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## RESEARCH ARTICLE

# Guadeloupe and Haiti's coffee genetic resources reflect the crop's regional and global history

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## Societal Impact Statement

Despite strong historical declines, Guadeloupe and Haiti's coffee sectors remain important to rural communities' livelihood and resilience. Coffee also holds value as part of the islands' historical legacy and cultural identities. Furthermore, it is often grown in agroforestry systems providing important ecosystem services, which will become more important as these vulnerable islands work to adapt to a changing climate. Current efforts to revitalize coffee farms and target strategically important specialty markets would benefit from understanding existing genetic resources and the historical factors that shaped them. Our study reveals the rich history reflected in current coffee stands on the islands.

## Summary

- The West Indies, particularly former French colonies like Haiti and Guadeloupe, were central to the spread of coffee in the Americas. The histories of these Islands are shared until the 19th century, where they diverged significantly. Still, both Islands experienced a strong decline in their coffee sector. Characterizing the genetic and varietal diversity of their coffee resources and understanding historical factors shaping them can help support revitalization efforts.
- To that end, we performed Kompetitive Allele-Specific PCR (KASP) genotyping of 80 informative single nucleotide polymorphism (SNP) markers on field samples from across main coffee-growing region of Guadeloupe, and two historically important ones in Haiti, as well as 146 reference accessions from international collections. We also compared bioclimatic variables from sampled geographic areas and searched for historical determinants of present coffee resources.
- At least five *Coffea arabica* varietal groups were found in Haiti, versus two in Guadeloupe, with admixed individuals in both. The traditional Typica variety is still present in both islands, growing across a variety of climatic environments. We also

Lucile Toniutti and Valérie Poncet contributed equally.

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found *Coffea canephora* on both islands, with multiple likely origins, and identified *C. liberica* var. *liberica* in Guadeloupe.

- These differences are explained by the Islands' respective histories. Overall, Guadeloupe experienced fewer, but older introductions of non-Typica coffee. By contrast, several recent introductions have taken place in Haiti, driven by local and global factors and reflecting the history of Arabica varietal development and spread. Diversity on these islands is dynamic, and our results reveal opportunities and limits to the future of Guadeloupean and Haitian coffee.

#### KEYWORDS

agrobiodiversity, Arabica, coffee, Guadeloupe, Haiti, historical determinants, Typica, varietal diversity

## 1 | INTRODUCTION

The history of agriculture is also that of the management and spread of plant genetic resources. Cropping systems shape crop genetics and are in turn shaped by them. As such, cultivated plant genetic diversity and structure can both reveal and be explained by cultivation history (e.g., Costa et al., 2022; Helmstetter et al., 2020; Magris et al., 2021). This has proven true for coffee, a major perennial crop (Figure 1). Ethiopian Highlands are the center of origins of Arabica coffee (*Coffea arabica* L., Rubiaceae), but cultivation and trade were mostly developed by Yemen before the 17th century (hence, the species name) (Friis, 2015; Ukers, 1922). From there, it spreads worldwide along two main routes, giving rise to two major cultivated lineages (Anthony et al., 2002). The first passed through Tropical Asia to eventually reach the Americas, producing the Typica lineage, and the second through Bourbon (Reunion) Island to produce the Bourbon lineage, later widely spread. Each step led the crop through important genetic bottlenecks, resulting in a loss of diversity (Anthony et al., 2002; Salojärvi et al., 2024). Another species, *Coffea canephora* Pierre ex. Froehner or “Robusta,” has a wide wild distribution in African rainforest and was spread beyond its center of diversity in the 20th century as a response to pathogen pressures on Arabica (Montagnon et al., 1998; Verleysen et al., 2023). Today, Arabica makes up 60% of world coffee production, with Robusta accounting for much of the rest (International Trade Centre, 2021). A third species, *Coffea liberica* Hierns, is farmed in modest proportions (Ferreira et al., 2019) though its cultivation predates that of Robusta by decades (Morris, 1881; Ukers, 1922). Today, coffee trees are pantropical, and grown in varied systems ranging from complex, diversified and shaded agroforestry systems (such as traditional homegardens), to full-sun, intensively managed commercial monocultures (Poncet et al., 2024; Toledo & Moguel, 2012). This economically vital crop is increasingly threatened by global climate change (Bunn et al., 2015; de Sousa et al., 2019; Tournebize et al., 2022) and faces concerns over the agricultural commodity system's human and ecological costs, creating a need for greater resilience, adaptability, and sustainability of coffee cultivation (Poncet et al., 2024).

### 1.1 | Arabica coffee: history in the West Indies

As the entry point of coffee in the Americas, the Caribbean region played an important role in the process of coffee's circumtropical spread. Despite prior unsuccessful attempts, the history of coffee in the West Indies definitively began in 1723 when the naval officer De Clieu introduced *C. arabica* to Martinique, from the offspring of a tree gifted by the Dutch to the French king (Ukers, 1922). From there, it was propagated to other French colonies, including Guadeloupe and to Saint-Domingue (now Haiti) in 1726. From these and Suriname, where it had been introduced in 1718 by the Dutch, it would spread throughout the Neotropics, eventually becoming a crop of global importance. While they are no longer major players in the global coffee trade, the West Indies were once important centers of production. As the final, drastic bottleneck experienced by the Typica lineage, the genetic legacy of the crop's introduction to the region has left its mark on modern Arabica diversity. Nevertheless, little work has been done on the genetic resources of coffee present in these regions, particularly in the former French colonies, which were historically so important to the global coffee trade.

### 1.2 | Guadeloupe and Haiti: common, then divergent histories

Guadeloupe and Haiti (hereafter “the Islands”, despite Haiti being only part of Hispaniola Island) both played a major role in the early cultivation and spread of coffee in the Americas. They also share similarities in their socio-political history: Both were French colonial, slave labor-powered plantation economies. Both Islands' native populations were replaced by European colonists, enslaved Africans, and their descendants, giving rise to similar creole cultures. However, the Islands' fates diverged significantly in the 19th century. Guadeloupe remained a colony until anti-imperialist efforts led to full status of French Overseas Department in 1946. By contrast, a successful slave rebellion in Saint-Domingue led to the Republic of Haiti becoming an independent nation in 1804, escaping direct colonial rule (though not foreign powers' spheres of economic and geopolitical influence). Since then, the history





**FIGURE 1** Photographs of coffee in Guadeloupe and Haiti. (a) Old (>60 years) Typica (*Coffea arabica*) tree in a coffee-banana polyculture in Matouba, Guadeloupe. (b) SL/Kenyan-like Arabica in Matouba, Guadeloupe. (c) Cherries on low-yielding Typica branch in Northern Haitian agroforest. (d) Robusta (*C. canephora*) cherries and leaves in Northern Haitian agroforest. (e) Guadeloupean coffee pickers returning from the field circa 1920s, taken from Ukers (1922) and digitized by the Gutenberg Project (<https://www.gutenberg.org/>). Source: Photo credits: (a) and (b) Lucile Toniutti, (c) and (d) Claude Patrick Millet.

of Haiti has been marked by socio-political instability, pervasive inequalities and rampant poverty, even during periods of relative agricultural vitality, and worsening environmental crises. Therefore, despite socio-economic issues of its own, Guadeloupe enjoys greater political stability and human development than Haiti. The Islands' social, economic, and political histories, first shared, then divergent, are reflected in the history of their agricultural sector. As such, they have shaped the various aspects of coffee cultivation on the Islands.

Coffee cultivation began on Guadeloupe in 1726 and quickly grew to historic highs (3000 t exported in 1777, harvested from >8 million trees), followed by an overproduction crisis (Kopp, 1929; Lafleur, 2006). Since that time, the extent and productivity of coffee farms has mostly receded from various causes such as 19th-century political upheavals, unfavorable policies, frequent biotic attacks, 20th-century turmoil (World Wars, economic crises), major hurricanes (e.g., 1921, 1928), and the rise of banana cultivation (1930s) as a main export crop (Hoy, 1962; Kopp, 1929; Lafleur, 2006). By 2005, Guadeloupe only exported 20–30 t of coffee grown on about 100–120 ha (Lafleur, 2006). Still, Guadeloupean coffee has historically enjoyed an excellent reputation. It is known as *Café bonifieur*, in reference to the *bonifieries*, which are traditional coffee-processing establishments unique to Guadeloupe.

Coffee was also introduced to Saint-Domingue in 1726 and thrived in the island's abundant mountains. Farms were established as full-sun

monocultures, to the detriment of forest and soil health (De Bivar Marquese, 2022; Trouillot, 1982; Ukers, 1922). The colony quickly became the major coffee producer until the 1790s Haitian Revolution laid waste to plantations. Though production recovered and exports continued to be the main driver of newly independent Haiti's economy (Lundahl, 1984), coffee systems transitioned to small, highly fragmented, diversified farms. Peasant farmers were vulnerable to global and local economic and political inequities, as well as pests, pathogens, extreme weather events, and soil erosion (Amaya et al., 1999; Dupuy, 1989; Moral, 1955; Plummer, 1984). The sector's vitality diminished throughout the 20th into the 21st century. A proliferation of internationally funded development was proposed, and failed, to strengthen Haitian agriculture (Eitzinger et al., 2019; Ester, 1978).

### 1.3 | The present state of the coffee in the Islands

Despite its precipitous decline, Guadeloupean coffee remains an appreciable supplement to rural livelihoods (Dulcire, 2005) and still holds cultural importance to its inhabitants (Breton, 2017; Dulcire, 2005; Lafleur, 2006). In recent years, there has been renewed interest in expanding coffee cultivation in Guadeloupe. With crop diversification being a potential response to the growing need for greater

sustainability in Banana cultivation, greater integration of coffee's part in these systems has been suggested (Tarsiguel et al., 2023). These initiatives, started by growers' cooperatives, have gained support from several stakeholders such as local government and scientific and private sector institutions. However, the viability of this undertaking is still debated, and the various growers themselves have contrasting views and priorities (Dulcire, 2005). Similar efforts exist in Haiti and are also faced with considerable difficulties. While some growers are able to export their coffee for the niche, gourmet market under the label "Haitian Blue," most farms, including in historical strongholds, struggle to maintain production (Agricultural Risk Management Team, 2010; Amaya et al., 1999). Most Haitian coffee farms have a low management intensity, with coffee stand regeneration happening mostly through spontaneous seed bank germination. Such systems are crucial to maintaining Haiti's forest cover (Feller et al., 2006) and rural livelihoods (Steckley & Weis, 2016).

#### 1.4 | The need to characterize the local structure and diversity of coffee, and their determinants

From similar beginnings, the histories of Guadeloupe and Haiti's coffee sectors unfolded in drastically different ways. In the present, these Islands share a common desire for the crop's revitalization through agroforestry, though these efforts will unfold in highly contrasted economic, social, governmental, and cultural contexts. These factors entail a need for greater knowledge not only of the Islands' coffee genetic resources but also of their historical determinants and environmental context. The agrobiodiversity contained in traditional systems can be leveraged to help achieve these goals, and there is a need for greater scientific understanding of this topic. Development and greater availability of genetic study methods has promoted the study of local diversity for Arabica (e.g., Anthony et al., 2001; Zewdie et al., 2022) and Robusta (Vi et al., 2023) alike. In particular, targeted genotyping of known polymorphic regions is a cost-effective and useful way to study coffee diversity (Millet et al., 2024; Verleysen et al., 2023).

There is much value to characterizing crop genetic diversity: By taking stock of existing resources, it can inform their management and decision-making to improve agrosystems. Furthermore, it provides an opportunity to consider the historical forces that have shaped them (Bonnin et al., 2014). Writing about Latin-American coffee cultivation, the historian McCook (2017) explains "The structure of any coffee farm at any given moment is intensely historical and encompasses both local and global processes." This can be expected of West Indian coffee farms as well, and particularly of their genetic resources. To what extent has the diversity of coffee in the Islands changed over time, and what is the present-day status of the historical Typica? In addition, understanding the bioclimatic context of these resources is of value, as such environmental conditions can affect quality (Bertrand et al., 2012), and serve to differentiate products. In short, knowledge of history and of local environmental specificities not only provides lessons for planning the crop's future but can increase the commodity's market attractiveness and value, including through labeling efforts.

Therefore, the present study aims to use targeted genotyping to the following aims: (i) to determine the present genetic structure of the historically significant Typica variety in Guadeloupe and Haiti, (ii) to characterize the overall local coffee tree genetic and varietal diversity, (iii) to compare Arabica diversity between Islands, and to that held in international collections, (iv) to interpret genetic data through a historical lens, and (v) to characterize and compare the crop's bioclimatic environments across study areas. The past and present determinants of the Islands' coffee genetic resources will thus be discussed, as will the implications they hold for the crop's future in the region.

## 2 | MATERIALS AND METHODS

### 2.1 | Materials and sampling

In Guadeloupe, sampling took place in 2022 in Basse-Terre, across the present extent of coffee cultivation, particularly along the southern part of *Côte Sous-le-Vent* (Leeward—western—coast). In total, 33 farms were prospected as part of a RITA project (*Réseau d'Innovation et de Transfert Agricole*). These were mostly historic coffee plantations that have been abandoned or reconverted into agroforests and polycultures, under organic or conventional management (Figure S1). One sample was also obtained from a farm on a satellite island (Terre de Bas, Les Saintes) south of Basse-Terre. In total, 145 Guadeloupean samples were collected. We also used Haitian field sample data from Millet et al. (2024), acquired in 2021 from the Nord (North) and Grande-Anse (Southern peninsula) departments. These historically important coffee regions (De Bivar Marquese, 2022) have since experienced severely diminished yields. Fourteen farms per department were visited with Haiti's Agricultural and Agroforestry Technological Innovation Program (PITAG). These were agroforests of varying levels of complexity and coffee stand age, with virtually no chemical inputs. Six hundred twenty Haitian samples were thus included in the study. The larger sampling size in study areas of Haiti is reflective of their much greater geographic extent.

Sampling on both Islands was done in collaboration with farmers, and aimed to maximize represented diversity in the study areas, including all putative (reported) varieties. Healthy, mature leaves were collected from plagiotropic axes, dried and preserved in silica gel before conditioning for DNA extraction.

### 2.2 | Reference samples

Leaf samples were obtained for reference individuals of commercial and wild coffee from the CATIE (Tropical Agricultural Research and Higher Education Center) international coffee germplasm collection (Turrialba, Costa-Rica) and IRD (French National Research Institute for Sustainable Development, Montpellier, France). In addition, genotype data were acquired from the Hawai'i Agricultural Research Center's (HARC) collection (Hawaii, USA) provided by the United States Department of Agriculture-Agricultural Research Service's Sustainable Perennial Crop Laboratory (USDA-ARS, SPLC, Beltsville, MD, USA),

and from studies by Mérot-L'Anthoene et al. (2019). Finally, sequencing data were obtained for the Arabica lectotype (Linnaean herbarium sample BM000558021), as well as a Costa Rica 95 specimen, from a recent study (Salojärvi et al., 2024).

In total, the reference sample set contained 123 *C. arabica* individuals encompassing several wild accessions, historical and modern commercial varieties, F1 hybrid cultivars, in addition to the Linnaean sample. Also included were 18 *C. canephora* from several geographically determined genetic groups, one *C. liberica* var. *liberica*, two *C. liberica* var. *devrewei*, and two *Coffea congensis* (Table S1).

## 2.3 | Genotyping

We applied the genotyping sequencing method to genotype the accessions at 80 core single nucleotide polymorphism (SNP) selected by Zhang et al. (2021) from the Mérot-L'Anthoene et al. (2019) array on the basis of their ability to discriminate across several commercial and wild *C. arabica* accessions. Mérot-L'Anthoene et al. (2019) previously produced a DNA array for *Coffea* in which 945 biallelic SNPs were specifically selected to assess diversity within *C. arabica*. Of these, Zhang et al. (2021) identified a core set of markers polymorphic across a panel of commercial and wild Arabica accessions, including many references included in the present study. The marker information and sequences are provided in Table S2. Processing of field and reference leaf samples, from DNA extraction to selective KASP assay genotyping of target markers, was performed using a proprietary protocol by LGC Biosearch Technologies (Middlesex, UK). Twenty-seven Arabica and two Liberica (one of each subspecies) were repeatedly genotyped as duplicates. Duplicate reference samples were compared to exclude a few loci with >1 difference between repeats. Genotype information from duplicate samples was then combined into “consensus” samples with fewer missing data (with the few loci having divergent calls considered missing data).

Because the markers were primarily designed for Arabica, other species had more missing data. Still, they were also informative for related species. Three marker subsets were selected to minimize trade-offs between individual data completeness and maximal inclusion of samples from all species to more fully characterize sampled diversity. We thus used three species-specific genotype sets.

In addition, genotype information at target loci was obtained for the Arabica and Robusta references from previously generated sequencing data. Target marker sequences were blasted onto the *C. arabica* reference genome sequence v0.6 of the accession ET-39 (Salojärvi et al., 2024) to obtain positions, which were used to extract genotype information from the Linnaean and CR95 sequencing data from a variant call format (VCF) file.

## 2.4 | “Arabica dataset”

All genotyped Arabica samples were combined, and loci missing in >30% of samples, then individuals with >26% missing genotypes were filtered out to produce the final dataset (field and reference samples,

hereafter the “arabica dataset”). After all filtering steps, the “arabica” dataset contained genotype information at 80 loci for 834 individuals (Table S2) from Guadeloupe ( $N_{GI} = 111$ ), Haiti ( $N_{Ht} = 601$ ), and international germplasm collections ( $N_{ref} = 122$ ).

## 2.5 | “Liberica dataset”

There are two cultivated subspecies of *C. liberica*, which are quite genetically distinct (N'Diaye et al., 2005). To determine which ones were present in the study areas, after preliminary identification, putative Liberica field samples from Guadeloupe ( $N_{GI} = 6$ ) were combined with *C. liberica* var. *liberica* ( $N_{ref} = 1$ ) and *C. liberica* var. *dewrewei* ( $N_{ref} = 2$ ) reference individuals, as well as two representatives from each other available species including *C. congensis* (outgroups), and a subset of markers with <30% missing data across these samples (40 in total) was selected to form the Liberica dataset.

## 2.6 | “Robusta dataset”

We also sought to identify the possible origins of field *C. canephora* samples by comparing them to references from known geographic-genetic groups as defined in Mérot-L'Anthoene et al. (2019). References from groups A, D (West African), E, R (Central), and O (East) were combined with putative Haitian and Guadeloupean Robusta field samples into a Robusta-only dataset (34 samples:  $N_{GI} = 17$ ,  $N_{Ht} = 6$ , and  $N_{ref} = 11$ ). We used a subset of 58 markers available with <40% missing data across this sample group, this more permissive threshold increasing the chances of retaining informative loci for *C. canephora*.

## 2.7 | Genetic analyses

We described each island' coffee resources in terms of both diversity and varietal composition. Descriptive genetic diversity statistics were calculated on the Arabica dataset for North and Southwest Haiti, Guadeloupe, and across reference accessions using GenAIEx software v. 6.51b2 (Peakall & Smouse, 2012).

A principal component analysis (PCA) was then performed on field and reference samples using the R packages LEA v. 3.10.2 (Frichot & François, 2015) and Tidyverse v. 2.0.0 (Wickham et al., 2019) ggplot function to visualize the Islands' coffee diversities in relation to that represented by reference accessions.

Varietal characterization of field samples was then carried out using a population structure analysis run with sNMF function ( $K = 1-10$ , 100 repetitions) of the R package LEA v. 3.10.2. Varietal groups were defined using a 75% threshold of contribution from ancestral populations reconstructed at the most appropriate K value and labeled according to reference samples assigned therein. Individuals with <75% contribution were considered admixed or of unclear varietal assignment.

An unweighted neighbor-joining dendrogram was constructed from a simple-matching distance matrix (1000 bootstrap replicates)



calculated on the Arabica dataset Using DARwin v. 6.0.21 software (Perrier & Jacquemoud-Collet, 2006). Robusta individuals ( $N = 26$ ) were added to the tree as outgroups. This was then repeated by including the Linnaean sample and Costa-Rica 95 (Salojärvi et al., 2024) in order to see the former's positioning in relation to the arabica diversity considered in this study.

Simple-matching distance matrices were independently calculated, and neighbor-joining trees constructed from the Liberica and Robusta datasets respectively, using DARwin v. 6.0.21.

## 2.8 | Bioclimatic variables

In order to characterize the climatic contexts in which Guadeloupe and Haitian coffee grows, climate data (1970–2000 average), for the 19 standard bioclimatic variables based on temperature and precipitation patterns, and elevation data were downloaded from Worldclim (version 2.1) at 30s resolution. Data at sampled coordinates were extracted with R package Raster (v 3.6-20). A PCA was performed (R function `prcomp`) and plotted with package `ggbiplot` (v. 0.55) to describe the climatic envelopes of the six following geographic zones: Basse-Terre's three *Ensembles Paysagers* (Nord Basse-Terre/Côte au Vent; Sud Basse-Terre and Côte Sous le Vent) (Région Guadeloupe & DEAL Guadeloupe, 2011) and Haiti's Nord, western Grande-Anse, and eastern Grande-Anse.

## 2.9 | Search for historical determinants of genetic structure

In order to interpret local genetic diversity through a historical lens, the results of the varietal characterization were used to guide iterative searches for sources providing historical insight regarding their introduction and cultivation on the Islands, primarily using Google Scholar ([scholar.google.com](https://scholar.google.com)), the Internet Archive ([archive.org](https://archive.org)), and the Manioc digital library ([manioc.org](https://manioc.org)). We sought out contemporary scholarly work on plant science and history, but also historical accounts from manuals, monographs, and development project reports.

# 3 | RESULTS

## 3.1 | Arabica diversity analyses

We described and compared the levels of diversity of Guadeloupe and Haiti, and to that represented in international collections. Gene diversity (as expected heterozygosity,  $H_e$ ) was highest for reference individuals ( $H_e = 0.384 \pm 0.014$  SE), slightly lower for North ( $H_e = 0.340 \pm 0.02$ ) and Southwest ( $H_e = 0.317 \pm 0.02$ ) Haiti, and lowest by far for Guadeloupe ( $H_e = 0.093 \pm 0.014$ , see also Table S3). This is consistent with the PCA plot, with references having the widest distribution, followed by Haitian samples (Figure 2a,b).

## 3.2 | Arabica varietal characterization

We assigned field samples to varietal groups using a population structure analysis on the arabica dataset. The latter had its lowest cross-entropy between 7 and 10, and increasing values up to  $K = 8$  allowed for the identification of distinct varietal clusters labeled according to reference samples included therein. Six of these groups included reference individuals and could thus be associated with known varieties, but two of them were composed of Haitian field samples exclusively and were thus unlabeled (Figure 2c). The eight arabica genetic varietal groups identified were as follows: a Typica-like group ( $N_{GI} = 91$ ,  $N_{Ht} = 247$ , and  $N_{ref} = 14$ , Figures 1a; S2A), a Bourbon-like group ( $N_{Ht} = 29$ ,  $N_{ref} = 14$ ), a CR-95/Catimor-like group ( $N_{Ht} = 72$ ,  $N_{ref} = 4$ , Figure S2B), a Kent/I-60-like group ( $N_{Ht} = 8$  and  $N_{ref} = 3$ ), a SL/Kenyan-like group ( $N_{GI} = 11$ ,  $N_{ref} = 4$ , Figure 1b), an Ethiopian-like group ( $N_{Ht} = 1$ ,  $N_{ref} = 24$ ), and two unlabeled, Haiti-only groups ( $N_{Ht} = 49$  and 25, respectively). Several individuals ( $N_{GI} = 9$ ,  $N_{Ht} = 168$ ,  $N_{ref} = 59$ ) had <75% contribution from all groups and were thus considered admixed. These groupings are also consistent with the distribution of individuals on the PCA plot (Figure 2).

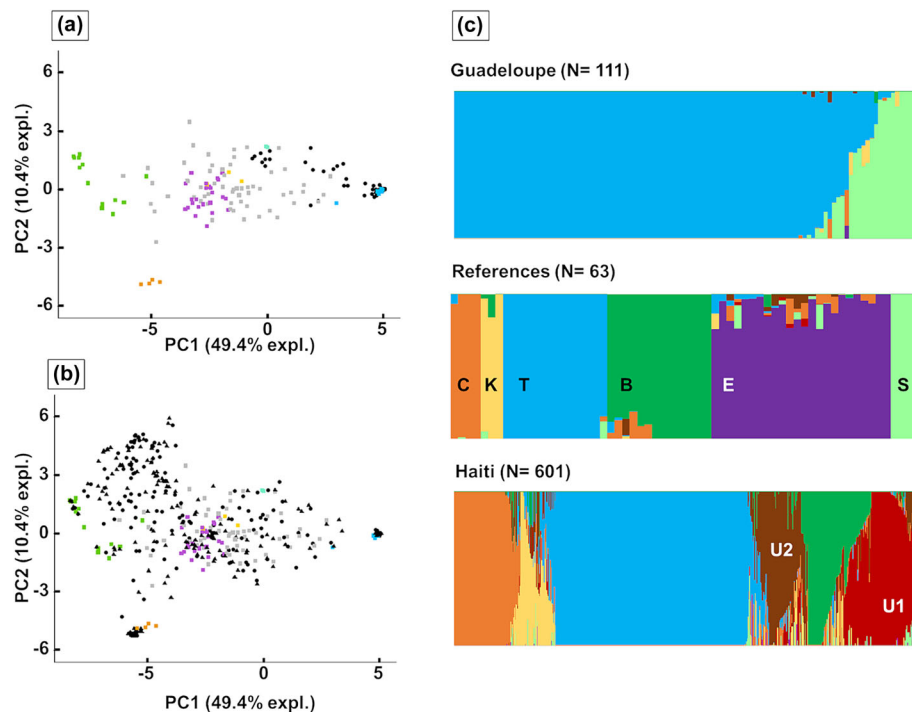
The clustering of samples on the “Arabica” neighbor-joining dendrogram is also in agreement with the population structure analysis (Figure 3). Using *C. canephora* samples as outgroups, wild Ethiopian individuals are basal, and followed by the split of cultivated Arabica into two main lineages with Typica and Bourbon individuals, respectively. The dendrogram shows correct sample clustering according to their assigned varietal groups, with the exception of one of Haitian Unlabeled group (hereafter “Unlabeled2”). “Unlabeled2” individuals were split across the two main branches of cultivated Arabica. Guadeloupean SL/Kenyan-like samples clustered together and with references from that group. Pairwise  $F_{st}$  between genetic groups show them to be well-differentiated (Table S4).

Typica-like individuals clustered together indiscriminately of origin. In fact, identical genotypes at all loci were found across several locations in Haiti (both departments) and Guadeloupe, as well as among reference individuals of different origins. The dendrogram including the sequenced samples (Figure S3) shows the correct placement of the Costa-Rica 95 control, and the Linnaean sample being closest to the Typica cluster.

Our results show that there is less diversity and fewer varietal groups in Guadeloupe than in Haiti, but both Islands share the historical Typica variety, which is widespread in all coffee-growing regions.

## 3.3 | Identification of Robusta genetic groups of origins

On the “Robusta-only” dendrogram, field individuals did not all cluster together with references from any single genetic group nor were samples from the same island or indeed the same farm grouped together (Figure S4). Field samples clustered with references from



**FIGURE 2** Genetic structure and diversity of *Coffea arabica* from Guadeloupe and Haiti in relation to reference samples from international collections. (a) Plot of Guadeloupean (in black) and reference samples (all others) along the first two axes of a principal component analysis performed on Guadeloupean, Haitian, and reference samples. (b) Plot of Haitian (in black) and reference (all others) samples along the first two axes of the same principal component analysis (PCA). (c) *C. arabica* population structure analysis at  $K = 8$  showing results for Guadeloupe (top), reference (middle), and Haiti (bottom) samples. Only references with  $>75\%$  contribution from any one group are shown. Groups are labeled according to references assigned therein: C = CR95/Catimor-like, K = Kent/I60-like, T = Typica-like, B = Bourbon-like, E = Ethiopian-like, S = SL/Kenyan-like. Two groups were composed of only Haitian samples (U1 = Unlabeled1 and U2 = Unlabeled2). The reference individuals on the PCA plots (a and b) are colored according to the genetic groups described in (c), with all references with  $<75\%$  contribution from any group shown in gray.

groups D (Upper Guinean), A (“Conilon,” Congo-Brazza), E/R (RDC), and O (Ugandan) but were often positioned more basally, suggesting admixture with contribution from several geographically determined genetic groups. Robusta samples were found on only one (Northern) Haitian farm but were present throughout Basse-Terre in Guadeloupe.

### 3.4 | Identification of Liberica samples to subspecies level

On the “Liberica” dataset dendrogram (Figure S5), Guadeloupe field samples clustered with *C. liberica* subspecies *liberica* but not *C. liberica dewveii*. These samples originated from locations across the study area. No Haitian sample belong to either subspecies.

### 3.5 | Islands' coffee composition

Nearly all Arabica varietal groups were present and widely distributed in Haiti, with farms ranging from one to five varietal groups, but Robusta was found on only one farm, and Liberica is absent. By

contrast, only the Typica and SL-like groups were present in Guadeloupe, but both Robusta and Liberica were found across coffee-growing areas of the island (Figure 4). The historical Typica variety is present in all six geographic zones.

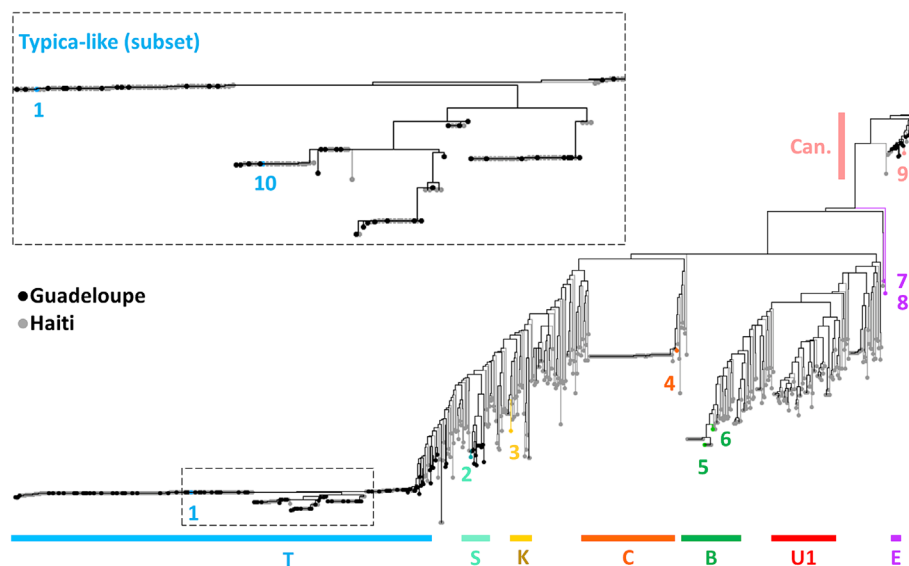
### 3.6 | Climatic envelopes

The Climatic envelopes of the six geographic zones were characterized and show a clear separation of Haiti and Guadeloupe's zones along a spectrum of high-to-low altitude and precipitation, and low-to-high temperature (Figure S6). There were also gradual differences between Southern and Northern Haiti, and between Basse-Terre (Guadeloupe)'s two coasts. Overall, Guadeloupe's East coast is warmest and driest with lower elevation, while Southeast Haiti is cooler, wetter, and higher in elevation (Figure S7).

### 3.7 | Historical determinants of genetic structure

Global and local historical factors shaping the genetic composition and structure of the Islands' coffee resources were identified and used





**FIGURE 3** Unweighted neighbor-joining dendrogram of Guadeloupe (in black), Haitian (in gray) and reference (in color) *C. arabica* and *C. canephora* individuals. Calculated from simple-matching distance matrix. Colored bars represent varietal groups identified by sNMF population structure analysis: C = CR95/Catimor-like, K = Kent/l60-like, T = Typica-like, B = Bourbon-like, E = Ethiopian-like, S = SL/Kenyan-like U1 = Unlabeled1 (Haiti-only) group, plus Can. = Canephora outgroups. A portion of the Typica branch is magnified (in frame). To aid legibility, a few representative reference individuals are included, colored according to their assigned varietal group (excluding Canephora) as identified by sNMF population structure analysis. These are as follows: 1. (Ku214) Typica/Jamaica Blue Mountain, 2. (T.04313) SL28, 3. (T.04268) Kent, 4. (T.08667) CR95, 5. (Mw264) PR6791/Bourbon Select, 6. (T.02542) Caturra, 7. (T.04667) E-160, 8. (T.04290) Jimma Kaffa, 9. (GUI2) Guinean *C. canephora*, and 10. (T.00990) Surinam.

to generate timelines representing the various historical and geographic scales (Figure 5). Though a comprehensive history was outside of our study's scope, the generated timelines include all major determinants, to the best of our knowledge. In some cases, it was possible to trace the introduction of species (e.g., Liberica in Guadeloupe, Nicholls, 1881) or varieties (e.g., Catimor in Haiti, Ester, 1978) through contemporary books and reports. In other cases, monographs, reports, and personal accounts testified to their presence on the Islands at a particular time (e.g., of Robusta in 1920s Guadeloupe, Ukers, 1922, and of Caturra in 1970s Haiti, Ester, 1978) or testified to the status of certain varietal groups during a particular time (e.g., of Kent's popularity in the 1910s–20s, Haarer, 1923). Certain historians have also produced works identifying major historical drivers of varietal development, such as the global progressive spread of coffee leaf rust (CLR) (McCook, 2006, 2017), as well as works relating the history of coffee in Haiti (De Bivar Marquesse, 2022; Moral, 1955) and Guadeloupe (Hoy, 1962; Lafleur, 2006).

## 4 | DISCUSSION

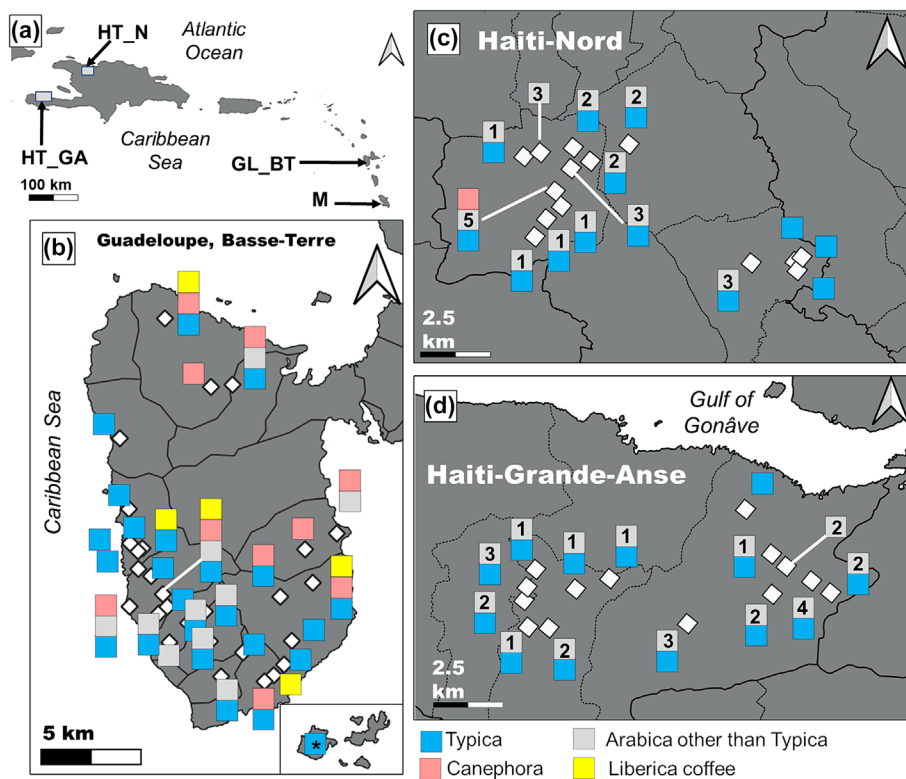
### 4.1 | A shared history reflected in the Typica variety

Our analyses of Guadeloupean Arabica have revealed that the heritage Typica variety is still widespread on the island, being found across all sampled coffee regions (Figures 1a, 4). The same is true in

Haiti where it persists in large stands in multi-varietal farms and in monovarietal systems.

There was little genetic diversity in the Typica varietal group regardless of origin: Identical genotypes across all markers were found in individuals from all sampled regions, as well as collection references, including the prestigious Jamaican Blue Mountain coffee (Figure 3) as well as references labeled “Suriname” (T.00990) and “Guadeloupe” (T.00989). This is consistent with historical accounts and genetic studies confirming that Typica originated from a very limited number of individuals (Anthony et al., 2001; Salojärvi et al., 2024), themselves resulting from successive genetic bottlenecks along its global spread. Indeed, after the Dutch acquired Arabica from Mocha, Yemen, the crop was introduced to India, Sri Lanka, and Java around 1696–1699, Amsterdam, and eventually the Americas (1718–1726, Ukers, 1922). This originated the Typica lineage, which was established both in the Suriname fields and De Clieu's plantation in Martinique.

With the globalization of tropical crops being a key part of European colonialism, Guadeloupe and Saint-Domingue (Haiti) were deeply impacted by this process. In these Islands, coffee was first cultivated in unshaded monocultures (Laborie, 1798; Moral, 1955), though agroforestry eventually came to predominate as Guadeloupean coffee receded (Hoy, 1962; Lafleur, 2006) and Haitian independence did away with plantations (Lundahl, 1984). This shift was permitted by Typica's ability to perform well under shade. The plant would spread from the early 18th century onwards to Brazil from the Guyanas, and to Central America from the West Indies (Herrera & Lambot, 2017; Ukers, 1922). The position of the Linnaean lectotype



**FIGURE 4** Sampling locations and coffee genetic group distribution in Guadeloupe and Haiti. (a) Location of study areas in the West Indies (HT\_N = Haiti Nord department, HT\_GA = Haiti Grande-Anse department, GL\_BT = Guadeloupe, Basse-Terre) with Martinique (=M) also shown (first coffee introduction in West Indies). (b) Sampling locations and their genetic resources in Basse-Terre, Guadeloupe, with Les Saintes in the insert (\* Typica sample corresponded to small-seeded “Moka” phenotype). (c) Nord department in North Haiti and (d) Grande-Anse department in Southwest Haiti. Stacked squares indicate presence of a coffee category in samples. Gray squares represent all *C. arabica* with >75% contribution from Typica-like group, including other varietal groups (counts indicated for Haitian sites, always 1—SL/Kenyan-like—in Guadeloupe) and admixed individuals. Source: Maps created in QGIS v. 3.30.1 using Natural Earth (free vector and raster map data @ [naturalearthdata.com](https://www.naturalearthdata.com)) and shapefiles from Hijmans, and University of California, Berkeley, Museum of Vertebrate Zoology (2015a, 2015b) and Patterson and Kelso (2012).

close to the Typica cluster on the dendrogram (Figure S3) suggests that it was related to the plants that were introduced to Suriname by the Dutch and the Caribbean by De Clieu, perhaps being or sharing a common progenitor.

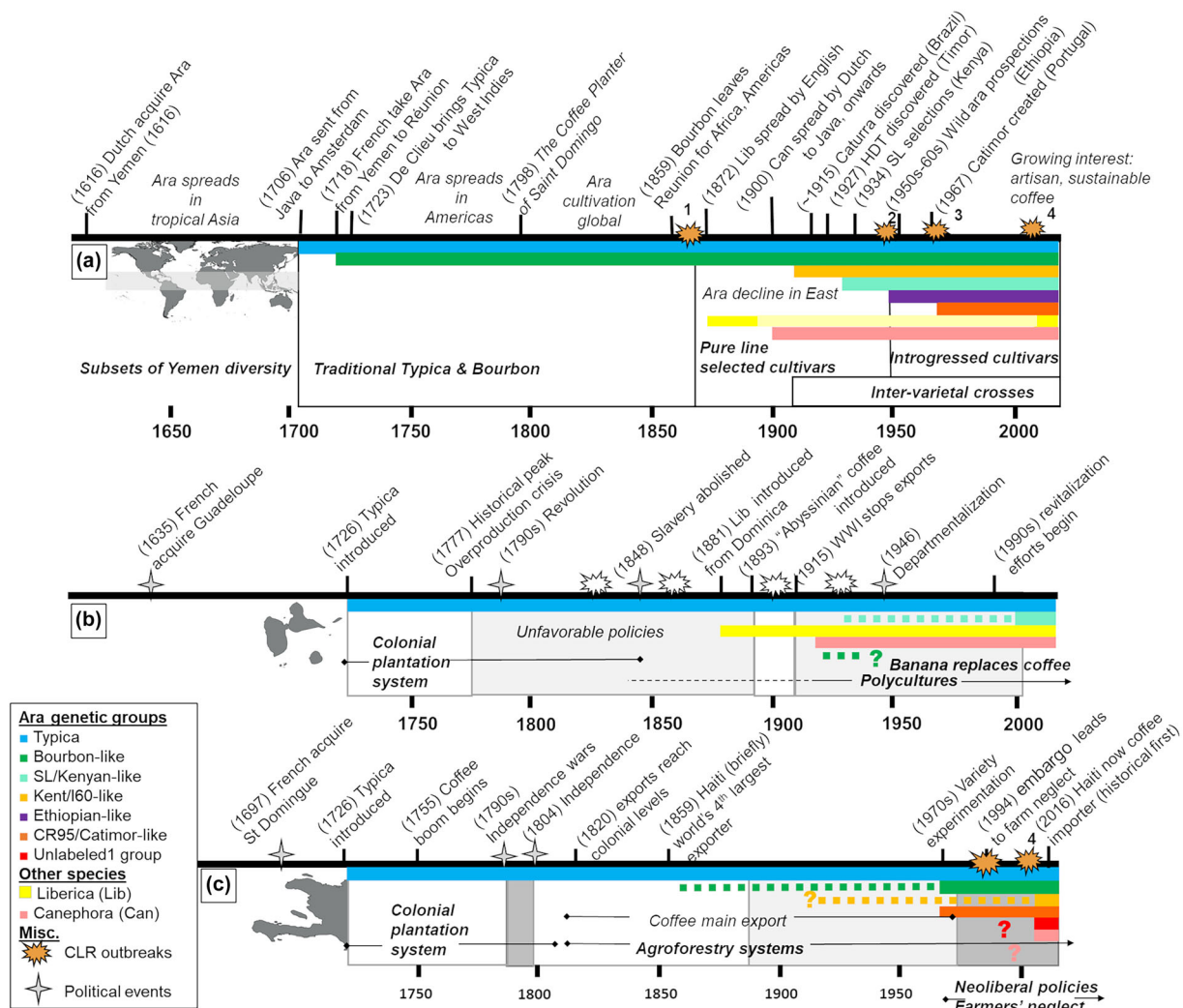
#### 4.2 | Guadeloupean “Moka”: a phenotypically distinct form of Typica

One Guadeloupean individual from the Saintes satellite Islands, assigned to the Typica group, was observed to have consistently small-sized cherries. Arabica with this trait are generally called *Ti café* (“small”) or “Moka” in Guadeloupe (Lafleur, 2006) and enjoy the best reputation for quality. Our markers do not differentiate these Moka from other Typica. The Moka phenotype may originate from punctual mutations in Typica, similar to Caturra being a dwarf mutant of “tall” Bourbon (World Coffee Research, 2019), also indistinguishable with our markers. The term “Mocha” was historically used for Yemeni coffee, which was described as small-beaned and of superior quality (Haarer, 1923; Ukers, 1922) but is genetically diverse (Montagnon

et al., 2021). Guadeloupean Moka is not likely closely related to Yemeni accessions. Therefore, the name “Mocha” should not be taken to have genetic meaning but may rather be used to describe plants with similar traits.

#### 4.3 | Old East African accessions provide a modest increase to Guadeloupean coffee diversity

While Typica forms the core of Guadeloupean coffee resources, several other Arabica belong to the “SL/Kenyan-like” varietal group (Figure 1b), which does not appear to be present in Haiti. This varietal group was not identified by Millet et al. (2024). SL/Kenyan-like references ( $N_{ref} = 4$ ) included T.04313-SL28, T.04314-SL34, and T.02742-“Dilla Alge,” which are all Eastern African accessions. SL selections were developed in the 1930s in Kenya by the Scott Agricultural Laboratories by breeding trees from various collections in Eastern Africa: SL28 for drought tolerance, and SL34 for cup quality. The Dilla Alge accession was collected in Ethiopia and introduced to Kenya in 1942 (Sylvain, 1958; USDA, 1958).



**FIGURE 5** Historical timeline of events affecting Guadeloupe and Haiti coffee genetic resources. (a) Global timeline. Boxes below timeline represent major developments in the genetic profile of cultivated Arabica worldwide. (b) Timeline showing major events affecting the composition and vitality of the coffee sector in Guadeloupe and (c) in Haiti. For (b) and (c), boxes underneath timelines represent periods of coffee sector positive (empty) and negative (grayed) growth. For all timelines, Ara = *Coffea arabica*, Lib = *C. liberica*, Can. = *C. canephora*. Ticks represent historical events in coffee cultivation, and colored lines represent period of cultivation for genetic groups identified in this study (uncertainties represented by dashed lines). Coffee leaf rust (CLR, *Hemileia vastatrix*) events represented (1) CLR discovery near Lake Victoria (East Africa, 1861) and first big outbreak in Ceylon (Sri Lanka) and South India (1869), beginning its spread in tropical Asia and Pacific islands; (2) CLR spread through Western African farms (1950–60s); (3) arrival in Americas (Brazil, 1970) and spread through the 80s; and (4) the Big Rust (2008–2013) epidemic in Latin America. For (b), white explosions represent various (often unspecified) waves of coffee illness reported for Guadeloupe, insufficient data for Haiti (Amaya et al., 1999; Avelino et al., 2015; Ester, 1978; Haarer, 1923; Harvey et al., 2021; Hoy, 1962; Kopp, 1929; Lafleur, 2006; Lalanne, 1934; McCook, 2006, 2017; McCook & Montero-Mora, 2024; McCook & Vandermeer, 2015; Moral, 1955; Morris, 1881; Muñoz-Pajares et al., 2023; Nicholls, 1881; Robert, 1935; Sylvain, 1972; Ukers, 1922).

To our knowledge, the origin of SL/Kenyan-like coffee to Guadeloupe is not attested in the literature. Our results corroborate a previous study carried out in 2017 by World Coffee Research (WCR) using Simple Sequence Repeat markers (SSR), which also revealed the presence of SL-type coffee plants in Guadeloupe (L. Toniutti, pers. obs.). The Guadeloupean samples were fairly spread out, though predominantly on the Western coast. When asked, farm owners could not identify or recall the origin of the SL/Kenyan-like plants (pers. comm.). Several Guadeloupean samples were identified as admixed, with varying levels of Typica and SL/Kenyan-like contribution. These

elements suggest a relatively old introduction of this varietal group, and subsequent interbreeding with local Typica.

Discrepancies exist between historical accounts and our genetic results. Documents from 1930s describe four coffee “species” on Guadeloupe: “Arabica” (i.e., Typica), the rare but productive “Roy” or “Bourbon,” the sensitive “Abyssinica,” and the recently introduced “Liberica” (Lalanne, 1934; Robert, 1935). We did not identify the Bourbon-like varietal group in Guadeloupe. If it had indeed been introduced, it is either still rare, or no longer present. In the 1930s, “Abyssinica” referred to coffee from south-eastern Ethiopia

(Roussel & Verdeaux, 2007), and these trees had apparently been imported to Guadeloupe in 1898 (Lafleur, 2006), predating SL selections by decades. This could be explained by the replacement of “Abyssinian” coffee by Kenyan-derived trees, or perhaps by common ancestry between the two (especially given the inclusion of the “Dilla Alge” accession in the SL/Kenyan-like group).

#### 4.4 | Haitian Arabica diversity reflects a global legacy of coffee breeding

While some genetic diversity is provided by the SL/Kenyan-like varietal group to the otherwise homogeneous, Typica-dominated Guadeloupean Arabica, it is far below that observed in Haiti. Multiple varietal groups of commercial or historical importance have been identified there, including Bourbon-like, Kent/l60-like, and CR95/Catimor-like groups. We also identified two unlabeled, exclusively Haitian groups. One was identified in previous work (Millet et al., 2024) and was hypothesized to be related to Timor hybrid (HDT)-introgressed Colombian cultivars such as Tabi and Castillo, reported in Haiti (Queneherve et al., 2015) but absent from our reference collections. The second unlabeled group (U2), unrecognized by the dendrogram, therefore appears dubious and may be an artifact of admixture. Indeed, varietal groups have experienced considerable genetic mixing in Haiti, as evidenced by the large number of individuals with <75% contribution from any one group (see also Millet et al., 2024).

The varietal diversity of Haitian coffee is a legacy of the genetic history of Arabica since the 18th century. Soon after the Typica line was established, a second wave of Arabica dispersal also started from Yemen, from where the French introduced coffee into Bourbon Island (called today “La Réunion”) around 1708–1718 (Haarer, 1923; Ukers, 1922). This introduction gave rise to the Bourbon Arabica lineage, which did not leave the island until its propagation to Africa and the Americas in the 1860s (World Coffee Research, 2019). Over time, and despite Arabica's narrow genetic base, a process began of varietal diversification of the main lines through massal selection and propagation of mutant strains. Starting in the late 19th century, it led to several varieties such as Maragogipe (Typica mutant from Bahia, Brazil, first identified in 1870) and Caturra (Bourbon dwarf mutant from Minas Gerais, Brazil, ca. 1915–1918, Haarer, 1923). The Caturra variety would eventually be introduced to Haiti in the 1970s (Ester, 1978).

In parallel, as coffee spread, so too did its pests and pathogens, and particularly the CLR (*Hemileia vastatrix*, Figure S1C). Originating around Lake Victoria in Eastern Africa, rust quickly spread to South and Southeast Asia in the 1860s (McCook, 2006). Notably, this initial spread of rust may have been exacerbated by the adoption in the Eastern Hemisphere of the “West Indian” coffee cultivation system (full-sun monoculture), of which an early, influential proponent was the Saint-Domingue planter P.J. Laborie (Laborie, 1798; McCook, 2017). CLR then spread in Africa in the 1920s, and finally, the Americas in the 1970s (McCook, 2006).

The impact of biotic aggressors was exacerbated by the low genetic diversity of cultivated Arabica (Anthony et al., 2002). These epidemics led to the widespread abandonment of older varieties, which were highly susceptible to the disease. With growing biotic pressures, growers sought new, more resistant Arabica varieties such as “Kent's coffee,” which was identified in India in 1911 (Haarer, 1923). Displaying (since-lost) CLR resistance, it was widely spread, particularly to Eastern Africa. The introduction to Haiti of the Kent-like group is likely to have taken place a long time ago (Millet et al., 2024), possibly as early as the first half of the 20th century, when it enjoyed great popularity, and Haiti's coffee sector greater vitality.

There were also efforts to make Arabica coffee more resistant through hybridization with other species. The spontaneous HDT, (*C. arabica* × *canephora*) identified in Timor in 1927 (Bettencourt, 1973), gave rise to HDT-introgressed varieties such as Catimors (crossed with Caturra; such as the CR95 cultivar Figure S1B), Sarchimors (with Villa Sarchi), and Colombian varieties (Muñoz-Pajares et al., 2023). Indeed, in the mid-20th century, there was a shift from simply fixing mutations to generating new, better-yielding genetic combinations through institutional breeding (Carvalho et al., 1962; McCook, 2017). In the 1970s, as the major pests and diseases had reached much of Latin America, national and international agencies like US Agency for International Development (USAID) implemented agricultural “technification” projects in low- and middle-income countries, aiming to offer “technical packages” consisting in improved varieties and/or agronomic intensification through agrochemical control of pests and pathogens (McCook & Montero-Mora, 2024; McCook & Vandermeer, 2015).

Many such projects came to Haiti, occasioning introductions of varieties such as Caturra and the then-new Catimor (Amaya et al., 1999; Ester, 1978; Sylvain, 1972). However, these projects failed to consider Haitian agroforestry's long history, which arose as a repudiation of the plantation system and out of need for resilience and risk management in the face of longstanding instability, and was incompatible with these technical packages. This explains the abundant genetic mixing in Haitian coffee farms.

#### 4.5 | Guadeloupe and Haiti's divergent histories reflected in their contrasted Arabica resources

As previously discussed, many Arabica varietal introductions took place in Haiti in the 20th century, brought about by global and local changes in policymaking, coffee breeding, and pathogen pressures. A more severe wave of CLR outbreaks nicknamed “The Big Rust” again ravaged Latin-American farms between 2008 and 2013, exacerbated by socio-economic, ecological, agronomic, and meteorological factors (Avelino et al., 2015; McCook & Vandermeer, 2015). As global markets experienced increased volatility from 1990s onwards, many farmers in Central America reduced investment in labor and inputs during periods of very low coffee prices and reverted to less intensive (and investment-hungry) production methods (McCook &



Montero-Mora, 2024). This relaxed pressure on pathogens played a role in the Big Rust of the 2010s (Avelino et al., 2015; McCook & Montero-Mora, 2024). Haiti was among the countries impacted, and again, development projects responded by introducing resistant varieties such as Colombian introgressed cultivars (Jean-Denis & Roesch, 2017; Queneherve et al., 2015), further increasing local diversity.

By contrast, and despite mentions of a “Rust” or even “*Hemileia*” attacking Guadeloupean coffee prior to the 1940s, (Lafleur, 2006; Lalanne, 1934), this disease is neither widespread nor particularly problematic in Guadeloupe today, possibly due to coffee's limited extent on the island. Furthermore, Guadeloupe, being a French department and having largely shifted from coffee to banana exports, was less concerned with 20th and 21st century developments in global coffee, such as technical package adoption. This may explain the absence of otherwise widespread varieties such as HDT-introgressed Catimors, which were increasingly prioritized following rust outbreaks. In fact, the abandonment of coffee for banana cropping began even before the development of introgressed Catimors, having been greatly promoted by a severe 1928 hurricane, which laid waste to a quarter of Guadeloupe's coffee stands. This caused farmers to increasingly turn towards bananas (which had primarily been a subsistence crop until then), which had shorter production cycles and thus earlier marketability (Desarthe, 2020; Lafleur, 2006).

The lack of coffee farm revitalization also permitted the continued persistence of Typica in Guadeloupe, and today it, along with Haiti, is among the few countries still cultivating Typica (WCR). The historically important variety has been abandoned throughout the world due to low yields and high susceptibility to rust. The Big Rust devastated Haitian farms but did not cause the abandonment of Typica. Haiti's neighboring country, the more prosperous Dominican Republic, is an interesting case: Many of its farms are traditional, diversified agroforests with Typica-dominated coffee stands and reported varietal (Typica-Caturra) interplanting, but technification has been increasing there as throughout Latin America (Siegel & Alwang, 2004). In response to pressure from CLR, the Dominican Coffee Council has recommended that farmers shift to introgressed varieties and has supported this enterprise through distribution of seed material (Consejo Dominicano del Café, 2017).

Today, many farms in Latin America consist in pure-line or introgressed cultivars grown in full sun or simplified, carefully managed shade systems, often with agrochemical inputs, with a trend towards intensification despite increasing consciousness of issues in sustainability (Cerda et al., 2020; Harvey et al., 2021; Perfecto et al., 2019). These transformations occurred in neither Guadeloupe, where coffee was simply not a priority crop, nor Haiti. In the case of the latter, this is likely due to the fact that Haitian farmers tend to prioritize autonomy, limited reliance on markets, and “bet-hedging” through diversification (Steckley & Weis, 2016). Furthermore, the partial failure and unintended consequences of technification in Haiti are also tied to institutional weakness, and the broader pattern of failure by foreign intervention and international aid to attain their development objectives (Ramachandran & Walz, 2015; Schöneberg, 2017).

#### 4.6 | Divergent histories also reflected in introduction of other species to the Islands

Concerns over coffee pathogens coincided with colonial efforts in Africa, and its forests were prospected for resistant species, which could be cultivated. Thus “Liberian” *C. liberica* and “Robusta” *C. canephora* coffee began supplementing or replacing Arabica in various parts of the world, the latter especially gaining prominence over the course of the 20th century (Chevalier, 1929; Cramer, 1957; Ukers, 1922).

While most sampled Guadeloupe coffee trees were Arabica, several belonged to *C. canephora*. This diploid, obligate allogamous species is native to much of equatorial Africa. Wild populations display a geographically determined genetic structure, with eight groups identified (Mérot-L'Anthoene et al., 2019). Though *C. canephora* was previously used by local populations, its global spread was initiated when it was introduced to Java in 1900 to replace CLR-stricken Arabica (Chevalier, 1929; Cramer, 1957; Haarer, 1923). Strains developed there were quickly spread to other rust-affected countries. Twenty years later, Robusta was reported from Guadeloupe (Ukers, 1922). Today, it is the second-most commercially important coffee species (approximately 40% of global production), though considered of lesser cup quality (International Trade Centre, 2021). It is not harvested for export in Guadeloupe, being restricted to local consumption.

Some Haitian Robusta individuals were also found (Figure 1d), all on the same farm in Northern Haiti. The species seems a more recent arrival to Haiti; as to our knowledge, it is unattested in historical literature and appears to have a limited distribution. In a report on a PITAG farmers' workshop, Eitzinger et al. (2019) write that “New varieties (e.g., the ‘Brasil’ [sic] variety) are more resistant [to CLR than Typica], but have less production.” *Brazil* is the name given by locals to the sampled Haitian *C. canephora*. The latter were already growing on the farm when the owner purchased it in 2014 (pers. com.), and their origins are thus unclear. Our results suggest that both Islands' Robusta samples are related to several genetic groups and may be of mixed origins (Figure S4). “Conilon” (group A)-type *C. Canephora*, which is widely cultivated in Brazil, appears to be only one several contributors, and references from this group were closer to some Guadeloupe samples than to any Haitian one. This points to possible introductions of either multiple Robusta of different origins, or of admixed individuals from Robusta breeding programs.

Six Guadeloupe samples belonged to the subspecies *C. liberica* var. *liberica*, and none to *C. liberica* var. *dewevrei*. This tall-growing, large-leaved, diploid, obligate allogamous species originates from Western and Central Africa (Davis et al., 2022). First found by botanists near Monrovia, it was first exported by the British. Sent to Kew Gardens in 1872, it spreads to British colonies worldwide (Morris, 1881), arriving in Dominica in 1874 (Nicholls, 1881). The plant was particularly appreciated for its vigor, productivity, and resistance to the “White fly” (coffee leaf-miner, *Cemistoma coffeellum*), which damaged Arabica farms (Nicholls, 1881, Kew bulletin). By 1881, Liberica was propagated from Dominica to Guadeloupe (Nicholls, 1881). It

enjoyed a relatively fast growth on the market in the early 1900s but was quickly supplanted by Robusta (Chevalier, 1929; Haarer, 1923). Like Robusta, Liberica is not harvested for export in Guadeloupe.

Our results are consistent with the known history. Ukers (1922) write that Liberica and Robusta were planted extensively in Guadeloupe to replace aging Arabica stands, but no similar mention is made for Haiti. This may be due to colonial administrations' roles in this dispersal at a time Haiti was no longer part of the colonized world.

#### 4.7 | Additional considerations

In this study, we characterized Guadeloupe and Haiti's coffee genetic resources and identified historical determinants of their structure. As such, we focused on events and processes directly affecting them: plant breeding and varietal introductions, evolution of biotic pressures that required genetic innovations, and incorporation of new species in cropping systems. However, it is important to note that these processes occurred within the broader context of the global coffee trade. The history of world coffee trade has been marked by periods of instability, transformations, and unpredictability. A comprehensive account of these is beyond the scope of this paper, but the 20th century deserves particular mention. Its first half was characterized by boom and bust cycles, in which Brazil (emerging as dominant producer in the wake of the Haitian Revolution) loomed especially large (Schurz, 1922; Topik, 2019). Efforts by the international community followed to regulate the coffee trade through treaties such as the 1962 International Coffee Agreement (Bilder, 1963). After the latter ended in 1989, another period of acute farmer vulnerability and price volatility began (contributing to farm neglect and, eventually, to the CLR crises) (Avelino et al., 2015; Ponte, 2001). However, changes in consumer values also led to demand for more socially and ecologically sustainable coffee, and development of various certification schemes (and ensuing debates over their efficacy; Grabs, 2020; Harvey et al., 2021; Ponte, 2001). This political-economic history was interrelated with that of coffee genetic innovations, affecting actors' willingness, incentives, pressures, and resources to develop, adopt, spread, and manage new genetic material.

Pushes to revitalize the Islands' coffee sectors must be understood in this global context as well as local ones. These efforts must be pursued in a manner that is ecologically and economically sustainable, resilient to climate change, and adapted to local needs and priorities. Local genetic resources can be harnessed to advance those goals, but this is contingent on understanding their limitations.

#### 4.8 | Despite compromises, Typica may remain a cornerstone of the Islands' coffee sector

In Guadeloupe, Arabica diversity is low, but historically notable. The Typica variety particularly justifies the reputation afforded to Guadeloupean coffee, and its cultivation could be maintained for supply on niche, gourmet markets with low volumes, with a focus on historical

and cultural importance (Dulcire, 2005). This also creates opportunities for further development of agro-tourism based on this patrimonial resource (Breton, 2017). Typica also retains potential in Haiti, which has in recent decades established itself on small-batch, quality-oriented markets and where the Typica variety continues to dominate despite significant diversification. Its persistence is due in part to its historical importance and status, attested by its local names of “Bonifieur” and “Café Créole” in Guadeloupe, and “Vieux Café” in Haiti. These vernacular names suggest that coffee agroforests deliver not only provisioning and regulating ecosystem services but also cultural ones.

The Typica variety is well-adapted to agroforestry systems, including both Islands' traditional *jardins creoles*: The same rusticity that allowed coffee stands to survive the Haitian revolutionary wars (Lundahl, 1984) also allowed it to persist in present systems and through continuing socio-political instability. It can also serve to diversify Guadeloupean banana farms and make them more resilient. However, Typica is low-yielding and biotic aggressor-sensitive, cannot satisfy expectations of competitive, high volume productivity, and is likely to leave farmers vulnerable to pests and diseases. Insights can be gleaned from another Typica-growing West Indian nation: Jamaica. Owing to the prestige and reputation of its Blue Mountain coffee, which is historically Typica (consistent with our genotyping results), the variety persists through intensive cropping methods, agrochemical use, and encouragement from a well-organized network of cooperatives, private sector firms, public actors, and an industry board that work to maintain its profitability. Despite this, production is decreasing, and several Jamaican farmers struggle with economic and biotic pressures and institutional barriers. They also express interest in varietal diversification through growing adoption of CLR-resistant Geisha and other varieties (Birthwright, 2023; Guido et al., 2020; Willis & Johnson, 2020).

Since the 18th century, Haitian coffee has been unfavorably compared to Martinique and Guadeloupe's coffee (Lafleur, 2006; Moral, 1955; Ukers, 1922) due to post-harvest treatment: Haitian coffee has long had the issue of its beans being processed improperly (Arias et al., 2006; Moral, 1955). However, both Guadeloupean and Haitian Typica coffees retain a very high cup quality potential provided adequate post-harvest processing. In the case of Guadeloupe, low profitability owing to high production costs is an issue, which can be alleviated by crop diversification and labeling or certification to increase value (Mazardin & Saj, 2023). However, this process is hindered by a relative lack of institutional structuring of the coffee sector, insufficient capacity building, and lack of integration of its actors (Chaumeil, 2023; Dulcire, 2005; Dulcire & Ribeyre, 2003; Kiki, 2015).

The potential effect of environment must also be considered: Typica has persisted for centuries in a variety of bioclimatic conditions on the Islands, but some areas may not allow for its quality and production potential to be best expressed. Indeed, our analyses revealed a clear bioclimatic differentiation of Guadeloupe and Haiti (Figure S6), as well as revealing internal regional differences. Most regions were within the appropriate reported range of mean annual

rainfall (1200–1800 mm) and slightly above that for annual temperature (18–21, up to 23°C) for Arabica, though microclimate and agroforestry conditions can compensate for improper macroclimatic conditions (DaMatta & Ramalho, 2006; De Camargo & Pereira, 1994). Locations on Guadeloupe's *Côte au Vent* (Windward) coast were warm and low in elevation, consistent with its historical status as marginal coffee land, where coffee could only grow in moist ravines (Gottmann, 1945; Lafleur, 2006). Environment and microclimate can affect coffee quality, potentially producing a *terroir* effect to differentiate the otherwise genetically homogeneous Typica (Bertrand et al., 2012), and further justifying labeling (or certification of geographic origin) efforts. Organoleptic testing is required to confirm this effect.

#### 4.9 | Legacy of diversification in Haiti and Guadeloupe must be considered

In Guadeloupe, the SL/Kenyan-like and Moka varieties identified in our genetic analysis could also be considered to create a niche cluster of excellence with high added value, but with the same agronomic limitations as the Typica variety, particularly in regards to CLR susceptibility. The genetic homogeneity of these coffee stands would need to be assessed to support labeling or marketing efforts. These limitations also apply to many of the varieties introduced to Haiti.

Farms with introgressed varieties may be less affected by CLR, but these varieties may be more susceptible to other pathogens such as *Mycena citricolor* (Ribeyre & Avelino, 2012). Furthermore, some countries have reported loss of CLR resistance in Catimors (Cabral et al., 2016). Compact, “modern” varieties such as Caturra and Catimor also have higher nutritional requirements than traditional ones and may therefore require fertilizer or manure application to perform well (World Coffee Research, 2019). Anecdotally, several Haitian farmers participating in the present studies remarked that compact varieties were very productive in their first 5–6 years, after which their yields dropped, while production lasted longer in Typica. This may be due to nutrient limitations in compact varieties, or possibly lack of adequate pruning to rejuvenate vegetative organs (Somarriba & Quesada, 2022). In diversified systems in which coffee is but one crop among many, and in which farmers may be uninterested in increasing their management intensity, or unable to do so due to lacking necessary resources (labor, money, or technical knowledge), traditional varieties are thus better suited.

Regarding other *Coffea* species, the role of Robusta in Guadeloupe seems unlikely to change, but Liberica has re-emerged as a trendy species in specialty shops, albeit to a limited extent (Davis et al., 2022) and may help diversify production, especially on the Windward coast. The continued presence of these species suggests that farmers are open to cultivating coffee trees other than Typica if they can be incorporated into relevant food networks, including household economies. In Haiti, “Brasil coffee” (Robusta) adoption has been slow, and its future is uncertain. However, it may be well-suited to the local market, where quality expectations are lower.

#### 4.10 | Appropriateness of varietal introductions depends on local contexts

With traditional varieties being low-yielding and CLR sensitive, and introgressed varieties requiring intensification (and potentially losing CLR tolerance), questions could be raised on the appropriateness of maintaining a purely conservative approach to Arabica cultivation. The advent of modern genetics, with increasing availability of marker-based genotyping, has greatly facilitated the study and valorization through breeding of coffee diversity. In the 1950s–60s, realizing the value of crop diversity and the untapped genetic potential of crop wild relatives, scientists had prospected wild Ethiopian accessions and put them in germplasm collections along with commercial accessions (Engelmann et al., 2007). In the 1990s, this collected diversity began to be channeled into F1 “hybrid” clone lines combining pest and disease resistance, agronomic performances (vigor, yield, adaptation to shade), good organoleptic qualities (Breitler et al., 2022), and climate change adaptation (Kahsay et al., 2023). This development has been called a paradigm shift (McCook & Montero-Mora, 2024), in which coffee breeding adapts to local farm systems (rather than farms adapting to coffee trees' requirements), though it arguably continues the process of inter-varietal crosses stretching from 1943's Mondo Novo (Typica × Bourbon, WCR). To date, this development of new resilient varieties in the world has impacted neither Haiti nor Guadeloupe.

Importing modern varieties or even F1 hybrid clones to Guadeloupe could be an option to bypass the traditional varieties' limitations, provided the chosen material is adapted to farming systems. Guadeloupe is equipped with scientific institutions that can greatly help their adoption. However, doing so entails the foregoing of traditional varieties and the historical value and narrative they provide. The decision is ultimately in the hands of coffee growers and of politics. Another possible avenue is the prospection of admixed Typica-SL/Kenyan-like trees to identify possible traits of interest via phenotyping. If found, such trees could benefit from the narrative of being “purely” from Guadeloupe.

As for Haiti, history has shown that farmers are attached to traditional farming systems and that new genetic material is absorbed into existing systems rather than replacing them. Newer varieties like F1 clones are un-adapted to local field management practices that result in dynamic genetic diversity within coffee stands (Millet et al., 2024). However, this history has yielded a high Arabica diversity that should be also explored to identify potential phenotypes of interest and adaptation mechanisms (if any) resulting from various socio-economic and ecological filters to which it is subjected. This could lead to new cultivars that can be spread to other similar cropping systems.

Both Islands have had prior, ultimately unsuccessful attempts at relaunching their coffee agriculture, and current ones are taking place in the context of a changing climate working against them (Bunn et al., 2015; de Sousa et al., 2019). Growing interest in sustainable and niche coffee (International Coffee Organization [ICO], 2023) provides opportunities for these marginal producers. Knowledge of

standing genetic resources and their historical determinants can help inform their research, management, and marketing for better, more resilient coffee farming systems.

## AUTHOR CONTRIBUTIONS

**Claude Patrick Millet:** Conceptualization; formal analysis; investigation; methodology; writing—original draft preparation; review and editing. **Boris Delahaie:** Supervision; writing—review and editing; writing—review and editing. **Frédéric Georget:** Conceptualization; investigation; methodology; supervision; writing—review and editing. **Clémentine Allinne:** Conceptualization; funding acquisition; methodology; supervision; writing—review and editing. **William Solano-Sánchez:** Resources. **Dapeng Zhang:** Methodology; resources. **Wesly Jeune:** Project administration; funding acquisition; supervision. **Lucile Toniutti:** Conceptualization; funding acquisition; investigation; methodology; project administration; supervision; writing—review and editing. **Valérie Poncet:** Conceptualization; funding acquisition; methodology; supervision; writing—review and editing.

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## CONFLICT OF INTEREST STATEMENT

The authors declare no competing interest.

## DATA AVAILABILITY STATEMENT

The data and related documentations that support the findings of this study are available on request in DataSuds repository (IRD, France) at <https://doi.org/10.23708/MRPVHL>.

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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