

RESEARCH ARTICLE

Ecological and genomic vulnerability to climate change across native populations of Robusta coffee (*Coffea canephora*)

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Abstract

The assessment of population vulnerability under climate change is crucial for planning conservation as well as for ensuring food security. *Coffea canephora* is, in its native habitat, an understorey tree that is mainly distributed in the lowland rainforests of tropical Africa. Also known as Robusta, its commercial value constitutes a significant revenue for many human populations in tropical countries. Comparing ecological and genomic vulnerabilities within the species' native range can provide valuable insights about habitat loss and the species' adaptive potential, allowing to identify genotypes that may act as a resource for varietal improvement. By applying species distribution

models, we assessed ecological vulnerability as the decrease in climatic suitability under future climatic conditions from 492 occurrences. We then quantified genomic vulnerability (or risk of maladaptation) as the allelic composition change required to keep pace with predicted climate change. Genomic vulnerability was estimated from genomic environmental correlations throughout the native range. Suitable habitat was predicted to diminish to half its size by 2050, with populations near coastlines and around the Congo River being the most vulnerable. Whole-genome sequencing revealed 165 candidate SNPs associated with climatic adaptation in *C. canephora*, which were located in genes involved in plant response to biotic and abiotic stressors. Genomic vulnerability was higher for populations in West Africa and in the region at the border between DRC and Uganda. Despite an overall low correlation between genomic and ecological vulnerability at broad scale, these two components of vulnerability overlap spatially in ways that may become damaging. Genomic vulnerability was estimated to be 23% higher in populations where habitat will be lost in 2050 compared to regions where habitat will remain suitable. These results highlight how ecological and genomic vulnerabilities are relevant when planning on how to cope with climate change regarding an economically important species.

KEYWORDS

adaptation, African rainforests, climate change, *Coffea canephora*, conservation, ecological vulnerability, genomic vulnerability, species distribution model

1 | INTRODUCTION

The 20th century has experienced the strongest warming trend in the last millennium, with average temperatures rising about 0.6°C globally (Jones et al., 1999) and with a projected global average increase ranging between 1.5 and 2°C by the end of the 21st century (IPCC, 2018). Under the most likely emission scenarios, the African rainforest is likely to warm 3 to 4°C during the 21st century (James et al., 2013; Zelazowski et al., 2011). Plant species have a limited number of options to respond to such rapid climate change. They can shift their ranges to follow their preferred climate conditions, locally adapt to new environmental conditions (by genetic changes or phenotypic plasticity) or go extinct if they cannot disperse or adapt (Bellard et al., 2012; Pinsky et al., 2019). These changes will have a large impact on overall biodiversity, but will also affect crops, fisheries and all commercial species that fuel human economies around the world (Challinor et al., 2014; Cheung et al., 2010; Godfray et al., 2010; Sousa & Raizada, 2020).

The tropics are particularly vulnerable to climate change because they are at the confluence of at least three factors at play. First, non-analogue conditions (i.e. conditions never met in recent history) are more likely to appear in tropical regions (Mora et al., 2013), where current climate already has among the highest average temperatures worldwide. Any increase will therefore result in new environmental conditions that are not currently represented on earth. Overall, the predicted increased periods of drought, thermal stress and extreme events are likely to produce a range of new selection

pressures in the tropics that do not exist elsewhere (Corlett, 2011; Feeley et al., 2012). Second, extinction rates are already significantly higher in tropical species than in temperate species (55% vs. 39%; Wiens, 2016) and compositional changes are readily observed in tropical rainforests (Esquivel-Muelbert et al., 2019). Some have hypothesized that this is not only due to a higher taxonomic diversity and an increased human pressure on tropical systems, but also due to an inherent inability of tropical species to deal with changes in water availability and heat stress (Schwalm et al., 2017). In addition, there is some evidence suggesting that the lower frequency of past drought events in tropical systems could have led to fewer current adaptations to variations in water availability (Engelbrecht et al., 2007). Third, tropical environments concentrate the poorest and fastest growing human populations, lacking the institutional and political infrastructure that is needed to adapt local economies to shifts in climate conditions (Foley et al., 2011; Godfray et al., 2010). Any changes in productivity for economically important species in tropical systems will increase the risk of food insecurity for human communities that are already highly vulnerable.

Climate change is predicted to negatively impact *Coffea* species, particularly because the rate at which change takes place might be too high for species to migrate in time or adapt via novel mutations (Bunn et al., 2015; Davis et al., 2012, 2019; de Aquino et al., 2022; Moat et al., 2017, 2019; Ovalle-Rivera et al., 2015). Coffee is the most important commodity crop globally, providing income to more than 125 million people, mostly in tropical nations, and having a retail market value of over 83 billion USD in 2017 alone (Voora et al., 2019).

The coffee industry is mainly underpinned by two *Coffea* species, that is *Coffea arabica* (58.5% of the annual production in 2020) and *C. canephora* (41.5%; ICO, 2021). Among *Coffea* species, *C. canephora* has the widest native distribution and climatic range. *C. canephora* is found in the understorey of western and central African rainforests, mainly in humid, evergreen forest, but sometimes in seasonally dry humid forest, occasionally in gallery forest with elevations ranging from 50 to 1500 m above sea level (Berthaud, 1986; Davis et al., 2006), which define our study area. Within its native distribution range, a high level of genetic variation exists. We focus on wild populations of *C. canephora*, because they contain most of the genetic diversity within the species (Gomez et al., 2009; Kiwuka et al., 2021; Mérot-L'Anthoene et al., 2019), as compared to the cultivated varieties that exist in other parts of the world. Therefore, in a scenario of climate change, wild populations have the potential to host genotypes that could cope with new climatic conditions better than the varieties currently cultivated. It has therefore become common practice to search for desirable traits in wild types to improve cultivated varieties (Satori et al., 2021). In this context, the study of genomic vulnerability of wild *Coffea* species in their native range could help identify pre-adapted individuals and genetic variants with potential for resilient crop improvement. The identification of ecologically and genomically vulnerable populations within the native range is therefore key to preparing tropical economies in this endeavour as well as to protecting the most vulnerable native *C. canephora* populations in situ or collecting them for ex situ conservation.

From a biodiversity perspective, vulnerability to climate change can be defined as the intersection of three factors (Dawson et al., 2011; Ofori et al., 2017): (1) *exposure*, or how much climate change a region is likely to experience; (2) *sensitivity*, or the degree to which a species depends on current conditions to survive; and (3) *adaptive capacity*, which includes phenotypic plasticity, adaptive potential and genetic diversity. Global climate models (GCMs) allow assessing

exposure by providing maps of how, and at what rates, climatic conditions are likely to change in a specific region and during a certain time frame (Hamann et al., 2015). Species distribution models (SDMs), in conjunction with GCMs, have often been used to evaluate sensitivity (Dawson et al., 2011). By using correlative models that relate current occurrence and/or abundance patterns to environmental gradients, we can project climatic suitability into future climate change scenarios, assuming constant species–environment relationships over time (Elith et al., 2010; Guisan & Thuiller, 2005). Here we will call ‘ecological vulnerability’ the difference between current and future climatic suitability, as calculated using SDMs with different climate change scenarios (Figure 1). A positive value indicates a decrease in climatic suitability under future conditions; the greater this difference, the more ecologically vulnerable the species is to the change in climate conditions. Finally, adaptive capacity is the potential of a species or population to tolerate or adapt to climate change (Dawson et al., 2011), and can be defined from various components, such as adaptive genetic diversity and dispersal. This component of vulnerability has been more elusive and difficult to tackle in previous studies (Ofori et al., 2017). While the chance of a species to withstand climate change is likely dependent on the intraspecific diversity and, particularly, whether there are populations that are already adapted to extreme environments, few studies have examined this assumption combining SDMs and genomic data (e.g. Hällfors et al., 2016; Razgour et al., 2019). Some SDM studies have accounted for neutral intraspecific differences in climate responses by separately modelling smaller units of a species range, for example by considering subspecies (Alsos et al., 2012; Balint et al., 2011; Meynard et al., 2017) or subpopulations (Chardon et al., 2020; Jay et al., 2012) in SDM projections. However, those studies still assume that each unit (subspecies, subpopulations) is homogeneous and conserves the same response to the environmental gradients, therefore eluding the question of adaptive capacity and vulnerability.

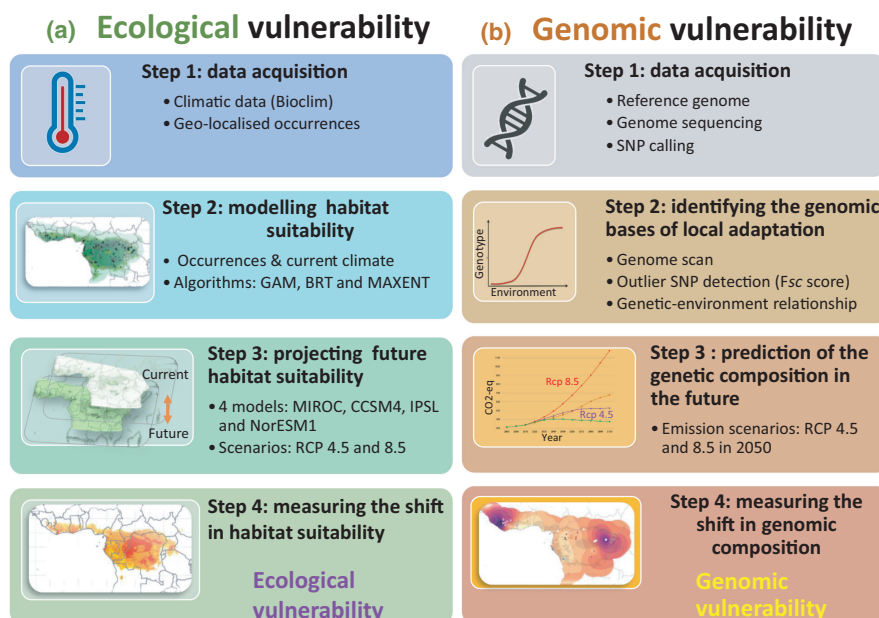


FIGURE 1 Representation of the different steps to calculate the ecological (a: left column) and genomic (b: right column) vulnerability indices

Access to new genomic data and high-throughput sequencing methods offers an opportunity to characterize intraspecific adaptive capacity in novel ways. Landscape genomics use associations between climate and genome (Capblancq, Després, et al., 2020; Rellstab et al., 2015) to identify adaptations that have shaped the spatial distribution of adaptive genetic variation in plants (Guerrero et al., 2018; Hancock et al., 2011; Manel et al., 2012; Sork, 2018). The broad principle is that, if certain genetic variants confer adaptation to environmental extremes, we expect their frequencies to change along the corresponding environmental gradients. If we can capture this signal in current genome–climate associations, we can then use it to predict genomic vulnerability under scenarios of change across the same environmental gradients assuming the space-for-time substitution approach (Rellstab et al., 2016, 2021; Waldvogel et al., 2020). One way these climate–genome associations can be used in this context is by contrasting the current versus future genomic composition change that would be required under future scenarios, assuming the climate–genome association should stay the same for the populations in order to remain adapted to their local environments. This has been called the risk of non-adaptedness (RONA; Aquino et al., 2022; Rellstab et al., 2016), risk of (mal)adaptation (Capblancq, Fitzpatrick, et al., 2020; Jordan et al., 2017) or genomic vulnerability (Bay & Harrigan, 2018; Wood et al., 2021). For example, Bay and Harrigan (2018) examined associations between genomes and climatic gradients across the range of yellow warblers and showed that populations that are declining correspond to those that would require the greatest genomic changes to match associated climate changes, which have occurred in the same time period. In this context, single nucleotide polymorphisms (SNPs) represent a great opportunity to scan large portions of a genome for small genomic changes that might be associated with different environmental gradients. Based on the relationship between candidate SNP variants and climate features at present, we can therefore make future projections of the amount of genetic change that would be required to keep pace with climate change (Rellstab et al., 2016; Figure 1). The broader the differences, the more the populations are expected to be genomically vulnerable.

In this study, we set out to quantify and map ecological and genomic vulnerability of native *Coffea canephora* populations under climate change, as defined above, using four general circulation models (GCMs) and two emission scenarios (representative concentration pathways [RCPs]). In a novel approach, we compared genomic and ecological vulnerability distributions. We applied this analysis to wild plants of *C. canephora* in its native range to answer the question: are populations in ecologically vulnerable regions also more genomically vulnerable? We show how mapping genomic adaptive potential with ecological considerations can foster a better understanding of how these different facets of species response to climate change interact spatially. Lastly, we discuss how our approach can guide agricultural and conservation decisions under climate change scenarios.

2 | MATERIALS AND METHODS

In this study, we developed a methodological framework to calculate, map and compare two indices of population vulnerability (Figure 1): ecological vulnerability and genomic vulnerability. The methodological details for the computation of each index are provided below.

2.1 | Sampling design and environmental data

Coffea canephora is a self-incompatible evergreen tree species which likely originates from the sub-equatorial lowland rainforests of Africa (Berthaud, 1986; Davis et al., 2006). The species is distributed in the understorey of evergreen and semi-deciduous tropical rainforests of the Guineo-Congolian region (Gomez et al., 2009). Wild populations of *C. canephora* are found as distant patches of few individuals, generally consisting of the parents and offspring scattered up to a few kilometres (Berthaud, 1986). Combining all known georeferenced data from seven herbaria and two living collections, we obtained a total of 492 carefully checked occurrence records (see Table S1) covering the entire range known for wild *C. canephora*. We used the 19 bioclimatic variables from WorldClim v1.4 (Hijmans et al., 2005), which represent mean and variability of temperature and precipitation (by season and annually) for a baseline period between 1960 and 1990, as well as under future climate change scenarios for 2050 (see below). Occurrence and environmental data sets were then resampled at the same resolution of 2.5 min, resulting in 227 occurrences which were subsequently used for modelling (Figure 1a step 1).

2.2 | Climatic suitability modelling

Occurrence records and climate data were used to model the current distribution using an ensemble forecasting approach (Araújo & New, 2007) based on three different statistical models (Figure 1a step 2). These models relate, through statistical relationships, the occurrence of the species of interest with the environmental gradients associated with them and are generally referred to as SDMs (Guisan & Thuiller, 2005). The final distribution model is therefore data driven. However, to better characterize the climatic envelope of the species, we provide some general information regarding the characteristics of occurrence sites in Supplementary Material S5.

Since some of the statistical models require background data, we randomly sampled 10,000 background sites within a 500-km buffer of known occurrences. We then weighted those background sites according to their environmental distance to the medians of all 19 environmental predictors at occurrence sites (using a Mahalanobis distance). Thus, sites which were environmentally more distant to conditions observed at occurrence sites had a greater chance to be selected as background in each iteration. These 10,000 background points were then subsampled to have twice as many pseudo-absences as there were presences

(i.e. 454 pseudo-absences when all occurrences are used). Both background selection and model calibration process were iterated 1000 times during the variable selection process and 100 times for prediction purposes. This process ensured that neither variable selection nor predictions are driven by one particular set of background points.

Bioclimatic variable selection was carried out using a forward stepwise selection procedure, based on maximizing the deviance of the generalized additive model (GAM, using the R library *mgcv*) and iterated 1000 times with a different set of pseudo-absences, similar to that implemented in Meynard et al. (2017). At the end of this procedure, we picked the climatic predictors that were chosen most often across iterations and were not intercorrelated, resulting in a list of five environmental predictors that were used for ensemble forecasting in the rest of the modelling effort.

To draw the distribution maps, we used three common statistical models: GAM (library *mgcv*; Wood, 2006), Boosted Regression Trees (BRT, library *gbm*; Elith et al., 2008) and Maximum Entropy (MAXENT, library *dismo*; Elith et al., 2011). Default settings for MAXENT were used, except that we forced it to use the same background data as for the other models. For each of these models, we produced 100 iterations using 80% of the occurrence data for calibration and prediction, and the other 20% of the data for calculating classification success. GAM and BRT were given weights to set equal influence to presence and background records. The final distribution map was then drawn as an across-model consensus based on mean predictions. The continuous suitability values were transformed into presence-absence predictions at the end using the threshold that maximized sensitivity and specificity (Liu et al., 2013). Model presence-absence classification success was assessed using the true skill statistic (TSS; Allouche et al., 2006) and the area under the receiver operator curve (AUC; Fielding & Bell, 1997).

2.3 | Environmental change over time: ecological vulnerability

The distribution of climatic suitability for *C. canephora* (Figure 1a step 3) was projected for 2050 using the same iteration and consensus strategy described above (100 iterations with a different subset of background sites for each iteration) and considering four global climate models (GCMs) widely used in global climate change studies in this region, namely MIROC-ESM, CCSM4, IPSL-CM5A-LR and NorESM1-M (Agyekum et al., 2018; Aloysius et al., 2016; Raju & Kumar, 2020). These four GCMs are complementary to each other, with opposite biases which are expected to even out using the ensemble forecasting. We considered two future scenarios of CO₂ emissions (RCPs): (i) the intermediate RCP 4.5, leading to a temperature increase of 1.8°C which stabilizes before 2100 due to a decrease in greenhouse gas emission; (ii) the more extreme RCP 8.5, leading to a 3.7°C temperature increase until 2100 with no stabilization. Considering the latest projections from IPCC (2018), RCP 4.5 represents a plausible pathway for climate change and RCP 8.5

represents a worst-case climate change scenario on *C. canephora* genomic and ecological vulnerability. For each RCP scenario, a consensus map was drawn as the mean of all predictions (over the GCMs, the statistical models and their iterations).

We computed the ecological vulnerability V_E (Figure 1a step 4) for each site within the species distribution range as the difference between present (S_{present}) and future (S_{2050}) continuous climatic suitability values:

$$V_E = S_{\text{present}} - S_{2050}$$

Positive V_E values therefore indicate that climatic suitability will be lower in 2050 than at present.

2.4 | SNP genotyping and bioinformatic analyses

We used 50 genomes representing the wild *C. canephora* diversity across its native range (Tournebize, 2017; Figure 1b step 1, Table S1). Three genomes of closely related Central African coffee species were also included (Table S1): *C. congensis* (Congo-Brazzaville), *C. liberica* ssp. *liberica* (Ivory Coast) and *C. liberica* ssp. *dewevrei* (Central African Republic; Charr et al., 2020). Illumina raw sequence data were processed through a bioinformatic pipeline generated with TOGGLE (Monat et al., 2015). The quality of the raw sequencing reads was checked using FastQC. Low-quality bases from 5' and 3' read ends were trimmed ($Q \geq 20$) and adapters were removed given a minimum overlap length of two bases, using *cutadapt* 1.8 (Martin, 2011). Filtered and trimmed reads were aligned on the assembly of *C. canephora* (accession DH 200-94 v. 1.0; ACGC, 2018) using *BWA* 0.7.2 *aln/sampe*, with standard settings (Li & Durbin, 2009). Aligned reads from the resulting SAM files were locally realigned using *GATK* 3.3 *IndelRealigner* (McKenna et al., 2010). PCR duplicates were removed using *PicardTools* 1.83 *MarkDuplicates*. Only properly aligned read pairs with Phred-scaled mapping quality above 5 were retained, using *SAMTools* 1.1 (Li et al., 2009). A maximum likelihood SNP calling approach based on *de novo* haplotype assembly was performed with *GATK* 3.3 *HaplotypeCaller*. Average Phred-scaled base quality below 10 and Phred-scaled mapping quality below 20 were excluded during this process.

For population genomic analyses relying on the genotype calls, we applied additional filters to retain only high-quality biallelic SNPs (Table S2). The retained SNPs were processed with *PLINK* 1.90b4 to keep only SNPs in approximate linkage equilibrium, based on the pairwise correlation (r^2) between the SNP genotype counts in windows of 50 kb sliding by 10 kb shift (option *indep-pairwise*). SNPs were considered correlated when $r^2 > 0.2$.

2.5 | Population structure and diversity

To investigate the genetic structure among the sampled individuals, we used a clustering strategy to estimate the assignment of each of the 50 samples to putative ancestral genetic groups. We used the

unsupervised clustering algorithm sNMF (Frichot et al., 2014) on the SNP data set for a number of groups, K , ranging from 1 to 12, with 10 replicates per value of K and with default mask and regularization parameters. The most likely number of clusters was chosen to minimize the cross-entropy criterion. Individuals were assigned to a specific genetic group if their corresponding ancestry coefficient exceeded 0.7 on the unit scale, or were otherwise left as unassigned. These sNMF genetic groups were used for further population-based genetic analyses.

Linkage disequilibrium (the non-random association of alleles at different positions) is an informative summary statistic since its rate of decay as a function of the distance between loci depends on the size of the population. As such, by characterizing the level of LD along the genome, we can estimate the effective population size, which is the primary predictor of genetic diversity. For instance, a steeper LD curve could indicate a larger population size. We estimated the decay of linkage disequilibrium along the genome by calculating the squared correlation coefficients (r^2) against the physical distance between SNPs (*PopLDdecay*; Zhang et al., 2019). We estimated the population recombination rate $\rho = 4 \cdot N_e \cdot r$ (with r the probability of crossing-over between two adjacent sites per generation) according to a model of drift-recombination equilibrium (Hill & Weir, 1988), by relying on a non-linear regression of r^2 on the physical distance d between sites (in base pairs):

$$r^2(d) = \frac{10 + \rho \cdot d}{(2 + \rho \cdot d) \cdot (11 + \rho \cdot d)} \cdot \left(1 + \frac{(3 + \rho \cdot d) \cdot (12 + 12\rho \cdot d + \rho^2 \cdot d^2)}{n \cdot (2 + \rho \cdot d) \cdot (11 + \rho \cdot d)} \right),$$

where n is the number of sequences.

In addition, we calculated several common population genetic statistics to get a better understanding of the demographic history of the species. In order to mitigate uncertainty on heterozygous calls due to local low sequencing coverage, we estimated these statistics using ANGSD 0.918 (Korneliussen et al., 2014). We used for this analysis a GATK sequencing error model and considered only sites with a Phred-scaled sequencing quality above 30 and Pred-scaled mapping quality above 25. Using these thresholds, we calculated the observed heterozygosity of each sample (i.e. the proportion of heterozygous sites). We also calculated for 10 kb-long sliding windows of 5 kb sliding step: the pairwise nucleotide diversity θ_π (Nei, 1987) and θ_w (Watterson, 1975); Tajima's D (Tajima, 1989), Fay and Wu's H (Fay & Wu, 2000) and Zeng's E statistic (Zeng, 2006).

2.6 | Detecting loci associated with climatic variations

To ultimately identify a set of loci putatively associated with climatic variations, and thus putatively involved in local adaptation, we first scanned individual genomes to detect SNPs potentially under selection, that is: candidate adaptive loci (Figure 1b step 2). We highlight this process below.

2.6.1 | Outlier SNP detection

Outlier SNPs were detected using a multi-statistical Fisher score, F_{SC} (Deschamps et al., 2016; Patin et al., 2017) that combines the scores of different neutrality outlier methods. In our case, we used six different approaches: four within-population neutrality outlier statistics based on the distortion of the local site frequency spectra and applied to each of the identified genetic groups: (1) Tajima's D (Tajima, 1989), (2) Fay and Wu's H statistic (Fay & Wu, 2000), (3) Zeng's E statistic (Zeng, 2006) and (4) the likelihood of recent selective sweeps using the SWEED software (Pavlidis et al., 2013); and two between-population statistics based on the local excess of genetic differentiation compared to the average neutral expectation: (5) F_{ST} (Weir & Cockerham, 1984) and (6) an outlier z-score approach, *PCAdapt* (Duforet-Frebourg et al., 2016).

We detected recent selective sweeps using SWEED, an approach which scans genetic variations across samples along the genome to identify regions where the allele frequency spectrum is strongly distorted, which is indicative of natural selection. For this analysis, the derived allele of each SNP was first defined based on the genotypes of two related outgroup species (*C. congensis* and *C. liberica* ssp. *dewevrei*). When the outgroup genotypes were not homozygous for the same allele, the ancestral/derived states of the SNP were considered ambiguous. The analysis was performed considering 5000 estimation points per chromosome and monomorphic sites.

To measure the genetic differentiation between populations, we used the pairwise F_{ST} statistics, computed in 10 kb windows sliding by 5 kb using VCFtools 0.1.13 (Danecek et al., 2011). For groupwise detection of selection, we considered the pairwise F_{ST} measures between the focal group and each of the four others. A disadvantage of F_{ST} is that it requires to define discrete populations. When a continuous population structure (e.g. isolation-by-distance) is observed, other approaches can be more advantageous. In this sense, *PCAdapt* is based on principal component analysis and does not cluster samples into populations. For the *PCAdapt*, we retained five eigenvectors based on the eigenvalue decay curve ($K = 5$).

To integrate the signals of selection carried by each summary statistics in a robust way, we summed the genome-wide ranks of all six statistics at the SNP level into a Fisher's combined score, referred to as $F_{SC,g}$ (Deschamps et al., 2016). To downscale the genomic region-based statistics at the site level, we projected the values of the window statistics to the nearest SNPs of the *PCAdapt* SNP dataset. For each statistic and each genetic group, the highest rank was assigned to the values departing most from neutrality. The $F_{SC,g}$ score was calculated for each SNP and each genetic group g as $F_{SC,g} = \sum_{i=1}^T -\log_{10}\left(\frac{R_{i,g}}{N}\right)$, where $R_{i,g}$ is the rank of the SNP for statistic i in group g , N is the genome-wide and species-wide number of SNPs and T is the total number of statistics. Outlier SNPs were defined as those having a $F_{SC,g}$ at the highest 1% tail of the genome-wide $F_{SC,g}$. This analysis was carried out for each genetic group. Putatively adaptive SNPs were defined at the species-wide level as the intersection of group-specific outlier SNPs.

2.6.2 | Genetic–environment relationship

To evaluate the role of climate in driving selection for the putatively adaptive SNPs, we performed a genome–environment association (GEA) study using LFMM 2.0 (Caye et al., 2019). We considered only SNPs having a minimum allele frequency of 10%. We also defined a random set of 20,000 background SNPs and analysed them together with the putatively adaptive SNPs. Missing genotypes in the SNP data set were imputed according to the ancestry coefficient of individuals (R package, LEA Frichot & François, 2015). For the GEA analysis, genotype and climate variables were standardized. For each of the 19 bioclimatic variables, we performed an independent GEA using ridge functions and controlled the effect of population structure by considering $K = 5$ latent factors for the five groups with $n > 2$ sample sizes. We calculated the significance of the association using the genomic inflation factor and controlled for multiple testing across the SNPs by adjusting the p -values of the GEA into FDR-corrected q -values. We considered a level of false discovery rate (FDR) of 5%. For each bioclimatic variable, we then calculated the odds ratio in favour of an excess of bioclimatic association for candidate SNPs relatively to background SNPs and tested the enrichment significance using a Fisher's exact ratio test. The p -values of the enrichment across the bioclimatic variables were adjusted for multiple testing using the conservative Bonferroni correction.

2.6.3 | Gene ontology enrichment

We conducted a gene ontology (GO) enrichment analysis to determine whether the candidate SNPs for selection were associated with specific biological functions more significantly than expected by chance. First, we converted the coordinates of the published *C. canephora* gene models (Denoeud et al., 2014) to the present reference assembly using FLO 1.0 pipeline with default settings. Then, we actualized the GO annotation of *C. canephora* gene models using a BLASTx of gene sequences onto the *Arabidopsis thaliana* gene database, retaining only the most significant matches. GO-associated terms were retrieved from the UniProtKB protein accession database 1.1 (2017-05-08). We tested the GO enrichment with Gowinda (Kofler & Schlotterer, 2012) for candidate SNPs specific to each group and for candidate SNPs at the species-wide scale. We performed one million simulations to calculate the FDR-corrected p -value of enrichment, under the *gene* mode.

2.7 | Genomic vulnerability under future climate conditions

We assessed the genomic vulnerability as the average change in the genotype composition of candidate SNPs required to match the future climate conditions, modifying the RONA introduced in Rellstab et al. (2016) at population level to work at the individual level. First,

we trained the GEA model for the whole SNP dataset using the R package LEA (Frichot & François, 2015). We used as predictors the five bioclimatic variables that were selected as the most explanatory and the least collinear in the SDM. We next predicted the genotype composition for the candidate SNPs in 2050. We calculated the individual genomic vulnerability indices as the average dissimilarity between present and future genotypes: for each individual i , $V_i = \frac{1}{N} \cdot \sum_{j=1}^N |G_{ij}(2050) - G_{ij}(\text{Present})|$, where N is the number of climate-associated SNPs and $G_{ij}(2050)$ is the predicted standardized genotype in 2050 of individual i at SNP j . We then averaged the V_i indices over the four GCMs. This procedure allowed us to quantify the amount of genetic divergence that would be required for individuals to have their current level of adaptation match the different climate scenarios considered in 2050.

3 | RESULTS

3.1 | Current *Coffea canephora* modelled distribution

Coffea canephora is found under tropical climates at relatively low altitude. Samples used in the ecological and genomic vulnerability analyses were distributed in similar environmental ranges although climatic characteristics varied among genetic groups at present (see details in Supplementary Material S5). To model the current *C. canephora* distribution, five explanatory bioclimatic variables were retained as those maximizing the deviance explained by GAMs (Figure SB in Supplementary Material S5). Three are precipitation-related variables: BIO18 (precipitation of the warmest quarter, selected across 100% of the runs), BIO15 (precipitation seasonality, 62% of the runs) and BIO12 (annual precipitation, 58% of the runs). Two are temperature-related variables: BIO10 (mean temperature of the warmest quarter, 44% of the runs) and BIO2 (mean diurnal temperature range, 55% of the runs). The estimated extent of the *C. canephora* climatic suitability fell within the known natural species range (Figure 2a). The SDMs showed good discrimination between predicted presences and absences, with TSS = 0.60 ± 0.07 and AUC = 0.85 ± 0.06 . The estimated distribution of suitable areas was continuous across the Upper and Lower Guinean and the Congolese ecoregions, reaching Uganda and Tanzania in the east. Disconnected pockets of suitable areas were found in Angola (near the Kumbira Forest Reserve eastward of Porto Amboim) and in south-western Ethiopia. The current range was estimated to be around 4 million km².

3.2 | *Coffea canephora* ecological vulnerability to climate change by 2050

Based on the modelled distribution at present, we predicted the distribution of the suitable habitats in 2050 according to four

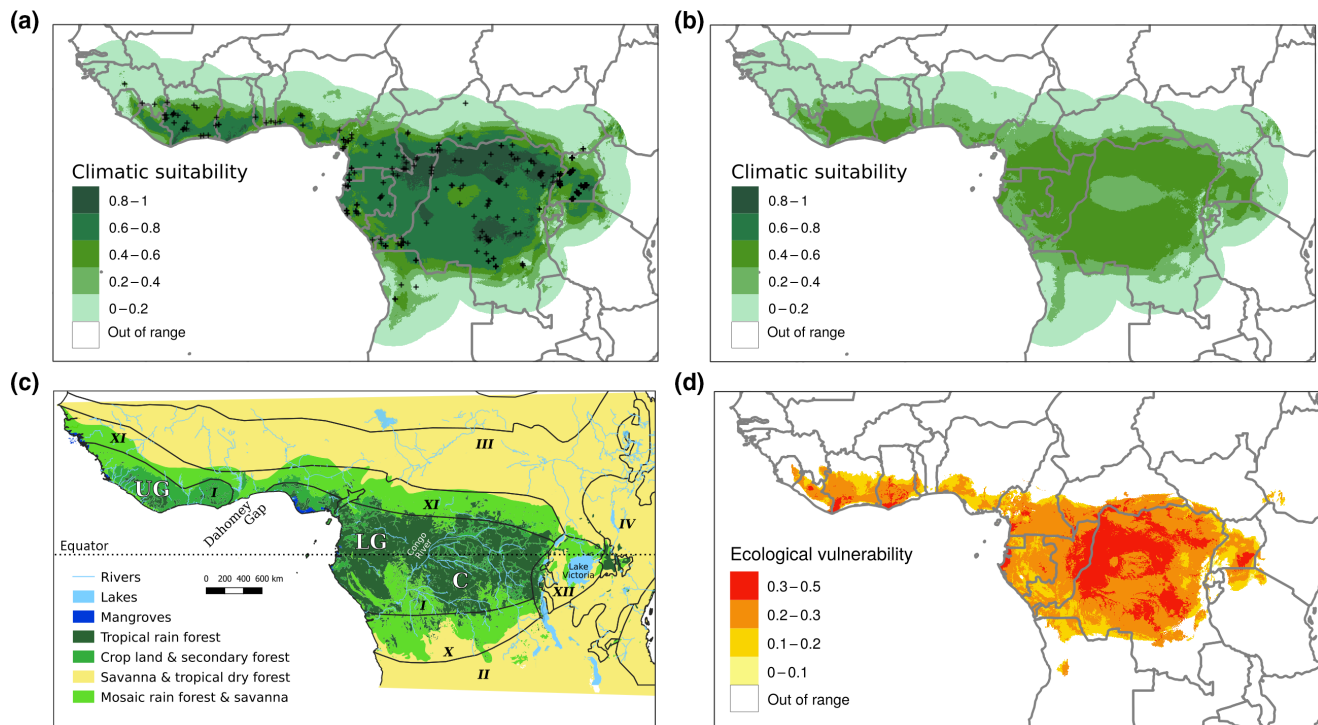


FIGURE 2 Distribution of climatic suitability for *Coffea canephora* (a) at present and (b) in 2050 under the scenario representative concentration pathway (RCP) 4.5. (c) Major modern vegetation types across tropical Africa (roman numerals) according to Guillaumet et al. (2009), main phytocorion limits are shown according to White (1983), delimitation I corresponds to the Guineo-Congolian regional centre of endemism; C, Congolia; LG, Lower Guinea; UG, Upper Guinea. (d) Spatial distribution of the ecological vulnerability in 2050 under RCP 4.5. Areas that were estimated to be unsuitable both at present and in 2050 were masked out

global climate models and two RCP scenarios, 4.5 (Figure 2b) and 8.5 (Figure S1). Overall, the area of climatically suitable habitats was predicted to retract in 2050 compared to present with a 38.6% to 52.0% reduction across the four GCMs for RCP 4.5 and a 45.7% to 56.0% reduction for RCP 8.5. Although the range is predicted to expand and contract in different regions, range expansion (2,698 km²) was more than 600 times smaller than range contraction areas (1,775,506 km²) for RCP 4.5 and more than 1300 times smaller for RCP 8.5 (gain area: 1,447 km²; loss area: 1,956,697 km²). The range-wide averaged ecological vulnerability V_E ranged from 0.139 (RCP 4.5) to 0.142 (RCP 8.5) and showed heterogeneity within the species range (Figure 2d). The strongest vulnerability was found at the centre of the distribution, along lakes (Uganda), rivers (Democratic Republic of Congo) or coasts (Cameroon and Gabon) (Figure 2c,d). We note that rivers are also areas with low population density and fecundity at present. SDMs predicted an increased suitability in 2050 along the margins in both the northern and southern hemispheres (Figure 2b). Considering the RCP scenarios, the species range was predicted to be severely disrupted by more than a thousand kilometres between Upper Guinea, on the one hand, and Lower Guinea and Congolia on the other hand. The Dahomey Gap, which is known to be unfavourable for the species at present (Gomez et al., 2009), also remained unsuitable in 2050. Suitable areas that were found in Zoka (northern Uganda) at present were predicted to become unsuitable by 2050.

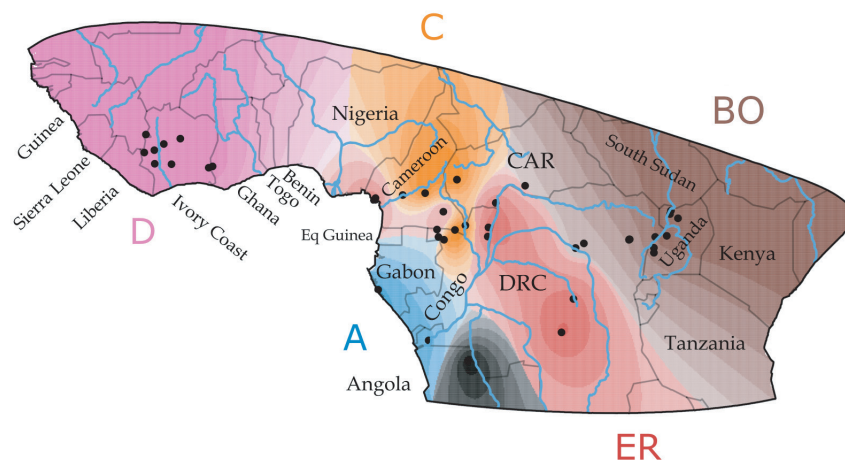
3.3 | Genetic structure and diversity

Using sNMF, we detected seven genetic groups (Figure 3), which were consistent with previous clusters identified using SSR markers (Cubry et al., 2013; Gomez et al., 2009; Kiwuka et al., 2021) as well as SNP array (Mérot-L'Anthoene et al., 2019). Note however that our analysis merged the previously separated B and O groups (using higher sample sizes in Gomez et al., 2009). The identified genetic groups were well differentiated, $F_{ST} = 0.22 \pm 0.11$ [min-max: 0.11–0.30] (Figure 3). Based on the nucleotide diversity θ_π and θ_w statistics, the highest genetic diversity was found in group Congo-Brazza (A) followed by the Congolese groups ER, C and BO. The nucleotide diversity in the Upper Guinean group (D) was on average 1.3-fold lower than in other genetic groups.

3.4 | Detecting loci candidate to selection

Genetic statistics calculated by window along the genome, like Tajima's D or Fay's and Wu's H , inform about genomic regions putatively under selection. Yet, they can also be affected by more general demographic processes, like population expansion or contraction, which tend to affect the genome as a whole. All populations had negative Tajima's D at the whole genome scale, suggesting a global excess of rare alleles and therefore a possible signature of recent population expansion. The lowest Tajima's D was found in

FIGURE 3 Genetic diversity indices estimated for the five major genetic groups A, C, D, BO and ER



	A	C	D	BO	ER	Mean $\pm$ SD
Sample size	6	6	9	9	11	
θ_{π}^1	2.3	2.0	1.5	1.9	2.0	1.9 $\pm$ 0.29
θ_w^1	2.4	2.1	1.6	2.0	2.4	2.1 $\pm$ 0.30
H_o^1	4.5	5.0	3.4	4.1	4.9	4.4 $\pm$ 0.6
Tajima's <i>D</i>	-0.24	-0.11	-0.47	-0.31	-0.58	-0.3 $\pm$ 0.2
Fay & Wu's <i>H</i>	0.05	-0.04	-0.16	-0.04	-0.08	-0.1 $\pm$ 0.1
LD decay^{1,2}	21.9	14.7	16.4	17.6	16.7	17.5 $\pm$ 2.7
ρ^1	0.11	0.10	0.14	0.12	0.13	0.12 $\pm$ 0.02
θ_w/ρ ($= \mu/r$)	22	21	12	17	18	18 $\pm$ 4

¹ Values are given per kilobase ($\times 10^{-3}$ to scale in bp^{-1}).

² Distance at which $r^2 = 0.5r_{\text{max}}^2$.

θ_{π} : pairwise nucleotide diversity.

θ_w : Watterson's estimator of the population mutation rate.

H_o : observed heterozygosity (mean proportion of heterozygous genotypes in one individual across the genome averaged over individuals).

ρ : the population recombination rate as estimated from a model of drift-recombination equilibrium based on the pairwise genotype correlations (Hill & Weir, 1988).

the Congolese group ER. The Fay and Wu's mean H statistic varied around zero from positive for the A group to strongly negative for the D group. The negative D and positive H values for group A suggest population expansion. For the other groups, the negative values of both D and H rather suggest the excess of high frequency-derived variants which could be associated with positive selection playing at large scale given the extent of linkage disequilibrium (LD). Indeed, LD was found to decay to half its maximum level at 17.5 ± 2.7 kb on average (min-max: 14.7–21.9 kb). These results may suggest the impact of recent positive selection on the pattern of genome-wide diversity in the C, D, ER and BO groups.

We next scanned individual genomes to detect SNPs that have potentially been under selection. A total of 165 SNPs were detected in all five genetic groups using our F_{SC} scores. These SNPs represented candidates to selection at the species scale. We identified a fourfold enrichment of these SNPs in genic compared to intergenic regions, as compared with background SNPs (Fisher's exact ratio test: odds ratio = 3.7, $p = 1 \times 10^{-14}$). Among the 165 candidate SNPs,

87 overlapped with annotated genes (32 genes in total, representing a mean of 2.7 SNPs per gene). We did not detect any gene function that was significantly more associated with candidate SNPs (i.e. which could be associated with local adaptation) compared to the background genome (at FDR-corrected p -value $< 5\%$).

We next investigated the association of the allele frequencies at these 165 SNPs with the climatic gradients across the species range. A total of 76 out of 165 SNPs had a MAF above 10% and were subsequently analysed using LFMM (Caye et al., 2019) in order to correlate them with climatic variables. We found that 51% (39 out of 76) of the SNPs were significantly associated with at least one of the bioclimatic variables (FDR-corrected p -value $< 5\%$). Over the 19 tested bioclimatic variables, 16 were significantly more associated with candidate SNPs than expected by random background SNPs (Table 1). The most associated bioclimatic variables were isothermality (BIO3), temperature seasonality (BIO4) and those related to the precipitation of the driest periods (BIO14 and BIO17). While BIO3, BIO14 and BIO17 were rather collinear ($|r| > 0.7$), there is no significant

TABLE 1 Functional enrichment in candidate single nucleotide polymorphisms (SNP)–environment associations. The Fisher's exact ratio tests measure how significant is the SNP–environment association at candidate SNPs compared to the background SNPs

Bioclimatic variable	Description	$-\log_{10}(p)$	Odds ratio	Number of coding candidate SNPs	Number of non-coding candidate SNPs	Total number of candidate SNPs
BIO3	Isothermality	31.1	45.8	17	10	27
BIO4	Temperature seasonality	30.6	43.7	17	10	27
BIO17	Precipitation of driest quarter	22.7	39.7	13	7	20
BIO14	Precipitation of driest month	22.5	38.6	13	7	20
BIO15	Precipitation seasonality	21.7	35.0	13	7	20
BIO13	Precipitation of wettest month	21.2	37.1	13	6	19
BIO2	Mean diurnal range	20.7	40.2	13	5	18
BIO8	Mean temperature of wettest quarter	15.4	28.0	8	7	15
BIO5	Max temperature of warmest month	14.3	20.4	10	6	16
BIO18	Precipitation of warmest quarter	11.4	26.6	6	5	11
BIO19	Precipitation of coldest quarter	10.0	23.9	6	4	10
BIO9	Mean temperature of driest quarter	9.4	20.2	6	4	10
BIO11	Mean temperature of coldest quarter	9.3	19.8	6	4	10
BIO1	Annual mean temperature	5.7	13.4	4	3	7
BIO10	Mean temperature of warmest quarter	5.6	12.9	4	3	7
BIO12	Annual precipitation	0.0	0.0	0	0	0
BIO16	Precipitation of wettest quarter	0.0	0.0	0	0	0
BIO6	Min temperature of coldest month	0.0	0.0	0	0	0
BIO7	Temperature annual range	0.0	0.0	0	0	0

relationship between the collinearity clusters in bioclimatic variables and the significance of their SNP association (Kruskal–Wallis rank-sum test: $p = 0.25$). The importance of bioclimatic variables in the SDM did not correlate with the significance of their association with candidate SNPs (Spearman's $\rho = 0.29$, $p = 0.23$).

A total of 20 candidate SNPs were associated with these four bioclimatic variables (BIO3, 4, 14 and 17). Based on the genome annotation (Denoeud et al., 2014), these 20 SNPs were located in genes involved in a range of functions including abscisic acid-mediated signalling in response to stress (CPK7, CPK8 genes), ethylene signalling (HMA5, RAN1), circadian clock (UBP12, UB13), chromatin remodelling (BRM), general response to drought stress (NEK5, NEK6) and others with unknown functions in plants (RHBDF1, RHBDF2).

3.5 | Genomic vulnerability across *Coffea canephora* distribution

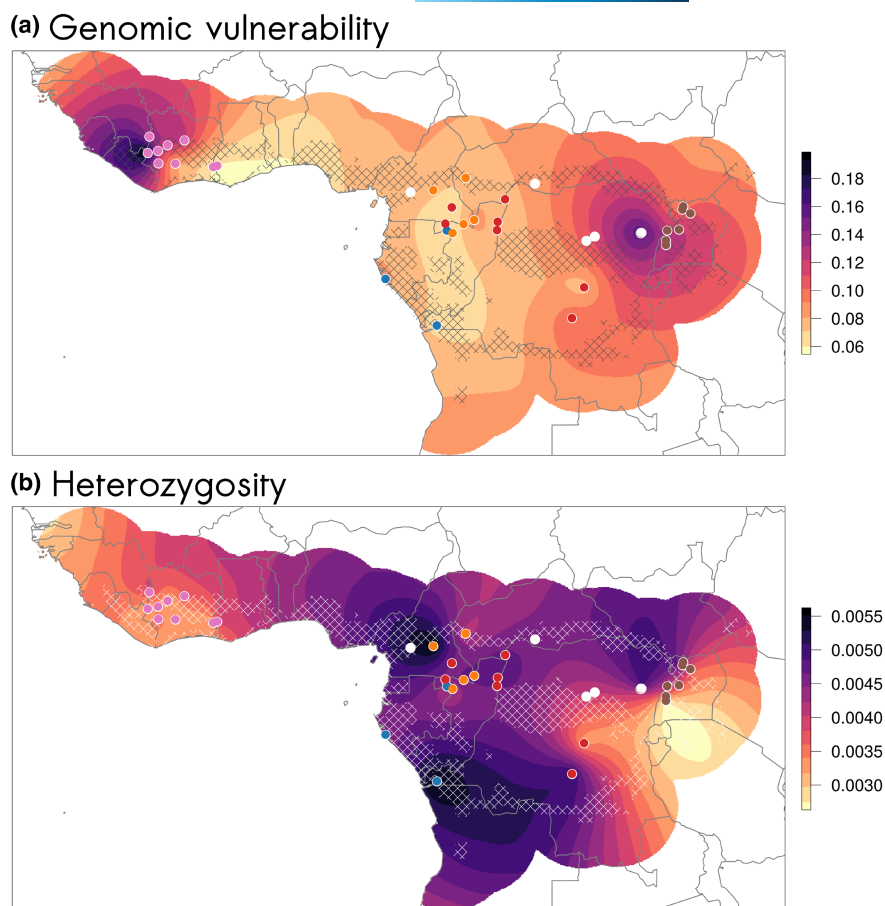
The genomic vulnerability, V_G , represents the magnitude of the shift in allelic composition required for genotypes to keep pace with change in climatic conditions between present and 2050. Here,

under RCP 4.5, the genomic vulnerability displayed large longitudinal variation across the present distribution range (Figure 4a). Regions with the highest genomic vulnerability extended over the westernmost and easternmost fringes of the distribution range (indicated in purple in Figure 4a), with a genomic vulnerability above the country-average ($V_G = 0.09$) in Guinea (0.14), the DR Congo (0.12), Ivory Coast (0.12) and Uganda (0.12). The lowest genomic vulnerabilities extended along the Atlantic littoral, from Ghana (0.06) to Gabon (0.08; yellow colour, Figure 4a). The most vulnerable genetic clusters were estimated to be the D (0.12) and the merged BO group (0.12). Comparable results were obtained when considering the scenario RCP 8.5 (Figure S2).

3.6 | Ecological and genomic vulnerabilities

Ecological vulnerability was not correlated with genomic vulnerability (Pearson's $r = -0.003$, $p = 0.98$). One fifth of the 34 studied samples had both low genomic and ecological vulnerabilities compared to the median values at the species scale (black in Figure 5a). One fifth of the samples had both high genomic and ecological

FIGURE 4 Genomic vulnerability of *Coffea canephora*. (a) Spatial Gaussian interpolation of the genomic vulnerability. (b) Spatial Gaussian interpolation of the observed individual heterozygosity (H_o). Hatched lines represent the estimated area of suitable habitats at present that are predicted to become unsuitable in 2050 under the representative concentration pathway (RCP) 4.5



vulnerabilities (red in Figure 5a). But most of the samples had low genomic vulnerability and high ecological vulnerability (yellow in Figure 5a) or low ecological vulnerability and high genomic vulnerability (brown in Figure 5a, located at the eastern and western edges of the distribution range). For those last ones, local habitats are estimated to become unsuitable by 2050 (triangles in Figure 5a,b). Samples from the north-eastern part of the distribution had overall higher genomic vulnerability than the species median albeit lower ecological vulnerability. Samples in areas estimated unsuitable by 2050 (outside the grey areas in Figure 5b) were 23% more genomically vulnerable than samples situated in areas estimated as suitable in 2050 (Figure 5b). However, the test is only marginally significant (Wilcoxon–Mann–Whitney test: $p = 0.07$).

Observed heterozygosity (Figure 4b) was found to be negatively correlated with genomic vulnerability (Pearson's $r = -0.39$, $p = 0.024$), suggesting that heterozygosity was actually lower for individuals that are expected to be most genomically vulnerable to future climate change. We found no correlation between H_o and ecological vulnerability. The heterozygosity of samples laying in areas that are estimated to become unsuitable by 2050 was not significantly different from the heterozygosity of samples in areas estimated to remain suitable (Wilcoxon–Mann–Whitney test: $p = 0.29$).

4 | DISCUSSION

To our knowledge, our comparative approach is the first to contrast two continuous indices of ecological and genomic vulnerability under climate change scenarios throughout the large native range of a commercially important crop species. Recent interest around intraspecific variability in response to climate gradients has resulted in a few studies that investigated genomic vulnerability (Dauphin et al., 2021; Nielsen et al., 2021; Wood et al., 2021). However, these studies did not take into account genomic and ecological vulnerability simultaneously. To the best of our knowledge, the closest study to this end was Razgour et al. (2019) who used SDMs to project potential shifts in distributions for a subset of populations that were identified as pre-adapted to different parts of a humidity–temperature gradient. While these approaches represent a great advance since they assess loci or genes that are potentially directly associated with gradients affected by climate change (rather than neutral genes), they still assume that the subgroups that are modelled as a unit are homogeneous with respect to their environmental response, and that the environmental niche will be perfectly conserved under climate change conditions (Bellard et al., 2012).

Here we adopted a different perspective. On the one hand, SDMs were used to measure what we called ecological vulnerability, reflected by the intersection between how much a given region

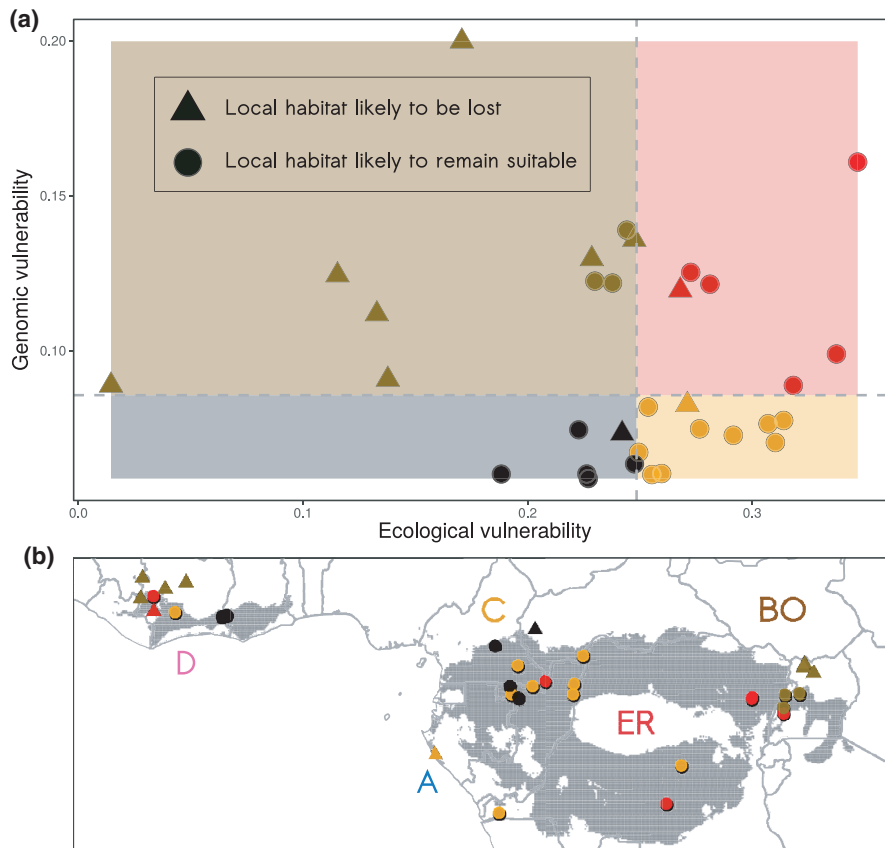


FIGURE 5 (a) Relationship between the genomic vulnerability and the ecological vulnerability indices. The panel is divided into four quarters with distinctive colours, in respect to the median of the genomic and ecological vulnerability indices. Point shapes represent whether the sample is located in an area that will be either unsuitable (triangle) or suitable (circle) by 2050 under the representative concentration pathway (RCP) 4.5. Locations where habitats are expected to become unsuitable (triangle) and which have low ecological vulnerability are locations where the habitat suitability at present was already lower than for other locations. (b) Spatial projection of the samples used to assess the genomic and ecological vulnerability. The greyed area represents the distribution of suitable habitats by 2050 under RCP 4.5

suitability will change under different climate change scenarios, and how this species is likely to respond to those changes. On the other hand, we used current GEAs to calculate and map the genomic vulnerability quantifying the level of genotypic change expected under future climate conditions for GEAs to remain similar to today. We discuss below the implications of each of these aspects of vulnerability and their intersection.

4.1 | *Coffea canephora* suitable habitat and ecological vulnerability to climate change

Afrotropical rainforests, which are highly endangered, represent the second largest continuous tropical rainforest block on earth after the Amazon basin (Malhi et al., 2013). While this lowland rainforest region mainly consists of old and widespread taxa (Dagallier et al., 2020), the *C. canephora* lineage has diverged more recently, after which it further dispersed into the tropical Africa, representing nowadays the largest natural distribution among the *Coffea* species (Davis et al., 2006; Gomez et al., 2009). The overall distribution of *C. canephora* coincides with the distribution of the African tropical rainforests (Guillaumet et al., 2009; White, 1983; Figure 2) and mainly overlaps with the Guineo-Congolian bioregion as defined by Droissart et al. (2018). While our modelled *C. canephora* distribution at present agrees with the study of Bunn et al. (2015), our projection is more continuous in Congolia and in Lower Guinea and includes potential distribution on the coast of Nigeria.

Major determinants of the current distribution are related to precipitation (e.g. precipitation of the warmest quarter and precipitation seasonality). This suggests that the species may present a strong physiological sensitivity to water balance, a known phenomenon among tropical tree species (Engelbrecht et al., 2007). Reproductive phenology of *Coffea* species is also highly dependent on rainfall seasonality (Gomez et al., 2016). Variables related to water stress, such as dry or warm-season precipitation levels, are also related to the distribution of global humid tropical forests (Zelazowski et al., 2011). A steady decline in rainfall has already been observed since 1985 in the Congo Basin (Chambers & Roberts, 2014; Zhou et al., 2014), and drought events are expected to become more frequent and severe in the 21st century (Alexander et al., 2009), in particular in West Africa and in the northern part of the Congo Basin (Dai, 2012). Changes in precipitation may therefore represent a significant threat to *C. canephora* populations under climate change.

We revealed a severe overall potential reduction in suitability for *C. canephora*, with a future species range that is predicted to be about two times smaller in 2050. However, the distribution of such change is heterogeneous. For example, a large extent of suitable habitats was predicted to become lost by 2050 in the south-western part of the Congo Basin, in agreement with Bunn et al. (2015) for *C. canephora* and Réjou-Méchain et al. (2021) who considered the vulnerability of central African plant communities. These contractions can be explained by intensified dry seasons in the western Congo Basin. However, this region also harbours heavy cloud cover during the dry season, which could facilitate the persistence of tropical rainforest

patches (Zelazowski et al., 2011) and possibly the persistence of *C. canephora*. Overall, the total area of suitable habitats is predicted to retract up to 52% and 56% by 2050 under RCP 4.5 and RCP 8.5 scenarios respectively (Figure 2b; Figure S1).

Meanwhile, we also predicted a few areas of range expansion, although these represent less than a third of the area predicted to be lost. These range expansions are located in specific areas such as Rwanda, Burundi and western Kenya (where the species is not occurring at present) on the eastern fringe of the species distribution, being in accordance with Bunn et al. (2015). Likewise, the opportunity of rainforest expansion was predicted to occur mainly outside the West and Central African core of distribution, at the margins of the current rainforest distribution, such as in the East African forests close to the border of DR Congo (Malhi et al., 2013; Zelazowski et al., 2011).

4.2 | Signature of local adaptation to drought and rainfall seasonality

Although a single species cannot be taken as a general model for the evolution of a whole ecosystem (Helmstetter et al., 2020), it can give us some important insights into the potential of populations to persist and adapt to climate change. Our data allowed us to confirm the species' population structure described in previous published work (Cubry et al., 2008; Gomez et al., 2009; Kiwuka et al., 2021; Mérot-L'Anthoene et al., 2019) and to assess the signals of selection and local adaptation at the genome-wide scale. Most studies which aim to detect signatures of natural selection use single or few independent statistics. However, each statistic has its own limitations and uncertainties, leading to variable predictions of natural selection along the genome. As with ensemble forecasting which integrates multiple SDM algorithms to overcome their variability and specific biases, we implemented a robust Fisher score F_{SC} (Deschamps et al., 2016; Patin et al., 2017), which integrates multiple genetic statistics sensitive to natural selection into a consensus measure quantifying the likelihood of selection acting at particular sites of the genome. We identified signals of genetic association with two rainfall-related variables, suggesting potential pre-adaptation to future climate change which could buffer the impact of precipitation extremes such as more frequent extreme drought episodes (Alberto et al., 2013). These results are consistent with other analyses at the global scale, where levels of rainfall were also found to be one of the strongest pressures of selection across species and world regions (Siepielski et al., 2017). Detecting putative adaptations to variation in water availability was not expected for a tropical rainforest species, since tropical plant species tend to show lower resilience to drought compared to other ecosystems worldwide (Schwalm et al., 2017). Indeed, among other hypotheses, the lower frequency of past drought events in this ecosystem could have led to fewer adaptations to cope with fluctuations in water availability (Engelbrecht et al., 2007).

By scanning whole genomes for signatures of adaptive potential across the native range of the species, we pinpointed genetic

regions that are potentially associated with adaptive traits. Although no significant physiological nor ecological functions were found significantly more associated with the genomic regions candidate to selection (compared to the rest of the genome), the genes associated with a potential local adaptation are involved in multiple biological processes, among which is the response to biotic and abiotic stress (CPK7 and CPK8 genes: in abscisic acid-mediated signalling in response to stress; HMA5 and RAN1: in ethylene signalling; or NEK5 and NEK6: in general response to drought stress), that require further functional characterization to confirm their potential to increase resistance to drought. For instance, we identified two SNPs in the CPK7 and CPK8 genes as well as two SNPs in the NEK5 and NEK6 genes, which are strong candidates of selection based on our population genetic analyses, as well as significantly associated with environmental (BIO3, 4, 14 and 17) gradients, supporting their putative role in local adaptation.

4.3 | Mismatch between ecological and genomic vulnerabilities

Assessing ecological and intraspecific genomic vulnerabilities simultaneously allows us to tackle the question: are populations in ecologically vulnerable regions more genomically vulnerable? Indeed, we could expect that regions with a high ecological vulnerability (i.e. impacted by a severe predicted habitat loss in the future) are also regions where genomic vulnerability would be the highest if the genetic makeup is at equilibrium with the local environment. However, we found no significant correlation between the two vulnerability indices. This means that regions that are predicted to remain suitable for the species in 2050 (i.e. with low ecological vulnerability) might still suffer a panoply of genetic adjustments in order to keep pace with climate change at the same locations (i.e. high genomic vulnerability; top-left quadrant, Figure 5a). And vice versa, the most ecologically vulnerable regions are not necessarily those for which the genomic vulnerability of populations is highest (bottom-right quadrant, Figure 5a). For instance, our SDMs predict major range contraction in the northern part of Lower Guinea and the northern part of DR Congo (Figure 2). Yet, some of these ecologically vulnerable regions are among those harbouring the lowest genomic vulnerability (northern Lower Guinea, western part of the northern DR Congo; Figure 4a). In other words, distribution models should not solely be used as predictors of the ability of local populations to withstand climate change, but rather should be associated with genomic vulnerability assessments. Conversely, regions with low ecological vulnerability but high genomic vulnerability could stem from strong local adaptation, leading climate-associated loci to be more sensitive to climate change than what is expected in terms of climatic suitability change. Our results also demonstrated that the genetic groups which are defined in *C. canephora* by neutral markers could not be modelled as a single unit in terms of vulnerability assessment, as they are heterogeneous with respect to their environmental response (variable genomic vulnerability). This observation is of crucial

importance when discussing conservation units (see below). Overall, our analyses pinpoint towards six populations which have the lowest estimated ecological and genomic vulnerability scores (Figure 5a, lower-left quadrant) and therefore might be the most pre-adapted to future climate conditions. These populations are located (i) at the border of Cameroon and the Central African Republic, (ii) in a region at the border of Gabon, Cameroon and the Republic of the Congo; and (iii) at the border between Ivory Coast and Ghana (Figure 5b). Individuals from these populations could guide future varietal improvement to design new varieties resilient to climate change.

4.4 | Milestones for conservation policies

Understanding the ecological and evolutionary processes that shape biodiversity is crucial to establishing priorities in conservation regulations (Wood et al., 2021). African forests, which are already experiencing a much drier and more seasonal climate than other tropical forests (Parmentier et al., 2007), are also forecasted to experience large and rapid climate change (Diffenbaugh & Giorgi, 2012). However, to what extent tropical plants will effectively respond to climate change remains unclear, for two reasons. First, the ability of lowland tropical tree populations to migrate over long distances to maintain constant environmental conditions in a changing climate remains poorly characterized (Loarie et al., 2009). Second, little is known about how populations of species with long generation times, such as trees, cope with rapid climate change (Dauphin et al., 2021).

There is a growing concern within the field of conservation biology to incorporate genetic studies into species conservation management (Corlett, 2017; Foden et al., 2019; He et al., 2016; Williams et al., 2014). For instance, the assessment of wild genetic diversity is of utmost importance to maximize lineages present in germplasm collection for ex situ conservation (Eynard et al., 2016). The level of genetic diversity can also contribute to the resilience of populations to climate change (Alberto et al., 2013; Savolainen et al., 2013) and can thus contribute to the definition of in situ conservation areas, as those are expected to be a better conservation strategy than ex situ germplasm collections, especially for *C. canephora* (Davis et al., 2019; Kiwuka et al., 2021). Nevertheless, for crop species both strategies are necessary, as there are still a lot on uncertainties on the impact of climate change regarding both habitat suitability and species adaptive potential.

The concept of genomic offset or genomic vulnerability holds great potential for recommendations in conservation or assisted migration, with its risks and limitations (Rellstab et al., 2021). A recent study has assessed the extinction risk across the 124 *Coffea* species (Davis et al., 2019) and showed that 60% of these species are threatened with extinction while *C. canephora* is of low concern. As *C. canephora* is a species of major commercial value, this is good news for the economies that depend on it, but it is worth noting that genetic vulnerability was not taken into account in that study, and that only a few species are amenable to coffee production. Our study is the first of its kind to address the vulnerability of *Coffea* populations in terms of genetic and ecological sensitivity to climate change. Our

ecological and genomic vulnerability measures allowed us to pinpoint regions most threatened by future climate changes, which can be informative about the vulnerability of several understory species in African humid forests, like *C. canephora*. These regions are estimated to extend at the longitudinal fringes of the species distribution, and in particular over Western Africa and over the north-eastern part of the Congolese Basin. Seeds from these populations should therefore be a priority for ex situ conservation efforts.

Our approach and results thus represent important milestones for practical conservation management of an African lowland tropical tree by (i) delimiting conservation units, which do not systematically correspond to the known genetic groups in *C. canephora*; (ii) identifying populations of higher genetic diversity and or adaptive capacities that can be used as reintroduction source populations (He et al., 2016); and (iii) identifying regions of habitat gain and habitat loss that can be taken into account to create in situ conservation areas. In regions where in situ conservation strategies have to be complemented with ex situ strategies, these analyses can delimit the areas of priority for collecting samples for ex situ conservation.

In addition, we identified genetic variants (located in genes like CPK7, CPK8, NEK5 or NEK6, cf. Table S3 for a complete list) that could increase resilience to drought and pinpointed crop wild relative populations which harbour a higher genetic diversity and a higher proportion of adaptive variants. These results can be further used for varietal improvement to this major agro-economic crop species. Although coffee is a commodity crop, it represents an important source of income for vulnerable human populations in the Global South. The value of identifying suitable varieties of coffee under climate change conditions should therefore not be underestimated.

Our study paves the way to investigate genomic vulnerability at large, including multiple species, in order to gain a more complete picture of ecosystem response to climate change when accounting for genetic patterns. It shows that distribution-based predictions of plant ranges in the future are not necessarily congruent with indices of local population adaptation to climate conditions. Our work calls for jointly studying ecological and genetic patterns of response to climate change in order to identify regions of in situ conservation priority, that is areas which are both ecologically and genomically vulnerable, to identify genotypes most relevant for ex situ conservation and to facilitate gene flow among regions of low and high genomic vulnerability (Aitken & Whitlock, 2013; Rhoné et al., 2020). In addition, to mitigate the impact of climate change onto the sustainability of worldwide coffee production, varietal improvement involving the introgression of adaptive traits of crop wild relatives will remain of primary importance (Cheserek & Gichimu, 2012; Kiwuka, 2020).

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

VP, SM, RT, DC and AdK conceived the study. RT, LB and CNM designed and carried out the analyses. CK, US, BS, J-LK, JM, HL, PM, SBJ and PS gathered species data. MK, PD, CT-D, CF and HP contributed to genomic analyses. SM, CNM, YV and VP contributed to model development. RT, SM, CNM and VP wrote the first draft of the paper and all co-authors commented on and approved the manuscript.

DATA AVAILABILITY STATEMENT

All relevant data are available within the manuscript and its Online Resource files. The raw occurrence data are available on Dryad: <https://doi.org/10.5061/dryad.qv9s4mwh1>. The raw sequence files in FASTQ format were deposited in the NCBI SRA database under project accession number [PRJNA803612](https://doi.org/10.5061/dryad.qv9s4mwh1) except for accessions from Cameroon. Access to accessions and data from Cameroon may require a special agreement with Cameroon, in accordance with a recent NAGOYA-Cameroon law.

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