatures of climate adaptation in wild *C. canephora* populations from seven Ugandan forests. We used this approach to assess local maladaptation to projected climate change. To achieve these goals, coffee candidate genes were capture-enriched and sequenced for each of the 207 individuals to identify genetic variants (SNPs). The association of these SNPs to climate gradients were further tested. Finally, we leveraged publicly available global climate models to predict the genetic offset of wild *C. canephora* populations in Uganda.

2 | MATERIALS AND METHODS

2.1 | Study species and sample selection

Uganda is divided into 16 climate zones based on precipitation patterns as defined by Basalirwa (1995), five of which host *C. canephora* stands (Figure S1B). Within these five climate zones, 207 georeferenced trees were sampled from seven wild forests (Figure 1a) in 2012 and 2014 by the National Agricultural Research Organization (NARO, Uganda) and collaborators of the Institut de Recherche pour le Développement (IRD, Montpellier, France). These forests include: Budongo ($n = 65$), Itwara ($n = 23$), Kibale ($n = 19$), Kalangala ($n = 10$), Mabira ($n = 25$), Malabigambo ($n = 16$) and Zoka ($n = 49$) (Table S1). Populations in Zoka, Budongo, Kalangala, Mabira and Malabigambo occurred in distinct climatic envelopes, while the climatic envelopes in Itwara tended to overlap those of Kibale (Kiwuka et al., 2021). In each targeted forest, leaf samples were collected from five subsites that were separated by distances of at least 5 km.

2.2 | Selection of candidate genes and bait design

The 323 candidate genes (CGs) selected for the present study have been annotated and/or functionally characterized in previous studies (Table S2). They all code for candidate proteins already reported to play important roles in central metabolism or in plant responses and adaptation to abiotic stress. The CG sequences were retrieved from the whole genome assembly of *C. canephora* (Denoeud et al., 2014) according to the annotation available on the Coffee Genome Hub (http://coffee-genome.org/) (Dereeper et al., 2015).

Probes were designed to cover each CG coding region as well as 1 kb upstream and 500 bp downstream flanking regions, so as to include putatively regulatory regions. The 120 bp MyBaits probes were designed with 2× tiling (Figure S2) and synthesized by MYcroarray provider (Ann Arbor, Michigan, USA). A total of 21,306 probes were designed. Each candidate probe was BLASTed against the *C. canephora* genome (Denoeud et al., 2014) and filtered based on the manufacturer's stringent criteria (Mariac et al., 2022). The final number of synthesized probes was 19,360 and covered all the CGs with a mean length of 4,106 bp (Table S3).

2.3 | Library preparation and sequencing

DNA extractions for the 207 samples were performed at the IRD facilities from silica-gel dried leaves according to a previously described protocol (Mariac et al., 2006). Genomic libraries were constructed using the protocols outlined in Rohland and Reich (2012) and Mariac et al. (2014). The 207 individual libraries were then capture-enriched by pools of 48 libraries using the synthetic RNA MyBaits probes and according to the MYcroarray protocol (Mariac et al., 2022). The enriched pools were quantified using real-time PCR and combined in equimolar ratios prior to sequencing on one lane of 150 bp paired end reads on an Illumina HiSeq 3000 sequencer (GeT-PlaGe Platform, GenoToul, Toulouse, France).

2.4 | SNP genotyping, calling and filtering

Sequence analysis was performed using scripts published by Mariac et al. (2014) and Scarcelli et al. (2016) and also available on GitHub (https://github.com/Maillol/demultadapt; https://github.com/SouthGreenPlatform/arcad-hts/blob/master/scripts/arcad_hts_2_Filter_Fastq_On_Mean_Quality.pl).

The mapping step was carried out using BWA MEM 0.7.5a-r405 (Li & Durbin, 2009) with the default option (-B 4) and the *C. canephora* assembly (http://coffee-genome.org/coffeacanephora) as reference. SNP calling was done using UnifiedGenotyper in the Genome Analysis Toolkit (GATK v3.6). SNPs located on the selected CG sequences were considered as "in-target" and the other ones as "off-target". A total of 4,078,725 raw SNPs was identified across the *C. canephora* genome, both in- and off-target of the capture experiment.

Two successive sets of filters were applied to raw SNPs (Figure S3). We first discarded low quality variants according to the quality criteria recommended by GATK (Figure S3A), and selected only biallelic SNPs using VCFtools v0.1.13 (Danecek et al., 2011).

We applied additional filters for population genetic analyses and for association analyses (Figure S3B), that is, keeping SNPs with no excess of heterozygous genotypes (<0.8), a minor allele frequency (MAF) greater than 5% and under linkage equilibrium. For the latter filter, SNPs were processed with PLINK 1.90b4 (Purcell et al., 2007) to prune only SNPs in approximate linkage equilibrium based on the pairwise correlation between the SNP genotype counts for 100 bp sliding windows with 10 bp steps (option -indep-pairwise). The SNPs were considered correlated when $r^2 > 0.5$. These filters led to a total of 5860 SNPs: 4753 in-target and 1107 off-target loci.

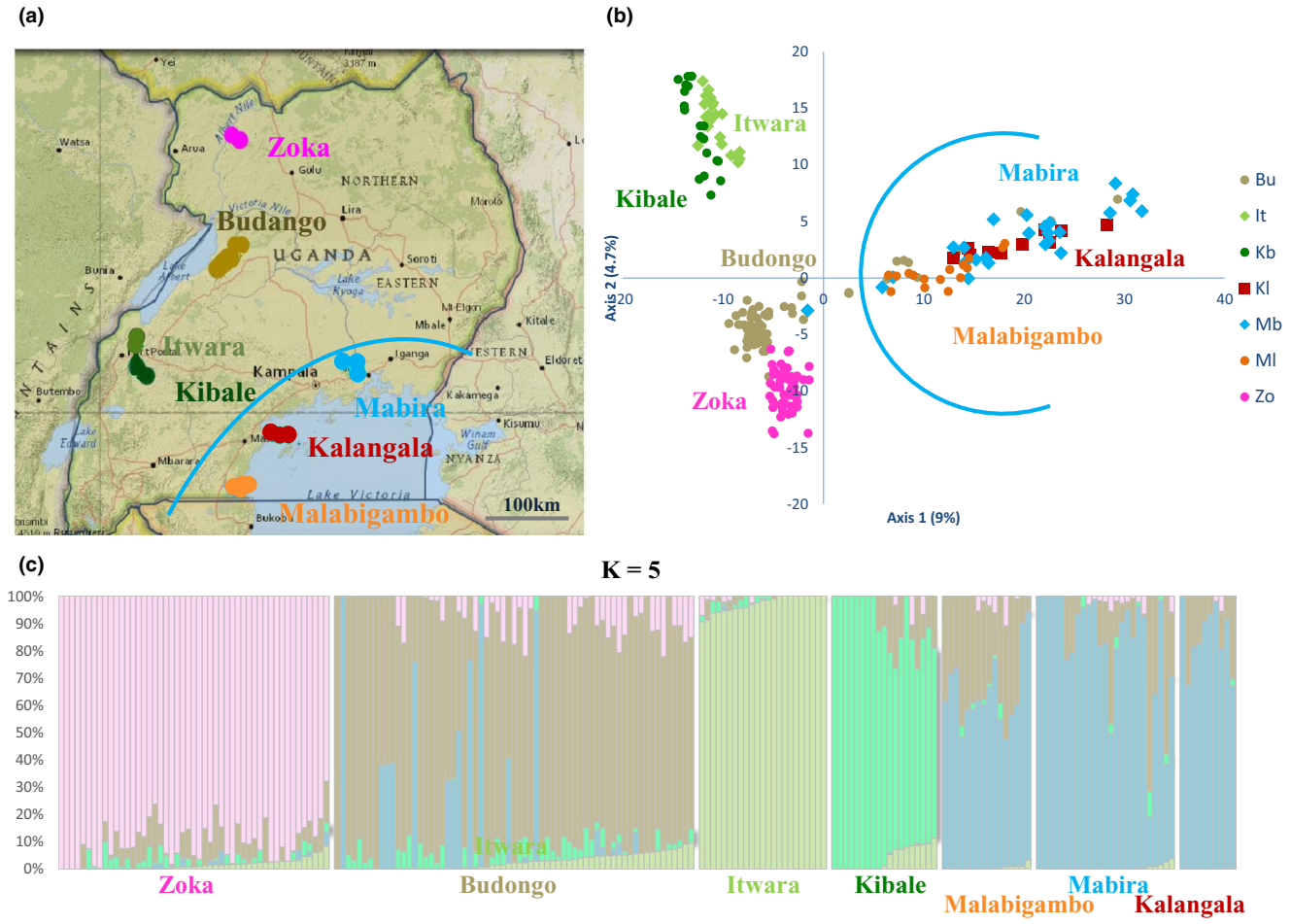

FIGURE 1 Genetic structure of native *Coffea canephora* in Uganda. (a) Geographical distribution of wild *C. canephora* forests. The blue line separates the northwestern forests from the south /centre (SC) forests (Uganda map source: https://maps.co/wileyonlinelibrary.com]). (b) Principal components analysis (PCA) of the 207 sampled individuals along the first two axes explaining 9% (axis 1) and 4.7% (axis 2) of the genome-wide genetic variance for the set of off-target SNPs. Colours correspond to the geographical origin. (c) Individual ancestries inferred with sNMF for five clusters ($K = 5$). Colours represent different genetic clusters, bars represent individuals (grouped by forest), and the proportion of each colour in each bar represents the estimated ancestry coefficient for that cluster for that individual [Colour figure can be viewed at wileyonlinelibrary.com]

All file conversions and the computation of descriptive statistics, if not stated otherwise, were performed using VCFtools v0.1.13.

2.5 | Bioclimatic data and climate change scenarios

Environmental factors (bioclimatic variables BIO1-19, Table S1) were downloaded from the WorldClim database (http://www.worldclim.org, Fick & Hijmans, 2017) at 30 arc-second resolution (~1 km) for "Current conditions ~1960–2000". We assessed correlations between bioclimatic variables and their differences between forests (Kruskal-Wallis tests) using R 3.4.4 (R Development Core Team, 2015). Future climate predictions (2061–2080) were interpolated from five global climate models (GCMs): CCSM4, HadGEM2-ES, IPSL-CM5A-LR, MIROCESM-CHEM, and NorESM1-M (Hijmans et al., 2005) previously used in the Fifth Assessment IPCC report (IPCC, 2014). Bioclimatic variables were extracted from three different scenarios, also known as representative concentration pathways (RCPs). The global annual greenhouse gas (GHG) emissions peak between 2010 and 2020, with emissions declining after this period for RCP 2.6, and around 2080 for RCP 6.0, while emissions continue to rise throughout the 21st century for RCP 8.5 (Meinshausen et al., 2011).

To evaluate which bioclimatic variable will differ most between "present" (1960–2000) and "future" (2061–2080) conditions for each GCM × RCP combination, a multivariate environmental similarity surfaces analysis was performed in R (MESS, Elith et al., 2010), as implemented in the modEvA v1.3.2 package (Barbosa et al., 2016). For this analysis, we included climate values within a circular buffer zone of 50 km radius around the sampling plots.

2.6 | Genotype-environment association study

2.6.1 | Population structure

In order to obtain a reliable estimation of the neutral population structure, only SNPs in off-target regions (i.e., found outside CGs) were first considered. Analyses of population structure was also

performed from in-target SNPs, and provided similar estimates (Figure S4). Two different methods were used to investigate population genetic structure: principal components analysis (PCA), as implemented in the R package LEA (Frichot & François, 2015), and the sNMF algorithm (Frichot et al., 2014), which estimates individual ancestry coefficients from the genotype matrix. Fifty runs of sNMF were performed for each number of putative ancestral populations (K), ranging from 1 to 20. The best fitting number of putative ancestral populations was assessed using the cross-entropy criterion. Population differentiation (F_{ST}) between forests was calculated using the software smartPCA (Patterson et al., 2006).

2.6.2 | Genotype-environment association (GEA) analysis

Latent factor mixed models (LFMM 2.0, Frichot et al., 2013; Caye et al., 2019) were used to evaluate associations between allelic frequencies at filtered and unlinked SNPs and each bioclimatic variable available in the BioClim database (BIO1-19). LFMM is an efficient inferential method and robust with respect to various demographic scenarios and sampling designs (Bay et al., 2018; De Mita et al., 2013; De Villemereuil et al., 2014; Lotterhos & Whitlock, 2015; Rellstab et al., 2016). The models need no detailed prior neutral genetic structure information, since structure is statistically incorporated in the model via latent factors. We used ridge penalties available in the LFMM2 algorithm to compute least-squares estimates of five latent factors (Caye et al., 2019). The number of latent factors was obtained from the population structure analyses, as previously described. The latent factors were subsequently used as covariates in the GEA model. Associations between each SNP frequency and each bioclimatic variable were assessed by statistics test calibrated using genomic inflation factors (lfmm2.test in LEA, Gain & François, 2021). Corrections for multiple tests were implemented through the false discovery rate (FDR) control method, at a 5% FDR level (Benjamini & Hochberg, 1995). Candidate SNPs were retained if they were associated with at least one of the 19 bioclimatic variables. Using Fisher's method, we also computed a combined significance value for each SNP by considering the first two principal components of temperature and precipitation-related variables (Fisher, 1925).

2.7 | Genetic offsets

Considering five general circulation models and the predictions of bioclimatic variables from three RCPs, we computed two different measures of genetic offset of coffee populations (Capblancq et al., 2020; Gain & François, 2021). To minimize the issue of collinearity among bioclimatic predictors, the predictive models included only BIO1 (annual temperature) and BIO12 (annual precipitation). The choice of those predictors aimed at limiting the overfit of allele frequencies, and corresponded to the two variables having the largest number of hits in common with the GEA study. A proportion of 40 out of 71 GEA hits were associated with BIO1 or with BIO12, and 29 out of the 71 GEA hits were found in the list of top Z-scores for BIO1 and BIO12.

Using annual temperature and precipitation, we modified the measure of risk of nonadaptedness (RONA) proposed by Rellstab et al. (2016) in order to account for population structure among the samples. The new genetic offset, defined as a genetically weighted environmental distance, extends RONA by considering locus-specific effect sizes computed from an LFMM instead of a simple linear regression model.

To implement the new genetic offset, we adjusted an LFMM with ridge penalty and five latent factors on the 5180 candidate SNPs. For the hits obtained from this GEA study and for each plant, we computed the median absolute value of locus-specific effect sizes (Bj) weighted by the difference between current and predicted values of the corresponding bioclimatic variables (BIO1 or BIO12). Genetically weighted environmental distances, corresponding to genetic offsets, were obtained for each population after averaging individual statistics obtained in this way

$$\begin{aligned}\text{Genetic offset} = {} & \text{median}(|\text{Bj}, 1|) \times d(\text{BIO1}, \text{BIO1pred}) \\ & + \text{median}(|\text{Bj}, 12|) \times d(\text{BIO12}, \text{BIO12pred}).\end{aligned}$$

We compared the genetically weighted environmental distances to the genetic offsets implemented in the R package LEA 3.5.4 (Gain & François, 2021). The quantity defined in LEA provides interpretations of genetic offsets as measures of genetic differentiation (F_{ST}) between populations in their current and predicted environments (Gain & François, 2021). Like genetically weighted environmental distances, LEA's genetic offsets were calculated for each population and for RCPs 2.6, 6.0 and 8.5. The results for each RCP were averaged over the five GCMs. A marked difference between the genotypes of current populations and the genotypes "required" under predicted change would imply a large adaptive change or a long period of genetic drift for the population concerned. Consequently, *C. canephora* forests with larger genetic offsets can be considered as maladapted or more "vulnerable" to future climatic conditions than those with smaller values.

3 | RESULTS

3.1 | Candidate gene capture and SNP genotyping

Targeted enrichment and sequencing of 323 CGs from a total of 207 *C. canephora* individuals resulted in a total of 544,669,164 reads, with the number of reads sequenced per library ranging from 306,114 to 4,233,240. The targeted genes represented a total length of 1.3 Mb, that is, 0.2% of the whole genome (1C = 710 Mb), and the enrichment factor of our 48-bulked captured libraries was especially high (Mariac et al., 2022), with 70% of reads mapping back to the targeted sequences on the reference genome on average. We enriched the targeted sequence by 320-fold compared to a nonenriched library (Mariac et al., 2022).

The calling of variants identified 41,452 high quality biallelic SNPs with a depth of 10× or greater (Figure S3). Finally, 5860 SNP markers were retained for GEA studies (i.e., with a minimum allele frequency (MAF) greater than 5% and in linkage equilibrium), representing from 1 to 81 SNPs (average 14.7 SNPs) per candidate gene (3.6 per kb on average) (Table S5): 4753 in-target SNPs located on 315 CGs and 1107 off- target SNPs.

3.2 | Population structure

Clustering analyses based on off-target SNPs indicated a genetic structure of native *C. canephora* populations reflecting their geographic distribution in Uganda (Figure 1a, similar to that obtained with in-target SNPs (Figure S4). These results were consistent with previously described population structure based on SSR markers (Kiwuka et al., 2021), with five genetic clusters ($K = 5$) (Figures 1c and S6). Most individuals from Zoka, Budongo, Itwara and Kibale forests, located in northwestern and western Uganda, were grouped according to their forest of origin (Figure 1b,c). Other individuals from Malabigambo, Mabira and Kalangala forests, located close to Lake Victoria clustered in a same large south/centre (SC) cluster (Figure 1b). These forests are all located in the lower part of Uganda, including south and central regions. The inferred population structure was supported by pairwise F_{ST} differentiation indices between forests. The F_{ST} values (mean pairwise F_{ST} of 0.142) ranged from 0.005 between Mabira and Kalangala, which had a common genetic background, to 0.267 between Kibale and Kalangala. Overall, the F_{ST} values suggested that there was substantial genetic differentiation among forests across the sampled distribution range (Table S6).

3.3 | Bioclimatic factors and habitat characteristics

We explored the environmental conditions at the sampling locations by performing a principal component analysis (PCA) of the bioclimatic factors. The first two PC axes explained 83.7% of the total variation in the studied region (Figure S6A). All bioclimatic factors significantly differed ($p < .05$) among the seven forests where *C. canephora* was collected. Mean annual temperature (BIO1) and annual precipitation (BIO12) were the variables that best illustrated the climatic heterogeneity. Mean annual temperatures varied mainly with elevation and latitude, ranging from 20 to 24°C (BIO1, Figure S6B), with higher temperatures reported in northern forests such as Budongo and Zoka (23 and 24°C, respectively). On the other hand, the topography, prevailing winds and water bodies, such as lakes Albert and Victoria, were associated with substantial differences in rainfall patterns across the country, without a clear gradient. For instance, for BIO12, rainfall ranged from 1159 mm in Kibale forest to 2,085 mm in Kalangala forest on the rim of Lake Victoria (Figure S6C).

3.4 | Genotype-environment associations

We assessed associations between each SNP and each climatic variable (BIOs) to detect SNPs that were putatively involved in local adaptation, and identified some bioclimatic factors that were potentially driving this process.

Seventy-one of the 5860 SNPs were significantly associated with at least one climatic variable. A total of fifteen bioclimatic variables were involved in these associations (Table 1 and Figure S7), while four variables were not associated with any SNP (BIO2, BIO13, BIO15 and BIO16). Bioclimatic factors greatly differed in the number of SNPs with which they were associated (Figure S7). The 11 temperature-related variables had a greater number of associations (74 associations overall), especially mean temperature of the wettest quarter (BIO8: 18 SNPs), minimum temperature of the coldest month (BIO6: 16 SNPs) and isothermality (BIO3: 14 SNPs). A smaller number of associations (60 SNP associations overall) were found with precipitation-related variables, most of them associated with precipitation of the driest month (BIO14: 26 SNPs) or annual precipitation (BIO12: 21 SNPs). Many SNPs were associated with more than one bioclimatic factor. Of the 71 SNPs correlated with at least one bioclimatic variable, 28 were located in the vicinity of or within the CGs and were therefore considered as being "in-target" SNPs. For the remaining 43 SNPs, 31 were close to non–CG genes and 12 SNPs were located in regions with no adjacent genes (<2 kb). These latter 12 SNPs were considered as being "off-target" loci (Table 1 and Figure S7). Note that three SNPs - associated to three different bioclimatic variables - were found close to the *CcDXMT1* (*Cc01_g00720*) gene involved in caffeine biosynthesis, efficient as a pest repellent (Ashihara et al., 2017; Uefuji et al., 2005). Two SNPs were close to a gene of the putative HD-ZIP transcription factor. Some SNPs were identified in the regulatory (promoter [5′ end] and terminator [3′ end]) regions of several CGs. This included SNPs associated with (1) *CcDXMT1* (*Cc01_g00720*) involved in caffeine biosynthesis, (2) *Cc07_g07540* encoding a putative HD-ZIP transcription factor, and (3) *DREB*-like genes *Cc02_g24810* (*CcERF034*), *Cc10_g14150* (*CcDREB2A.2*) and *Cc10_g14160* (*CcDREB2A.3*) (Table 1).

3.5 | Key genes associated with adaptation to the local environment

We highlighted SNPs located in different CGs that were associated with six or more bioclimatic factors (Table 1). For example, a SNP at chr2:22074987 in the *CcERF034* (DREB-like transcription factor) gene was found to be associated with 10 bioclimatic factors, nine of which were temperature-related factors (temperature Fisher's $p < 8.68 \times 10^{-11}$). Similarly, a SNP located at chr1:1210203 in the *CcDXMT* gene (3,7-dimethylxanthine methyltransferase, temperature Fisher's $p < 4.70 \times 10^{-9}$), at chr1:33303630 in the *CcC4H1* gene (cinnamate 4-hydroxylase, temperature Fisher's $p < 1.06 \times 10^{-7}$), and at the chr10:6440204 location in an intergenic region (BIO6

TABLE 1 Information on 71 SNPs and bioclimatic variable (BIO) associations

	Chr:Pos	Gene name	Gene code	SNP location	Gene function	Bioclimatic variables (BIO) 1	3	4	5	6	7	8	9	10	11	12	14	17	18	19
1	chr0:314444	CcC4H4	Cc00_g00170	Exon	Cinnamate 4-monooxygenase															
2	chr0:65785189		No																	
3	chr0:105979583		No																	
4	chr0:108260738		Cc00_g15560	3′ end	F-box stress induced protein															
5	chr0:108313490		Cc00_g15590	Intron	Hydrolytic enzymes															
6	chr0:123585792	CcSLP1	Cc00_g19100	5′ end	Stomatal density distribution															
7	chr0:145779068	CcMAS2	Cc00_g23010	3′ end	Momilactone A synthase-like															
8	chr0:185516773		Cc00_g30810	3′ end	Protein unknown function															
9	chr0:187060110		Cc00_g31190	Intron	Detox protein DUF1677															
10	chr0:190087864	CcCYP75B1	Cc00_g32130	3′ end	Flavonoid 3′-monooxygenase															
11	chr0:196818760		Cc00_g33810	Intron	Catalase															
12	chr0:200736190		Cc00_g34710	5′ end	Salicylate O-methyltransferase															
13	chr1:400342		Cc01_g00380	3′ UTR	Alcohol O-benzoyltransferase															
14	chr1:1209597	CcDXMT1	Cc01_g00720	3′ end	Xanthine methyltransferase															
15	chr1:1210203			3′ end																
16	chr1:1210465			3′ UTR																
17	chr1:33303630	CcC4H1	Cc01_g15360	Intron	Cinnamate 4-monooxygenase															
18	chr2:3258798		Cc02_g04100	5′ end	Pectin methylest. inhibitor															
19	chr2:5433829		Cc02_g06870	5′ end	BAHD acyltransferase															
20	chr2:6935776	CcCHI	Cc02_g08570	5′ UTR	Chalcone-flavon. isomerase															
21	chr2:8656338	Cc4CL-L4	Cc02_g10610	3′ UTR	4-coumarate-CoA ligase															
22	chr2:9155640	CcPAL1	Cc02_g11230	5′ end	Phenylalan. ammonia-lyase															
23	chr2:15059858	CcMYB4	Cc02_g16270	Exon	Transcription factor MYB4															
24	chr2:22074987	CcERF034	Cc02_g24810	5′ end	DREB-like transcription factor															
25	chr2:23011825	CcINVI1	Cc02_g25640	5′ end	Putative invertase inhibitor 1															
26	chr2:26354192		Cc02_g28010	5′ end	Chaperonin-like RbcX protein															
			Cc02_g28020	3′ end	Cellulose synthase A															
27	chr2:26477513		Cc02_g28080	Intron	Carotenoid dioxygenase															
28	chr2:27027415		Cc02_g28450	Exon	Dihydroflavonol 4-reductase															
29	chr2:33882516		No																	

(Continues)

TABLE 1 (Continued)

	Chr:Pos	Gene name	Gene code	SNP location	Gene function	Bioclimatic variables (BIO) 1	3	4	5	6	7	8	9	10	11	12	14	17	18	19
30	chr2:39762763		Cc02_g31340	3′ UTR	Serine/threon.-protein kinase															
31	chr2:45823095		Cc02_g33390	5′ end	Endo-beta-mannosidase															
32	chr2:54062842		Cc02_g39570	3′ end	Protein unknown function															
33	chr3:4659905	CcSAMT1	Cc03_g05630	5′ end	S-adenosyl-methionine transferase															
34	chr3:12179728		No																	
35	chr3:16156549		Cc03_g11470	Exon	Cinnamoyl-CoA reductase															
36	chr3:28308186		Cc03_g14250	3′ end	Transcription factor MYB12															
37	chr4:8153508		Cc04_g09590	3′ end	Hydroxycinnamoyl transferase															
38	chr4:9149099	Cc4CL-L2	Cc04_g09970	Intron	4-coumarate-CoA ligase															
39	chr4:9300218		Cc04_g10120	5′ end	Protein unknown function															
40	chr4:26647064		No																	
41	chr5:3037776		Cc05_g01360	Intron	Caffeic acid 3-O-methyltransferase															
42	chr6:139786		No																	
43	chr6:3390817		Cc06_g04300	5′ end	MYB-like protein (CcMYB16)															
44	chr6:6302224	CcSPS1	Cc06_g07910	3′ UTR	Sucrose-phosphate synthase															
45	chr6:8927531	CCoAOMT	Cc06_g11010	Intron	Caffeoyl-CoA-O methyltransferase															
46	chr6:9057925	CcUNK4	Cc06_g11210	Intron	K(+) efflux antiporter 4-like															
47	chr6:15996252		Cc06_g17280	Intron	Aquaporin PIP-like protein															
48	chr6:20213294		Cc06_g19050	Intron	Alcohol O-benzoyltransferase															
49	chr6:24124930		Cc06_g20390	Intron	Shikimate 3′-hydroxylase															
50	chr6:34698945		No																	
51	chr7:1327041	CcUNK2	Cc07_g01940	Intron	Glutaredoxin GRXC2															
52	chr7:2738039	Cc4CL-L7	Cc07_g03940	Exon	4-coumarate-CoA ligase															
53	chr7:5313694	CcGMGT1	Cc07_g07210	Exon	Galactomannan galactosyltransferase															
54	chr7:5322165	CcGMGT4	Cc07_g07220	5′ end	Galactomannan galactosyltransferase															

TABLE 1 (Continued)

	Chr:Pos	Gene name	Gene code	SNP location	Gene function	Bioclimatic variables (BIO) 1	3	4	5	6	7	8	9	10	11	12	14	17	18	19
55	chr7:5541103		Cc07_g07540	5′ UTR	HD-ZIP transcription factor															
56	chr7:5542794			3′ end																
57	chr7:7171559		Cc07_g09810	5′ end	Dihydroflavonol-4-reductase															
			Cc07_g09820	5′ end	Peptide repeat-protein															
58	chr7:7897804		Cc07_g10740	5′ end	Flavanone 3-hydroxylase															
59	chr8:936183		Cc08_g00920	3′ UTR	Cellulose synthase A															
60	chr8:16280785		Cc08_g06630	Intron	Isoleucine N-monooxygenase 2															
61	chr8:25553032		Cc08_g10740	Intron	Beta-fructofuranosidase															
62	chr8:29720412	CcPIP1;2	Cc08_g14850	5′ end	Aquaporin PIP1-2 like															
63	chr8:31143136		No																	
64	chr9:585487	CcCPI3	Cc09_g00790	3′ UTR	Cysteine proteinase inhibitor CPI-3															
65	chr9:7514746		Cc09_g06560	Intron	Protein unknown function															
66	chr9:7737016		No																	
67	chr9:20998638		No																	
68	chr10:833613	CcRaf21-2	Cc10_g01060	Intron	MAPKKK-like protein kinase															
69	chr10:6440204		No																	
70	chr10:24710177	CcDREB2A.2	Cc10_g14150	3′ end	DREB-like transcription factor															
		CcDREB2A.3	Cc10_g14160	5′ end	DREB-like transcription factor															
71	chr11:10708301		No																	

Note: The SNPs are classified according to their position on the Robusta genome. When known, the gene names are indicated, as well as their corresponding gene code.

Chr:Pos, genome position on the *C. canephora* chromosomes (Denoeud et al., 2014). Gene codes, corresponding gene codes from the Coffee Genome Hub (http://coffee-genome.org/, Dereeper et al., 2015). SNP location, location of each SNP relative to the gene boundaries is also indicated: 5′ end (>1.5 kb upstream of the putative 5′ end of gene coding sequence); 3′ end (>1.0 kb downstream of the putative 3′ end of the gene coding sequence). The Bioclimatic variables (BIOs 1–19) are defined in Table S4. **Dark boxes** = very strong association (p-value < .03), **grey boxes** = strong association (p-value > .03).

$p < 5.45 \times 10^{-6}$) were also associated with temperature-related factors. Conversely, some other SNPs appeared to be preferentially associated with precipitation-related factors (Table 1). Associations between the SNP in *CcERF034* with the minimum temperature of coldest month (BIO6), as well as the SNP in *CcDREB2A.3* with the mean temperature variation (BIO3) are illustrated in Figure 2. The highest alternate allele frequencies of the SNP in *CcERF034* occurred in Itwara and Kibale forests, that is, low temperature areas. In the case of the SNP in *CcDREB2A.3*, the highest alternate allele frequency occurred mainly in Kibale forest, a region where the greatest isothermality was observed.

3.6 | Genetic offsets

To evaluate which bioclimatic variables will differ the most in the sampling zones between present (1970–2000) and future (2061–2080) conditions, we performed a multivariate environmental similarity surfaces analysis (MESS) for each of the three RCPs, averaged over the five GCMs. The MESS results are presented as the average difference (%) relative to present conditions for the nineteen bioclimatic factors (Figure 3a). As expected, the expected variation intensity differed between the different RCPs used, but all scenarios generally forecasted more drastic changes for temperature than for precipitation related factors (Figure 3a,b). The BIO2, BIO5, BIO6, BIO8, BIO12 and BIO13 factors consistently showed the greatest expected changes (Figure 3), with the RCP 8.5 scenario having the strongest expected impact on BIO6 (minimum temperature of the coldest month), with 38% of the predicted changes, that is, an increase of 2.1 degrees (sd = 0.9 degrees) from the current value of 15.4 degrees.

With respect to the scenarios of climate change for *C. canephora* populations, genetic offsets were measured by genetically weighted environmental distances estimated using two of the most explanatory bioclimatic factors: annual temperature (BIO1) and annual precipitation (BIO12). Genetic offsets associated with projected climate change increased with the predicted levels of greenhouse gas emission, between low (RCP 2.6), intermediate (RCP 6.0) and high (RCP 8.5) scenarios, reflecting differences in their predicted impact (Figure 4). The genetic offsets were higher for RCP 8.5 (56.2%–69.2%) than for RCP 2.6 (18.4%–28.4%) or RCP 6.0 (39.7%–46.1%), but similar global trends were observed for all forests. The Zoka and Budongo populations stood out from the other populations as having the lowest offsets (Figure 4b). In contrast, the Malabigambo

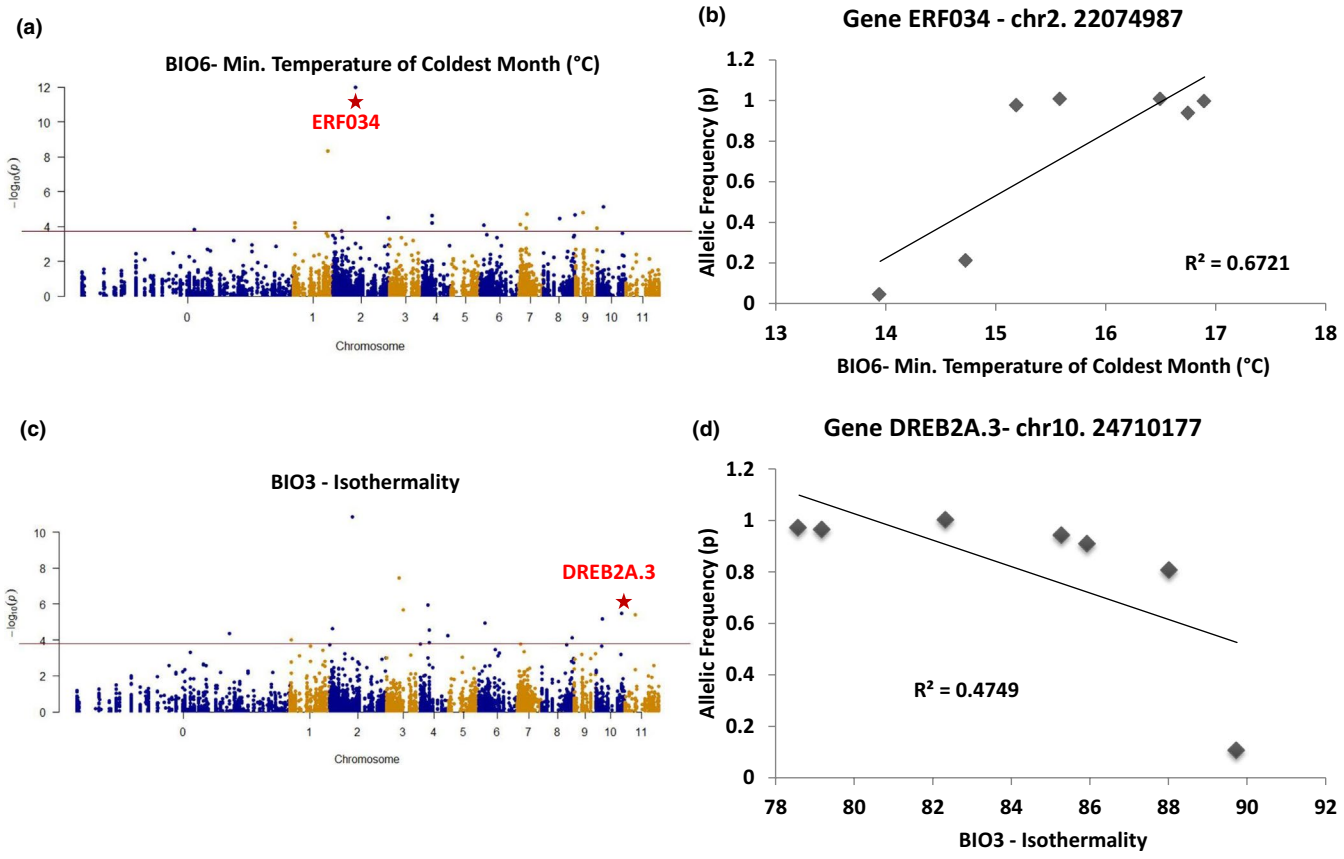

FIGURE 2 Examples of SNP-environment associations identified by the overall latent factor mixed model (LFMM) analysis in *Coffea canephora*. Distribution of SNPs in the *C. canephora* genome (chromosomes 0–11) associated with the BIO6 factor (Min. Temp. coldest months in °C) (a) and BIO3 (Isothermality) (c). The SNPs chr2:22074987 located in the *CcERF034* (*Cc02_g24810*) gene (a) and chr10:24710177 located in the *CcDREB2A.3* (*Cc10_g14160*) (c) are indicated by red stars. Linear regressions are presented for SNPs chr2:22074987 of *CcERF034* (b) and chr10:24710177 of *CcDREB2A.3* (d) [Colour figure can be viewed at wileyonlinelibrary.com]

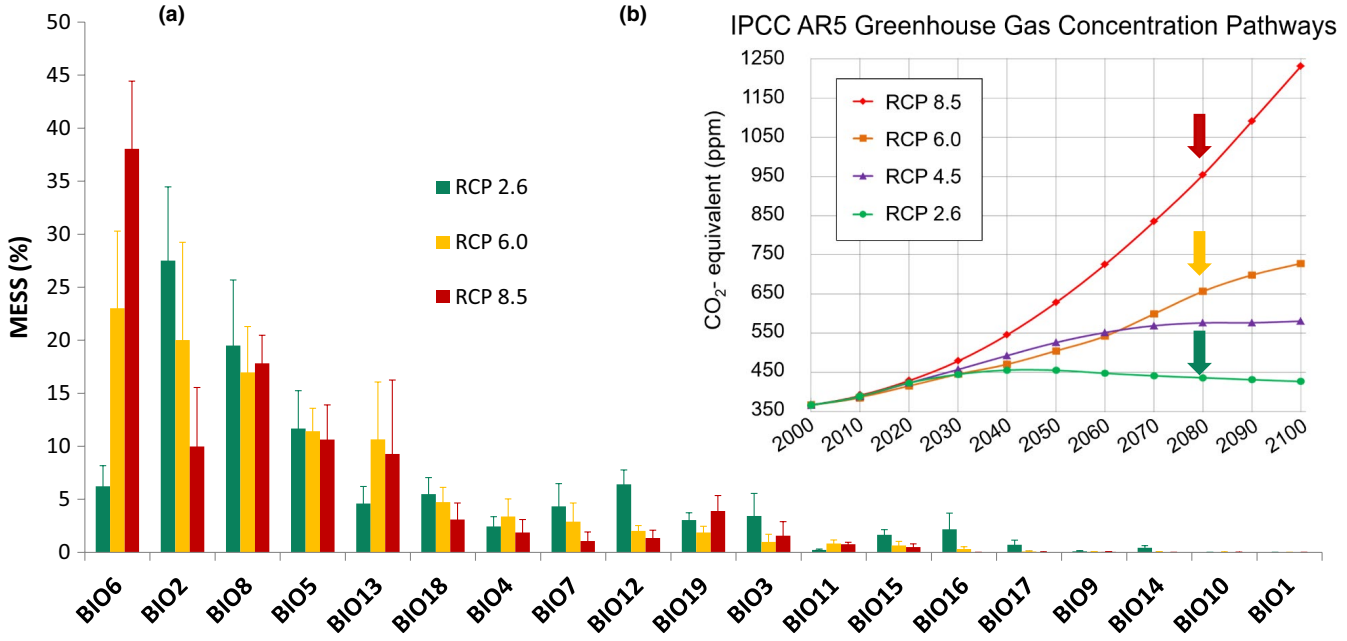

FIGURE 3 Predicted change in environmental factors between "present" (1960–2000) and future (2061–2080) under different representative concentration pathways (RCP). (a) Present-future difference (%) as calculated for each of the three RCPs using the multivariate environmental similarity surfaces, from data collected from a buffer zone of 50 km around the sampling plots, averaged over the five GCMs. (b) Four representative concentration pathways (greenhouse gas concentration trajectories) used for climate modelling (IPCC fifth Assessment Report [AR5] in 2014). RCP 2.6, 6.0 and 8.5 scenarii used in the analysis are shown with arrows, RCP 2.6 representing aggressive mitigation, and RCP 8.5 following a "business as usual" trajectory (Source: IPCC, 2014 – WikiCommons) [Colour figure can be viewed at wileyonlinelibrary.com]

population presented the highest genetic offsets under RCP 2.6 and RCP 8.5 and, together with the Kalangala population, the highest genetic offset under RCP 6.0. The computation of LEA's genetic offsets provided a similar ranking of *C. canephora* populations, and the correlation between the two measures was very high (Figure S8). The Budongo, Kibale and Zoka populations were associated with lower offset values, whereas Kalangala and Malabigambo population were associated with higher genetic offsets in all scenarios. The LEA offsets, which are comparable to pairwise F_{ST}'s between current and predicted populations, ranged between 13.0 and 22.9% in RCP 2.6 and between 27.4% and 36.8% in RCP 6.0, corresponding to differentiation levels measured between current populations. For RCP 8.5, the estimated offsets were higher than 30% (35.8%–47.1%), indicating a higher risk of maladaptation for all populations (Figure S8).

4 | DISCUSSION

The predicted impact of future environmental conditions significantly differed among the *C. canephora* native populations across the seven representative Ugandan forests. We detected associations between 71 SNPs and 15 BIO variables based on sequencing polymorphism of 323 CGs among 207 *C. canephora* individuals from these forests. These SNPs and associated CGs were putatively involved in local adaptation, and we considered that the associated BIO factors were potentially driving this process. Projection of future conditions based on forecasted local climate change showed that all populations might be to some extent maladapted to future local conditions, although the genetic offset varied across populations. Populations from Zoka and Budongo, in the driest northern zone of the distribution range, appeared to be the most likely to cope with the predicted climate change, as reflected by their low offsets, while populations in Kalangala and Malabigambo, in the Lake Victoria region, had the largest genetic offset (Figure 4).

4.1 | Severe predicted changes for Ugandan *C. canephora* populations

Coffea species and coffee production are expected to be severely affected by climate change (Bunn, Läderach, Ovalle Rivera, et al., 2015; Bunn, Läderach, Pérez Jimenez, et al., 2015; Davis et al., 2012, 2019; Moat et al., 2019; Tournebize et al., 2022). Temperature and rainfall are known to be important environmental factors affecting coffee vegetative growth, flowering and bean development (DaMatta & Ramalho, 2006; Gomez et al., 2016). In our study, an overall drastic climatic change was also expected in the next decades, although the extent of variation differed between the scenarios used to predict climate change (RCPs) and bioclimatic variables. More drastic changes have been forecasted for temperature than for precipitation-related factors. In particular, the minimum temperature of the coldest month (BIO6) was predicted to increase up to 2.1 degrees by 2080 from the current value of 15.4 degrees, under the RCP 6.0 and RCP 8.5 scenarios. However, precipitation of the

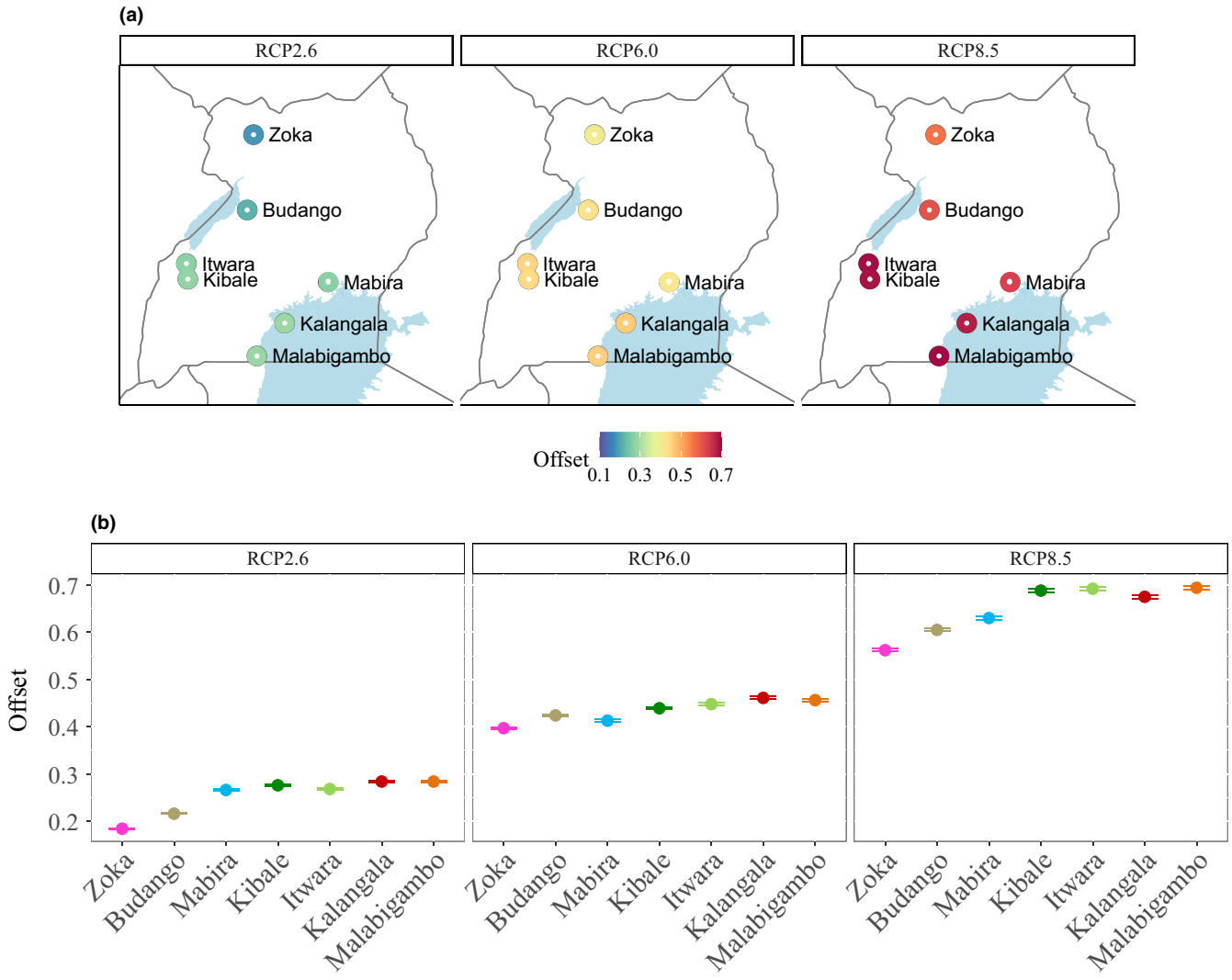

FIGURE 4 Predicted genetic offset (risk of maladaptation) of *Coffea canephora* populations in Uganda to future climatic changes under three RCP scenarii. They are defined as the average change in genotypes needed to match future environmental conditions in a set of 71 loci correlated with the specific environmental factor. (a) Map of the offsets for each forest in Uganda for the three RCP scenarii, averaged over the five GCMs and individuals. (b) Graph of the average offsets for the three RCP scenarii; error bars represent standard errors. Colours correspond to geographical origin as in Figure 1 [Colour figure can be viewed at wileyonlinelibrary.com]

wettest month (BIO13) was also predicted to be markedly impacted. This trend is in line with the findings of a previous study of Bunn, Läderach, Pérez Jimenez, et al. (2015), which modelled changes in habitat suitability for *C. canephora* crops between present and 2050 under RCP 6.0. While these authors sampled occurrence points in farms, which do not represent the equilibrium between species and climate in the wild, their results predicted coffee production to be severely affected by climate change via temperature fluctuations and seasonality.

4.2 | Signature of natural selection/local adaptation on candidate genes

Our approach was based on targeting a priori identified CGs, including some CGs previously identified as key genes in plant response to biotic and abiotic stresses and associated with available *C. canephora* genome annotations (Denoeud et al., 2014; Dereeper et al., 2015). Our approach was efficient since the targeted sequences were 320-fold enriched compared to a nonenriched genome sequencing, while providing high quality SNPs located on 98% of the CGs. This strategy confirmed the practical advantages of target sequence capture methods previously reviewed for evolutionary and ecological genomics studies (Jones & Good, 2016). For example, targeted enrichment was previously used to increase the phylogenetic resolution within the *Inga* (Fabaceae) neotropical tree genus (Nicholls et al., 2015). This focused approach targets CGs for which prior information is available (e.g., associated with specific fitness-related traits) and is hypothesized to have a greater likelihood of being under selection. It has been applied to detect loci putatively under selection (Christmas et al., 2016; Hill et al., 2018; Roffler et al., 2016), and led to a higher proportion of outliers. Similarly, in the present study, 39

SNPs were significantly associated with at least one climatic variable and were located in or nearby a total of 28 CGs.

In a previous study, we tested the association between climatic variables and genetic variability across the same populations via redundancy analysis (RDA) and 19 microsatellite (SSR) markers (Kiwuka et al., 2021). We observed that 16.3% of the total genetic variation was explained by climatic factors. In the current study, we detected significant specific associations: a total of 71 putative adaptive SNPs for 15 out of the 19 climatic variables tested were related to temperature or rainfall, thereby indicating local adaptation across *C. canephora* populations. In line with other findings, climate adaptation in *C. canephora* is a genome-wide phenomenon and probably involves multiple genes and polygenic adaptation (see for example Christmas et al., 2016). However, our approach had some shortcomings since correlation of alleles with environmental variables does not imply a causal relationship, and local adaptation is mainly based on polygenic interactions (Sork, 2018) that we might have underestimated because of our limited number of candidate genes. Our approach was nevertheless founded on physiological knowledge of coffee trees and represented a valuable step towards understanding the genetic basis of climate change tolerance.

4.3 | Key genes with a local environmental adaptation signature

The other main advantage of our CG approach is its potential for identifying SNPs that are associated to a specific gene or its regulatory regions, and they could be further explored for evidence of selection on specific alleles or functions. Some associations pinpointed here are remarkable even though a more in-depth analysis, that is, considering all SNPs and conducted on a gene-by-gene basis, could lead to a better understanding of the functional aspect of the putative adaptations, For example, the SNP located at position chr2: 22074987, showing the highest number of associations to bioclimatic factors among all analysed SNPs, particularly with temperature-related factors (Figure 2), is located in the *CcERF034* gene encoding a DREB-like protein (Alves, 2015; Torres et al., 2019). This gene is known to be a key transcription factor controlling plant responses to many abiotic stresses (Khan, 2011; Shinozaki & Yamaguchi-Shinozaki, 2007). We also found one SNP (chr10:24710177) associated with isothermality (BIO3) (Figure 2) in the promoter region of the *Cc10_g14160* DREB-like gene also corresponding to the 3′ end region of *Cc10_g14150* — these two genes were recently renamed *CcDREB2A.3* and *CcDREB2A.2*, respectively (Torres et al., 2019). By analysing the expression of *DREB*-like genes in *C. arabica* plants subjected to different abiotic stress, these authors showed upregulated expression of *ERF034* and *DREB2A.3* genes leaves subjected to short periods of cold, low humidity, high light and exogenous ABA (abscissic acid) treatments. The *DREB2A.3* expression also appeared to be highly upregulated in roots of the *C. canephora* drought-tolerant clone subjected to low relative humidity. The fact that several SNPs associated with bioclimatic factors were identified in these CGs clearly support the hypothesis that these genes play a key role in coffee response to abiotic stress, such as drought. Interestingly, the SNPs chr2:15059858 and chr6:3390817 located in the *CcMYB4* and *CcMYB16* genes, respectively, were found to be associated with only one bioclimatic variable, BIO12 (annual precipitation) and BIO6 (minimum temperature of the coldest month) respectively. While the *CcMYB4* putative protein shares high identity with MYB4/MYB32 proteins known to negatively regulate phenylpropanoid biosynthesis genes (Preston et al., 2004), *CcMYB16* encodes a putative protein also sharing high identity with the RAX2 transcription factor of the MYB superfamily. In *Arabidopsis*, a group of MYB transcription factors has been reported to regulate the biosynthesis of secondary metabolites, with MYB4 regulating expression of the cinnamate 4-hydroxylase (C4H) gene encoding a key enzyme of chlorogenic acids pathway well known to act as antioxidant compounds (Stracke et al., 2001). Analysing the compounds of the chlorogenic acid biosynthetic pathway in the leaves of different Robusta trees from Uganda according to their environmental origin would provide a better understanding of their adaptive role.

Although the direct impact of SNPs cannot be tested here, some could affect CG expression at the transcriptional level and/or by altering the stability of the corresponding mRNA.

In coffee, it has already been reported that SNPs and INDELs (insertion/deletion) present in the different haplotypes of *CcDREB1D* promoter regions cloned from *C. canephora* drought-tolerant and drought-susceptible clones were effectively responsible for fine-tuning the regulation of this gene in young coffee plantlets grown with different abiotic stresses such as drought stress (Alves et al., 2017, 2018; Torres et al., 2019). Based on these observations and on the results of our study, it would be very interesting to further evaluate the genetic diversity and expression of *CcDREB1D* in *C. canephora* plants representing each Ugandan forest location.

A comprehensive assessment of the physiological differential response to drought stress and a gene expression study at a larger scale on our study material would enhance our understanding of the molecular mechanisms and their mediating effect on phenotypic responses to drought.

4.4 | Coping with climate change and conservation challenges

Forests are particularly sensitive to climate change because trees are less likely to rapidly adapt to environmental changes due to their long lifespan (Davis et al., 2019). The limited ability of coffee trees to relocate means that most wild *C. canephora* populations will probably grow under less suitable climatic conditions in the near future, thereby undergoing increased stress. A key conservation issue concerns the need to identify and preserve populations that have the capacity to adapt to novel threats (Harrisson et al., 2014). It could then be possible to target specific adaptive traits once these threats are well understood, thus enabling rapid identification of genetically

diverse tolerant trees that could subsequently be used for conservation, reintroduction or even breeding.

In line with the risk of nonadaptedness (RONA, Rellstab et al., 2016), we proposed a new measure of genetic offset defined as a "genetically weighted environmental distance", in which weights correspond to the effect of the environment on adaptive loci. The measure improved RONA by including weights that are adjusted for the confounding effect of population structure (Rellstab et al., 2021). For *C. canephora*, the estimated genetic offsets allowed us to compare the level of genetic changes required between the different populations for them to maintain their genotype-environment association. Although current adaptation to the local environment might not represent a total preadaptation to future climates, we identified Zoka and Budongo forest populations with a greater capacity to cope with their local future conditions than the other populations, irrespective of the chosen RCP scenario. Populations with the greatest mismatch between current and predicted genotype compositions in Kalangala, Mabira and Malabigambo might be at greater risk of maladaptation, and less likely to cope with climate change.

Interestingly, populations in the northern and western regions of Uganda, especially in Zoka forest, were highly differentiated and contained several unique genetic variants that were not present elsewhere in the species distribution range. In contrast, populations from Malabigambo, Mabira and Kalangala, which clustered in the same SC group, were genetically mixed with cultivated and imported material (Kiwuka et al., 2021). The Zoka population is of special interest as it is located at the drier end of the climatic gradient in a small forest of about 12.6 km^2; but due to its location this population is especially vulnerable to human disturbance and habitat destruction. These populations are also of great agronomic interest because they could offer a resilience source for cultivated *C. canephora* material amidst the escalating effects of climate change (Kiwuka, 2020, Kiwuka et al., 2021).

The variability of the genetic offset among populations might stem from the magnitude of environmental change. The genotypic composition of a population undergoing a sharp increase in mean temperature in the future would have to change to a larger extent than that of a population that only experiences a minor increase. Moreover, other factors such as allele fixation, balancing selection, pleiotropic interactions or fitness costs may also influence changes in genotypic composition (Hoffmann & Sgrò, 2011; Mitchell-Olds et al., 2007). Beyond allelic changes, epigenetic and expression changes as well as phenotypic plasticity could provide alternatives for continued adaptation (Franks & Hoffmann, 2012; Huang et al., 2015; Kenkel & Matz, 2016; Nicotra et al., 2015), although a high phenotypic plasticity level may correlate negatively with intrinsic stress tolerance (Bongers et al., 2017; Kiwuka, 2020; Kiwuka, 2020). Major shifts in genotypic composition are likely to ensure adaptation, but other processes could also contribute to the adaptive potential of populations.

Using a gene-targeted SNP approach, we discovered genes potentially involved in local adaptation and estimated variations in vulnerability among natural populations. However, many traits involved in local adaptation are affected by multiple genes and interactions with the environment (Savolainen et al., 2013; Yeaman, 2015), which could not be accounted for here through our CG approach.

For conservation purposes, several evolutionary factors could still allow populations to remain adapted to changing climatic conditions even though these populations seem vulnerable with regard to genotypic composition changes. For instance, gene flow can facilitate climate adaptation within populations by broadening standing variation diversity (Kremer et al., 2012; Sgrò et al., 2011), increasing rates of allele frequency shifts and countering allele fixation.

The studied coffee populations might react in different ways to climate change: (i) suitable habitats could be colonized by new genotypes originating from a location that already exhibits conditions similar to those expected in the future at the resident population (Capblancq et al., 2020; Rhoné et al., 2020). For example, since the Budongo and Zoka populations prevailed in significantly warmer and drier places than the other populations investigated here, they might outperform the other populations in the present habitats of those populations under warmer climatic conditions. They might be best adapted to the future climate with respect to reduced precipitation and lower groundwater supplies on site; (ii) resident populations could also cope with climate change by adapting to the local changing environment via changes in their genotypic composition due to selection on standing genetic variation (or, less likely, novel variation due to mutations). This is basically the scenario that underlies the vulnerability analysis described above.

However, the critical question is how fast genotypic composition can change within a population? LEA's offsets in RCP 2.6 and 6.0 led to values close to pairwise F_{ST}'s measured in current populations (which reached 26%), suggesting that the risk of maladaptation may be manageable through assisted migration. Individuals could be transplanted like those already successfully introduced in areas such as Lake Victoria (Kiwuka et al., 2021). For RCP 8.5, LEA's offsets were higher than those observed in current populations and the populations may be at greater risk. Although the results obtained here indicate the potential magnitude of change that may be required to adapt to climate change, further work is needed to determine the actual ability of coffee populations to locally adapt, the role of gene flow or assisted migration in facilitating genotypic composition change, and the potential fitness effects. This is especially relevant in fragmented environments, where restricted gene flow and population size may reduce the capacity for populations to evolve at speeds required to keep pace with climate change (Aitken et al., 2008; Alberto et al., 2013). Such knowledge will improve the ability to assess future adaptive potential and identify vulnerable populations requiring management intervention.

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CONFLICT OF INTEREST

The authors have no conflict of interest.

AUTHOR CONTRIBUTIONS

Valérie Poncet, Alan C. Andrade, Alexandre de Kochko, Pascal Musoli and Niels Anten acquired the funding, designed the study, drew up and implemented the experimental design. Sinara Oliveira de Aquino carried out the experiments, performed the analyses and produced the figures. Catherine Kiwuka performed the fieldwork and contributed to the data interpretation. Pascal Musoli, Maud Lepelley, Olivier Darracq, and Dominique Crouzillat contributed to the Clément Gain set definition. Cédric Mariac, Kévin Bethune, and Marie Couderc assisted with the library preparations and sequence analyses. Rémi Tournebize, Stéphanie Manel, Valérie Poncet and Yves Vigouroux helped with the genetic data analysis. Olivier François, Clément Gain, Stéphanie Manel, Philippe Cubry and Rémi Tournebize helped with the genetic offset analyses. Sinara Oliveira de Aquino wrote the manuscript with the assistance of Valérie Poncet and Pascal Musoli. All authors reviewed and approved the manuscript.

BENEFIT-SHARING

Benefits Generated: A research collaboration was developed with scientists from the countries providing genetic samples, all collaborators are included as coauthors, the results of research have been shared with the provider communities and the broader scientific community (see above), and the research addresses a priority concern, in this case the conservation of organisms being studied. More broadly, our group is committed to international scientific partnerships, as well as institutional capacity building. Lastly, as described above, all data have been shared with the broader public via appropriate biological databases.

DATA AVAILABILITY STATEMENT

Single nucleotide polymorphism and climate data have been made available in Dryad doi:https://doi.org/10.5061/dryad.6t1g1jx0m.

ORCID

Rémi Tournebize https://orcid.org/0000-0003-0247-6400
Pierre Marraccini https://orcid.org/0000-0001-7637-6811
Cédric Mariac https://orcid.org/0000-0001-6439-115X
Philippe Cubry https://orcid.org/0000-0003-1561-8949
Yves Vigouroux https://orcid.org/0000-0002-8361-6040
Stéphanie Manel https://orcid.org/0000-0001-8902-6052
Olivier François https://orcid.org/0000-0003-2402-2442
Valérie Poncet https://orcid.org/0000-0002-1099-2846

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