agronomy

MDPI

Article

Vernacular Names and Genetics of Cultivated Coffee (*Coffea arabica*) in Yemen

Christophe Montagnon [1,*], Veronica Rossi [2], Carolina Guercio [2] and Faris Sheibani [3]

[1] RD2 Vision, 60 Rue du Carignan, 34270 Valflaunes, France
[2] Lavazza Group, Via Bologna 32, 10152 Torino, Italy
[3] Qima Coffee, 21 Warren Street, Fitzrovia, London W1T 5LT, UK
* Correspondence: christophe.montagnon@rd2vision.com

Abstract: While Ethiopia and South Sudan are the native habitats for *Coffea arabica*, Yemen is considered an important domestication center for this coffee species as most Arabica coffee grown around the world can be traced back to Yemen. Furthermore, climatic conditions in Yemen are hot and extremely dry. As such, Yemeni coffee trees likely have genetic merits with respect to climate resilience. However, until recently, very little was known about the genetic landscape of Yemeni coffee. The Yemeni coffee sector identifies coffee trees according to numerous vernacular names such as Udaini, Tufahi or Dawairi. However, the geographical landscape of these names and their correlation with the genetic background of the coffee trees have never been explored. In this study, we investigated the geographic occurrence of vernacular names in 148 coffee farms across the main coffee areas of Yemen. Then, we used microsatellite markers to genotype 88 coffee trees whose vernacular name was ascertained by farmers. We find a clear geographical pattern for the use of vernacular coffee names. However, the vernacular names showed no significant association with genetics. Our results support the need for a robust description of different coffee types in Yemen based on their genetic background for the benefit of Yemeni farmers.

Keywords: agro-biodiversity; genetic diversity; landraces

check for updates

Citation: Montagnon, C.; Rossi, V.; Guercio, C.; Sheibani, F. Vernacular Names and Genetics of Cultivated Coffee (*Coffea arabica*) in Yemen. *Agronomy* **2022**, *12*, 1970. https://doi.org/10.3390/agronomy12081970

Academic Editor: Maria Céu Lavado da Silva

Received: 4 August 2022
Accepted: 18 August 2022
Published: 20 August 2022

1. Introduction

Whilst the natural habitat of the coffee tree, *Coffea arabica*, is the Southwestern mountains of Ethiopia [1] and the Boma Plateau of South Sudan [2], Yemen is known as the main domestication center of the species [3–9]. As a consequence of the domestication process, a clear genetic separation has been consistently observed between *C. arabica* in its natural habitat and the cultivated coffee in Yemen [10–14]. Montagnon and co-authors [14] unveiled the genetic diversity of Arabica coffee cultivated in Yemen, showing that most of the Arabica coffee cultivated varieties around the world are derived from two Yemeni mother populations. A third mother population (New-Yemen) was also identified and found to be only in Yemen.

Increasing knowledge of coffee cultivated in Yemen is of great significance for the coffee community around the world, including the 12.5 million households that rely on coffee growing for their incomes [15]. Due to climate change, the world is projected to lose 50% of suitable coffee-growing land by 2050 [16]. The climate in the coffee-growing regions of Yemen is one of the driest in the world, with an annual rainfall below 400 mm per year, while the minimum annual rainfall from more than 62,000 points representing arabica coffee-growing area around the world was almost double that, at 754 mm per year [17]. There is little doubt that domestication in Yemen has favored drought-resistant genotypes, which would be of interest to the coffee community.

Coffee farmers in Yemen use various names to describe the coffee types they are growing. While dozens of names have been listed in previous studies [18,19], four varieties are claimed to be ubiquitous and represent the majority of cultivated Arabica coffee in

Yemen: Udaini, Dawairi, Tufahi and Burai [18–24]. However, to date, the list of names and their occurrence has not been based on a well-defined study covering the major coffee regions of Yemen. A study on the genetic diversity of 17 coffee genotypes corresponding to a given name found that the same name, such as Udaini, could be found in different genetic clusters [24]. No other study has addressed the coffee genetic background of coffee in relation to the names given by farmers. The names are often in reference to either the supposed geographical origin of the planting material or to some specific morphological features. Hence, without a comprehensive genetic study of these different coffee types, the given names can be considered to be vernacular names (=local names) rather than varietal names reflecting genetic identity.

Deciphering the relationship between vernacular names and genetic identity is extremely important for the coffee seed sector in Yemen. It enables farmers to benefit from reliable, stable, improved planting material and enables the coffee community to benefit from the genetic diversity potential of Yemen [14], namely in the context of climate change. In the present study, the hypothesis that vernacular names of coffee trees in Yemen are correlated to a specific genetic identity is tested. For this purpose, we intend (i) to confirm, using robust data, the naming of coffee planting materials in Yemen and their relationship to Yemen's coffee-growing areas and (ii) to assess the association between the local names and the genetics of the coffee planting material in Yemen.

2. Materials and Methods

In 2020, in the framework of a coffee development project funded by Lavazza Foundation and Qima Foundation and executed by Qima Coffee, 148 coffee farmers located in five governorates indicated the name of their cultivated coffee (Figure 1; Table 1).

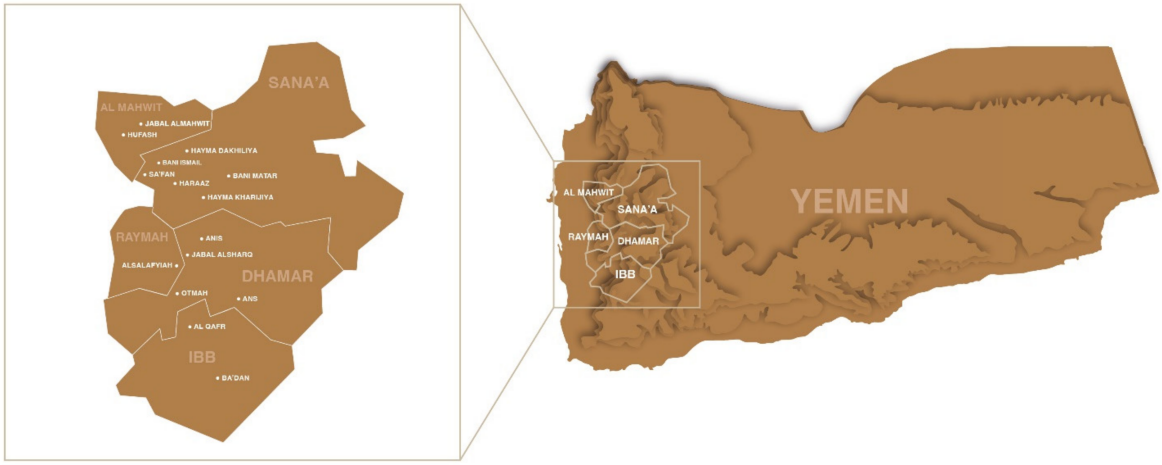

Figure 1. Map of Yemen and coffee-growing regions covered by the study.

Based on the occurrence and importance of the listed vernacular names, 88 trees representing the main cited names were sampled (Table 1). For each sample, the farmer was present and confirmed the name of the coffee tree while sample material was taken from the same tree.

DNA extraction and SSR marker analysis were performed by the ADNiD laboratory of the Qualtech company in the South of France (http://www.qualtech-groupe.com/en/, accessed on 12 August 2022). Genomic DNA was extracted from approximately 20 mg of dried tissue using 1 mL of SDS buffer. DNA was then purified with a magnetic bead (Agencourt AMPure XP, Beckman Coulter, Brea, CA, USA), followed by elution in Tris Edta (TE) buffer. The DNA concentration was estimated with an Enspire spectrofluorometer (PerkinElmer, Waltham, MA, USA) with a bisbenzimide DNA intercalator (Hoechst 33258) and by comparison with known standards of DNA.

Eight SSR primer pairs were selected after Combes et al. [25] and Pruvot-Woehl et al. [26]. Two new SSR primer pairs were included (Sat-207 and Sat-244) (Table 2).

Table 1. Number of coffee farms indicating vernacular names and coffee trees sampled for genotyping per governorate and region in Yemen.

		Indication of Vernacular Names	# Samples for Genotyping for Main Vernacular Names				
Governorate	**Region**	**# Farms**	**Udaini**	**Dawairi**	**Buna**	**Jaadi**	**Tufahi**
Al Mahwit	Hufash	8					
	Jabal Almahwit	22	8		5		
	Total	*30*					
Dhamar	Anis	4					
	Ans	13	5	5			
	Jabal Alsharq	2					
	Otmah	4					
	Total	*23*					
Ibb	Alqafr	25	11	5			6
	Ba'dan	6					
	Total	*31*					
Raymah	Alsalafyiah	5					
	Total	*5*					
Sanaa	Bani Ismail	5					
	Bani Matar	3	2	1		1	
	Hayma Dakhiliya	12				4	
	Hayma Kharijiya	11	13	3			3
	Haraaz	28				13	3
	Total	*59*					
	Grand Total	**148**	**39**	**14**	**5**	**18**	**12**

Table 2. List of microsatellite markers with their locus code, primer sequences and product size.

Code of Microsatellite	Primer Sequence Forward	Primer Sequence Reverse	Size Product (bp)
Sat-11	ACCCGAAAGAAAGAACCAA	CCACACAACTCTCCTCATTC	143–145
Sat-207	CAATCTCTTTCCGATGCTCT	GAAGCCGTTTCAAGCC	83–93
Sat-225	CATGCCATCATCAATTCCAT	TTACTGCTCATCATTCCGCA	283–317
Sat-235	TCGTTCTGTCATTAAATCGTCAA	GCAAATCATGAAAATAGTTGGTG	245–278
Sat-24	GGCTCGAGATATCTGTTTAG	TTTAATGGGCATAGGGTCC	167–181
Sat-244	GCATACTAAGGAATTATCTGACTGCT	GCATGTGCTTTTTGATGTCGT	178–306
Sat-254	ATGTTCTTCGCTTCGCTAAC	AAGTGTGGGAGTGTCTGCAT	221–237
Sat-29	GACCATTACATTTCACACAC	GCATTTTGTTGCACACTGTA	137–154
Sat-32	AACTCTCCATTCCCGCATTC	CTGGGTTTTCTGTGTTCTCG	119–125
Sat-47	TGATGGACAGGAGTTGATGG	TGCCAATCTACCTACCCCTT	135–169

PCR was carried out in a 15 µL final volume with 30 ng genomic DNA and 7.5 µL of 2× PCR buffer (Type-it Microsatellite PCR Kit, Qiagen, Quiagen, Hilden, Germany), with 1.0 µM each of forward and reverse primer (10 µM). A thermal cycler (Eppendorf) was used for amplification. It was set at 94 °C for 5 min for initial denaturation, followed by 94 °C for 30 s, annealing temperature depending on the primer used for another 30 s and then 72 °C for 1 min for 35 cycles, followed by a final step of extension at 72 °C for 5 min. The final holding temperature was 4 °C. PCR samples were run on a capillary electrophoresis ABI 3130XL with an internal standard: GeneScan 500 LIZ size standard (Applied Biosystems, Waltham, MA, USA). GeneMapper v.4.1 software (Applied Biosystems, Waltham, MA, USA) was used for alleles scoring with a visual inspection. Under the assumption of a significant association between vernacular names and genetics, each sample could be considered as a biological replicate of the corresponding indicated vernacular name (Table 1). There were no technical replicates as this method has proven to be robust and replicable in previous studies [14,25,26].

The scoring method previously described [14,26] was used. The presence or absence of alleles was coded as 1 or 0, respectively. Indeed, *C. arabica* being tetraploid, only an allelic phenotype, and not genotype, can be scored. If both alleles A and B are present, it cannot be decided if this phenotype AB corresponds to AABB, ABAB, AAAB or ABBB.

The association between genetic groups, vernacular names and geography (governorates) was tested using the Monte Carlo test for associations [27] adapted to situations where theoretical numbers per cell are inferior to 5. The number of simulations was 5000. The test was run using Xlstat [28].

DARwin6 software (Cirad, Montpellier, France) [29] was used with single data files. The dissimilarity matrix was calculated using Dice Index, which is well adapted to alleles' presence/absence data [29], and was the basis for the execution of the Principal Coordinates Analysis (PCoA).

Figures 2–6 were produced using Tableau software (Salesforce, San Francisco, CA, USA) [30].

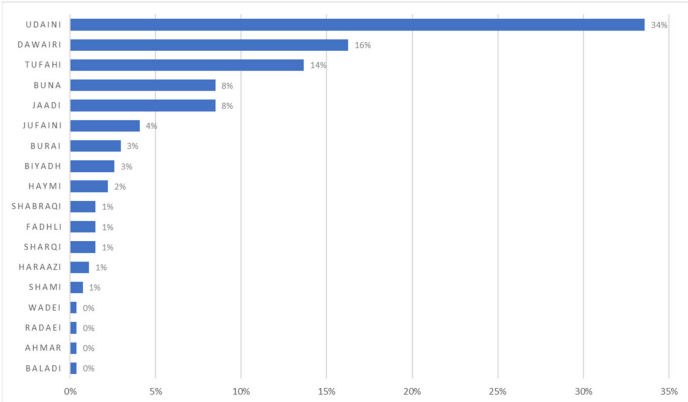

Figure 2. List and frequency of vernacular coffee names mentioned on 148 coffee farms in Yemen.

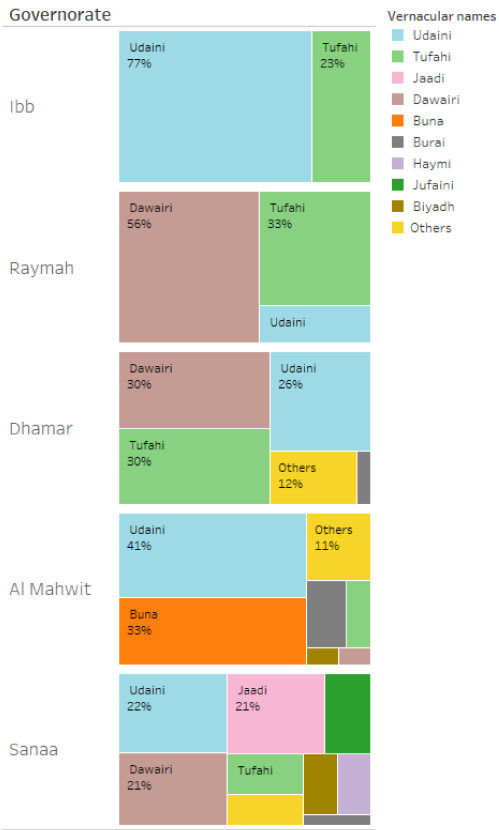

Figure 3. Share of vernacular coffee names mentioned on 148 farms from different governates in Yemen. In each cell (=governorate), the area for each name is proportional to its frequency. The sum of frequencies in each governorate is equal to 1.

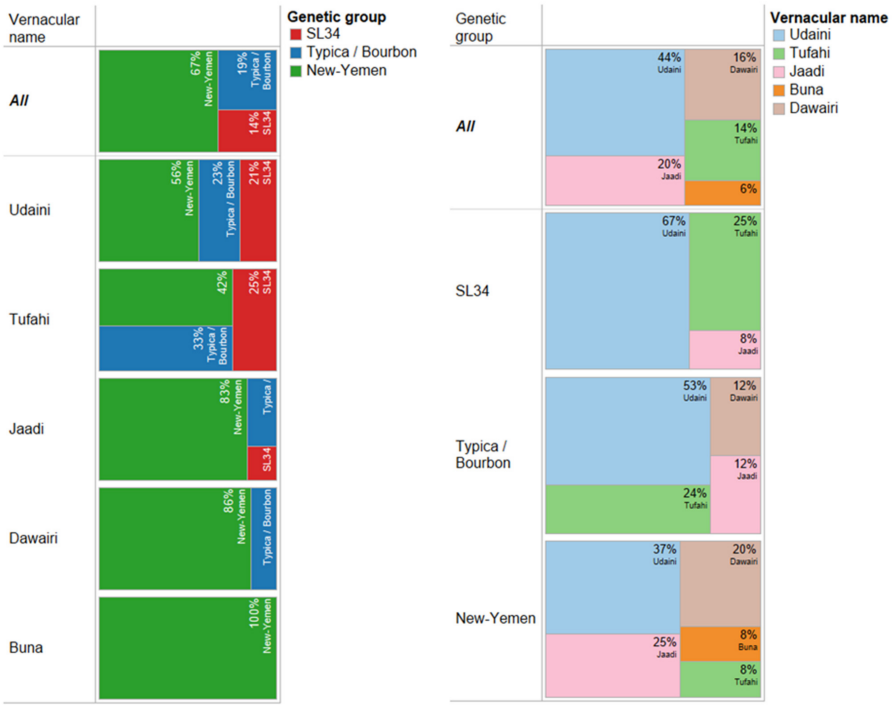

Figure 4. Share of coffee genetic group amongst samples with the same vernacular name (**left**) and share of vernacular names for each genetic group (**right**). The sum of frequencies in each cell is equal to 1.

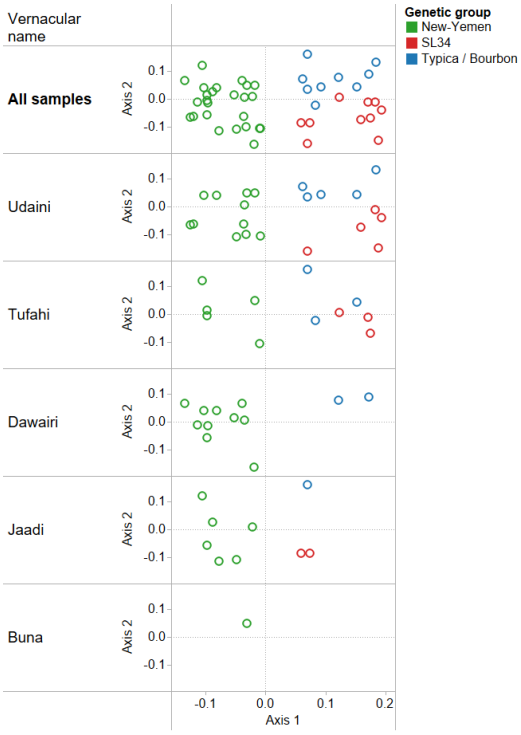

Figure 5. Representation of 88 coffee samples on the first two components of the PcoA based on their SSR profile. The first row includes all the samples, and subsequent rows show samples of each vernacular name separately. The color of each point corresponds to the different genetic groups.

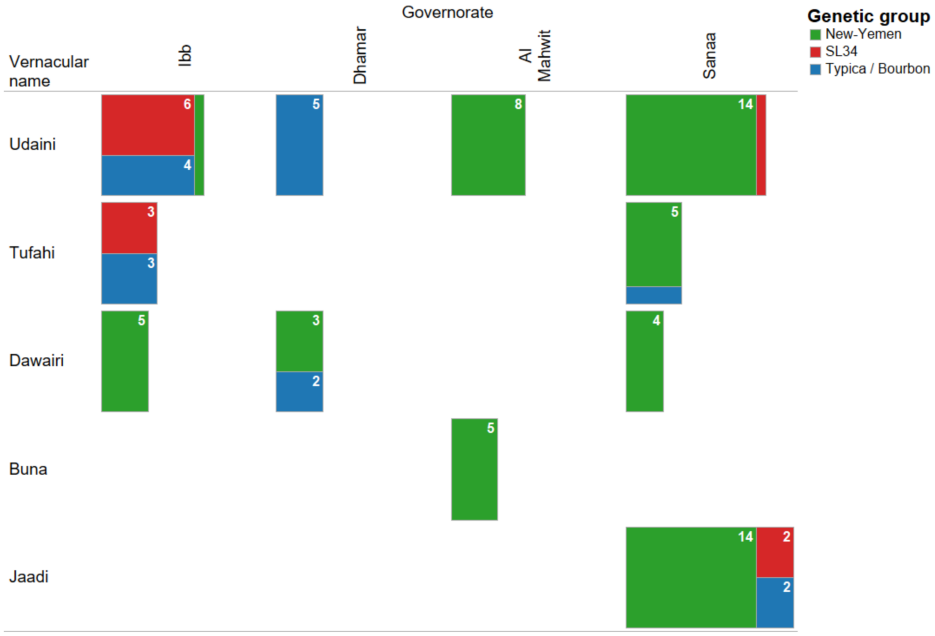

Figure 6. Genetic make-up of 88 coffee samples along with their vernacular name and the governorate of origin.

3. Results

In 93% of the 148 farms (137/148), the vernacular name of the cultivated coffee trees was given. Eighteen vernacular names were mentioned (Figure 2). Udaini represented more than one-third of the citations (34%). Dawairi and Tufahi were most cited after Udaini with 16% and 14%, respectively. Then, only Buna and Jaadi had more than 5% citations. Hence, the top 5 vernacular names represented 80% of the total, while the remaining 13 represented 20%.

The Monte Carlo test for association between vernacular names and governorates showed a highly significant dependence between the two (p-value < 0.0001). There was a strong South (Ibb, Raymah, Dhamar)–North (Al Mahwit, Sanaa) geographic pattern for given vernacular names (Figures 1 and 3). In Ibb, only two vernacular names were given (Udaini and Tufahi), and 80% of the farmers stated that they grow only one variety. Sanaa and Mahwit had the largest number of given vernacular names, and 80% of the farmers stated that they grow two or more varieties. Jaadi, Jufaini and Haymi were specific to Sanaa. On the other hand, Buna was specific to Al Mahwit, and Dawairi was cited only once in this governorate. Udaini and Tufahi were the most ubiquitous names, followed by Dawairi, even if the latter was absent in Ibb and rarely cited in Al Mahwit. There were also differences identified between regions within the governorate of Sanaa. Udaini was the main vernacular name given in Hayma Dakhiliya (40% of cited names) and Hayma Kharijiya (50% of cited names), while Jaadi, Tufahi and Jufaini were cited in Haraaz with a frequency of 32%, 17% and 22% respectively.

The genetic profile of all of the samples fell into one of the three genetic groups previously described in Yemen [14]: SL34, Typica/Bourbon and New-Yemen. The name–genetic group association (Figure 4) was not significant (Monte Carlo test p-value = 0.284). 67%, 19% and 14% of samples named Udaini were from the New-Yemen, Typica/Bourbon and SL34 genetic groups, respectively. For Tufahi, 56%, 23% and 21% of samples named Udaini were from the New-Yemen, Typica/Bourbon and SL34 genetic groups, respectively. Jaadi, Dawairi and Buna trees were predominantly from the New-Yemen genetic group with a representation of 83%, 86% and 100%, respectively.

Reciprocally, most samples from the SL34 genetic group correspond to the given names of Udaini (67%) and Tufahi (25%), with only 8% corresponding to Jaadi. The samples from

the Typica/Bourbon and New-Yemen genetic groups correspond to all given names. Buna was the only given name that was only from the New-Yemen genetic group.

The PCoA of all genotyped samples shows that the genotypes are diverse even within each genetic group (Figure 5). If the name–genotype relationship was perfect, then each name would be represented by a distinct single genotype. Only the five Buna samples corresponded to a single genotype. However, two Udaini samples were also of the same genotype. Udaini and Tufahi samples covered the entire diversity of genotypes. Dawairi and Jaadi had more samples from the New-Yemen genetic group but still had a large diversity of genotypes.

Figure 6 shows the genetic groups of the samples in relation to their vernacular name and their region of origin. The Monte Carlo test showed a highly significant association between genetic groups and geography (p-value < 0.0001). As previously observed, the Udaini and Tufahi samples correspond to all three genetic groups. However, both Udaini and Tufahi were found to be mainly from the New-Yemen group when grown in Al Mawhit and Sanaa, while those grown in Ibb and Dhamar were found to correspond to the SL34 and Typica/Bourbon groups. Irrespective of the region of cultivation, Dawairi samples were found to be mostly from the New-Yemen group, with the exception of two samples that were cultivated in Dhamar, which corresponded to the Typica/Bourbon group. Buna, only mentioned in Al Mawhit (Figure 3), corresponded to only one genotype of the New-Yemen group. Finally, Jaadi, only mentioned in Sanaa, was mostly (15/18) from the New-Yemen group, with 2 samples from the Typica/Bourbon group and only 1 sample from the SL34 group.

4. Discussion

To our knowledge, this is the first time that vernacular names of coffee grown in Yemen have been systematically explored in the main coffee-growing regions of the country. By far, Udaini was found to be the most widely referenced name (34%), while Dawairi, Tufahi, Buna and Jaadi made up the remaining widely used names, with each being referenced at more than 5% frequency. These results are in line with previous knowledge [18–21]. However, our results quantify the weight of each name and further show a clear geographical pattern related to the names. We found that Udaini and Tufahi were cited in all regions but were the only ones to be cited in Ibb and almost the only ones in Dhamar and Raymah. On the other hand, the northern regions of Sanaa and Al Mawhit had a greater number of vernacular names, including Udaini, Tufahi and Dawairi. Jaadi was only referenced in one single region within Sanaa–Haraaz, while Buna was specific to Al Mawhit.

Our study indicated no significant association between the given vernacular name and the genetic identity. In particular, Udaini and Tufahi samples were spread across all the genetic groups, and variability was found amongst the samples. Neither Dawairi nor Jaadi had a clear genetic identity, but they were more from the New-Yemen genetic group. Of the main vernacular names, Buna had the clearest genetic identity as the five samples corresponding to that name had the very same genotype. However, some samples named Udaini also shared the very same genotype in the same region.

All in all, our results show that the region of cultivation might be a better proxy (highly significant association) for the genetic identity, at least the genetic group, than the vernacular name. Indeed, whatever the given vernacular name, the majority of samples from Sanaa and Al Mawhit were in the "New-Yemen" group, while Typica/Bourbon and SL34 genetic groups were more represented in Ibb and Dhamar (Figure 6).

During the visit of the technicians to the farms, there was an attempt to characterize the coffee trees according to the main coffee descriptors [31]. However, the data were not usable because of the different conditions and environments of the individual plants (data not shown). Mutations in *C. arabica* have played an important role in varietal coffee development worldwide. Caturra has been one of the earliest referenced human-selected varieties [32]; Caturra is a dwarf mutation of the Bourbon variety [33,34]. Dwarfism can also occur in different genetic backgrounds; for instance, Pache is a dwarf mutation of

the variety Typica. Numerous other mutations have been described in the species [35], including the Laurina (= Bourbon Pointu) mutation of Bourbon with low caffeine content, which has been well described and referenced [36]. SSR markers are powerful markers for the authentication of *C. arabica* varieties [26]. However, to our knowledge, no molecular markers are available for the detection of mutations in *Coffea*. The mutations are observed through their phenotypic expression. The scarce descriptions of cultivated coffee in Yemen suggest that Udaini and Tufahi would be tall trees while Dawairi would be dwarf or more compact; additionally, Tufahi is said to have a specific fruit shape reminding of an apple, which gave the name Tufahi in Arabic [19,20]. However, even the general tall/dwarf description of the different types is not that clear cut. In some regions, the Dawairi trees are clearly told to be "compact", while in other regions, they are defined as tall trees (Montagnon, informal discussions with some Yemeni farmers). Table 3 summarizes the information regarding the origin of the names one Arabic-speaking co-author of the present study from his experience and discussions with farmers. In general, the geographical origin is a proxy for genetic background only if this origin corresponds to genetically uniform coffee trees. Most traits that are listed in Table 3 are either qualitative mutations (dwarfism/compact habit or yellow cherries) or related to the variation of quantitative traits that are independent of the genetic background.

Table 3. Origin of the vernacular coffee names in Yemen.

Variety	Frequency	Named after a Region of Origin	Named after a Specific Visible Trait	Comments
Udaini	34%	Al Udaini		
Dawairi	16%		Tree shape	"Dawairi" means "rounded" in Arabic, possibly related to bushy shape
Tufahi	14%		Coffee cherries are apple-shaped	
Jaadi	8%		Clustered cherries—close together	"Jadi" in Arabic can be translated to "curly" or "rough". Some farmers state it refers to curly leaves, others state it refers to rough cherry clusters that are difficult to pick.
Buna	8%		For smaller trees and cherries	"Buna" is the feminine of "bun" which is "coffee" in Arabic. In Arabic sometimes, the feminine noun can be used to represent smaller size/structure; hence possibly related to smaller trees
Jufaini	4%		Shape of cherries—elongated	"Jufain" means "eyelids"—possibly related to the shape of the cherry and/or the bean, like almonds in shape.
Burai	3%	Bura		
Biyadh	3%		Cherries are lighter in colour	"Bayad" comes from the word "white" in Arabic
Haymi	2%	Hayma		
Sharqi	1%	Sharqi Haraaz		
Fadhli	1%	Bani Fadl		
Shabraqi	1%		Lowest branches fall rip apart as if they were naturally pruned	"Shobraq" means "ripped apart" in Arabic
Harazi	1%	Haraaz		
Shami	1%		Yellow cherries	The word "sham" can mean corn (which are yellow in colour), likely refering to the yellow cherry mutation
Baladi	0%	Local		"Baladi" means "local" in Arabic
Ahmar	0%		Red	"Ahmar" is translated literally to "red"
Radaei	0%	Radaa		
Wadei	0%	Yadi		

Our results support previous observations that a "variety" name is not a guarantee of genetic identity [19]. Eskes [37], in the governorates of Lahij and Abyan in the southeastern part of the Yemeni coffee-growing regions, gave one of the most detailed descriptions of different cultivated coffees in Yemen. He described both tall and compact trees, such as the "Ludia" type. Interestingly, the author indicated that the "Udaini type appeared the most variable, whereas other local types showed less variation". The occurrence of mutations on coffee trees in Yemen is likely partly responsible for blurring the cultivated coffee naming–genetic correlations in this country. The absence of correlation between genetics and vernacular names is not specific to *C. arabica* in Yemen. In coffee in general, because of the absence of a professional seed sector in most countries, the variety name of a plant is often not a guarantee of its genetic background [26]. In Ethiopia, the native habitat of *C. arabica*, there are formally identified varieties originating from a referenced breeding program [38,39]. There are also numerous landrace vernacular names [39]. To our knowledge, there has been no study that has evaluated the correlation between local names given to coffee trees in Ethiopia and their genetic background. However, some studies did prove that the human-provoked movements of seeds in Ethiopia had blurred the reference to the geographical origin of coffee [40–42]. *C. arabica* is an autogamous species. Nevertheless, it has been shown that cross-pollination can represent 10% to 15% [43,44], and potentially up to 50% [45]. However, our results show that Udaini and Tufahi names correspond to different genetic groups, without any signs of cross-pollination between the groups. Rather, our results indicate that relying on some morphological similarities and/or the origin of the seeds is not a good indication of coffee genetic similarities in Yemen. Peroni et al. [46] showed, in Brazil, that Cassava (*Manihot esculenta*) vernacular names were powerful in discriminating sweet and bitter varieties in relation to their genetic groups because this trait (bitter or sweet) is easy to evaluate by farmers. However, the genetic diversity within these two main groups did not match the diversity of vernacular names. In Ethiopia, Birmeta et al. [47] also observed the limitation of vernacular names as a proxy for the genotype of *Ensete ventricosum* because morphological similarity is not always equivalent to genetic similarity.

Only a collection of genetically verified trees with different genetic backgrounds in a single site in Yemen will allow a rigorous and complete phenotypical description of the different genetic types. The use of vernacular names will not help reach this objective. Only through genotyping would it be possible to gather coffee trees according to their genetic background. A central and statistically rigorous description and phenotypical evaluation of the different coffee genetic types in Yemen will pave the way for a sound genetic improvement program in the country and prevent genetic erosion. Furthermore, the resultant knowledge may benefit the wider coffee community facing challenges related to climate change [16].

5. Conclusions

Three hundred years ago, the few seeds that were smuggled out of Yemen gave the genetic basis of the *C. arabica* varieties that spread around the world. Since then, very little information on the genetics of coffee cultivated in Yemen has been available. A recent study by Montagnon et al. [14] unveiled a significant genetic diversity in Yemen. In this study, we show that vernacular names given to cultivated coffee have no correlation with the genetic background of the coffee trees. The same name is given to very different genetic backgrounds, and the same genetic background is associated with different names. Hence, coffee tree naming in Yemen does not reflect the inherent properties and merits of cultivated coffee trees. Robust phenotypic characterization of Yemeni coffee genetic types will help Yemeni farmers benefit from the genetic diversity they maintained through the generations. We, therefore, recommend the collection and characterization of both the genotype and phenotype of Yemeni coffee trees in one or several controlled germplasm collections in Yemen.

Author Contributions: Conceptualization, C.M. and F.S.; methodology, C.M. and F.S.; formal analysis, C.M; data curation, C.M.; writing—original draft preparation, C.M.; writing—review and editing, C.M., V.R., C.G. and F.S.; visualization, C.M. and F.S.; supervision, F.S., V.R. and C.G.; project administration, F.S.; funding acquisition, F.S., V.R. and C.G. All authors have read and agreed to the published version of the manuscript.

Funding: This research was funded by the Qima Foundation and the Lavazza Foundation.

Institutional Review Board Statement: Not applicable.

Data Availability Statement: The datasets generated during the current study are available from the corresponding author on reasonable request.

Acknowledgments: The authors would like to thank Yemeni coffee farmers for maintaining coffee genetic resources in Yemen for generations.

Conflicts of Interest: The authors declare no conflict of interest.

References

1. Davis, A.P.; Gole, T.W.; Baena, S.; Moat, J. The impact of climate change on indigenous arabica coffee (*Coffea arabica*): Predicting future trends and identifying priorities. *PLoS ONE* **2012**, *7*, e47981. [CrossRef]
2. Krishnan, S.; Pruvot-Woehl, S.; Davis, A.P.; Schilling, T.; Moat, J.; Solano, W.; Al Hakimi, A.; Montagnon, C. Validating South Sudan as a Center of Origin for *Coffea arabica*: Implications for Conservation and Coffee Crop Improvement. *Front. Sustain. Food Syst.* **2021**, *5*, 445. [CrossRef]
3. De La Roque, J. *Voyage de l'Arabie Heureuse, par l'Océan Oriental, et le Détroit de la Mer Rouge: Fait par les François Pour la Première Fois, Dans Les Années 1708, 1709 et 1710*; André Cailleau: Paris, France, 1716. Available online: https://play.google.com/books/reader?id=3fsOAAAAQAAJ&hl=fr&num=10&printsec=frontcover&pg=GBS.PP7 (accessed on 1 July 2022).
4. Ukers, M.A. *All about Coffee*; The Tea and Coffee Trade Journal: New York, NY, USA, 1922.
5. Chevalier, A. Les caféiers du globe. I. In *Généralités sur les Caféiers. Encyclopédie Biologique*; Paul Lechevalier: Paris, France, 1929.
6. Cramer, P.J.S. *A Review of Literature of Coffee Research in Indonesia (from about 1602 to 1945)*; IICA: Turrialba, Costa Rica, 1957.
7. Haarer, A.E. Modern coffee production. In *Ebenezer Baylis and Son*; The Trinity Press: London, UK, 1958.
8. Meyer, F.G. Notes on wild *Coffea arabica* from Southwestern Ethiopia, with some historical considerations. *Econ. Bot.* **1965**, *19*, 136–151. [CrossRef]
9. Koehler, J. *Where the Wild Coffee Grows: The Untold Story of Coffee from the Cloud Forests of Ethiopia to Your Cup*; Bloomsbury Publishing: New York, NY, USA, 2017.
10. Anthony, F.; Bertrand, B.; Quiros, O.; Wilches, A.; Lashermes, P.; Berthaud, J.; Charrier, A. Genetic diversity of wild coffee (*Coffea arabica* L.) using molecular markers. *Euphytica* **2001**, *118*, 53–65. [CrossRef]
11. Anthony, F.; Combes, M.C.; Astorga, C.; Bertrand, B.; Graziosi, G.; Lashermes, P. The origin of cultivated *Coffea arabica* L. varieties revealed by AFLP and SSR markers. *Theor. Appl. Genet.* **2002**, *104*, 894–900. [CrossRef]
12. Silvestrini, M.; Junqueira, M.G.; Favarin, A.C.; Guerreiro-Filho, O.; Maluf, M.P.; Silvarolla, M.B.; Colombo, C.A. Genetic diversity and structure of Ethiopian, Yemen and Brazilian *Coffea arabica* L. accessions using microsatellites markers. *Genet. Resour. Crop Evol.* **2007**, *54*, 1367–1379. [CrossRef]
13. Scalabrin, S.; Toniutti, L.; Di Gaspero, G.; Scaglione, D.; Magris, G.; Vidotto, M.; Pinosio, S.; Cattonaro, F.; Magni, F.; Jurman, I.; et al. A single polyploidization event at the origin of the tetraploid genome of *Coffea arabica* is responsible for the extremely low genetic variation in wild and cultivated germplasm. *Sci. Rep.* **2020**, *10*, 4642. [CrossRef]
14. Montagnon, C.; Mahyoub, A.; Solano, W.; Sheibani, F. Unveiling a unique genetic diversity of cultivated *Coffea arabica* L. in its main domestication center: Yemen. *Genet. Resour. Crop Evol.* **2021**, *68*, 2411–2422. [CrossRef]
15. Browning, D. How Many Coffee Farms Are There in the World? In Proceedings of the ASIC Conference, Portland, OR, USA, 16–20 September 2018. Available online: https://www.youtube.com/watch?v=vKaeDkpqPSg (accessed on 1 July 2022).
16. Bunn, C.; Läderach, P.; Jimenez, J.G.P.; Montagnon, C.; Schilling, T. Multiclass classification of agro-ecological zones for Arabica coffee: An improved understanding of the impacts of climate change. *PLoS ONE* **2015**, *10*, e0140490. [CrossRef]
17. Ovalle-Rivera, O.; Läderach, P.; Bunn, C.; Obersteiner, M.; Schroth, G. Projected shifts in *Coffea arabica* suitability among major global producing regions due to climate change. *PLoS ONE* **2015**, *10*, e0124155. [CrossRef]
18. USAID. Moving Yemen Coffee Forward. In *Assessment of the Coffee Industry in Yemen to Sustainably Improve Incomes and Expand Trades*; USAID: Washington, DC, USA, 2005. Available online: https://pdf.usaid.gov/pdf_docs/Pnadf516.pdf (accessed on 12 July 2022).
19. Al-Zaidi, A.A.; Baig, M.B.; Shalaby, M.Y.; Hazber, A. Level of knowledge and its application by coffee farmers in the Udeen Area, Governorate of IBB-Republic of Yemen. *J. Anim. Plant Sci.* **2016**, *26*, 1797–1804.
20. Cambrony, H.R.; Vincent, J.C.; Wierer, C. Caféiculture au Yémen 1975. In *Problèmes Révélés à L'occasion d'une Mission d'étude de la Production du Traitement et de la Commercialisation, Suggestions Pour une Réhabilitation*; Gerdad-IFCC: Montpellier, France, 1975.

21. Robinson, J.B.D. Coffee in Yemen: A practical guide. In *Rural Development Project Al-Mahwit Province*; Klaus Schwarz Verlag: Berlin, Germany, 1993.
22. Ebrahim, N.; Shibli, R.; Makhadmeh, I.; Shatnawi, M.; Abu-Ein, A. In vitro propagation and in vivo acclimatization of three coffee cultivars (*Coffea arabica* L.) from Yemen. *World Appl. Sci. J.* **2007**, *2*, 142–150.
23. Al-Azab, A.; Habib, S.; Hussein, M.; El-Sherif, F. Micropropagation of Four Coffee Cultivars (*Coffea arabica* L.) from Yemen through Shoot Tip Culture. *Hortsci. J. Suez Canal Univ.* **2015**, *4*, 25–31.
24. Hussein, M.A.; Al-Azab, A.; Habib, S.; El Sherif, F.M.; El-Garhy, H.A. Genetic Diversity, Structure and DNA Fingerprint for Developing Molecular IDs of Yemeni Coffee (*Coffea Arabica* L.) Germplasm Assessed by SSR Markers. *Egypt. J. Plant Breed.* **2017**, *203*, 713–736.
25. Combes, M.C.; Andrzejewski, S.; Anthony, F.; Bertrand, B.; Rovelli, P.; Graziosi, G.; Lashermes, P. Characterization of microsatellite loci in *Coffea arabica* and related coffee species. *Mol. Ecol.* **2002**, *9*, 1178–1180. [CrossRef]
26. Pruvot-Woehl, S.; Krishnan, S.; Solano, W.; Schilling, T.; Toniutti, L.; Bertrand, B.; Montagnon, C. Authentication of *Coffea arabica* Varieties through DNA Fingerprinting and its Significance for the Coffee Sector. *J. AOAC Int.* **2020**, *103*, 325–334. [CrossRef]
27. Sham, P.C.; Curtis, D. Monte Carlo tests for associations between disease and alleles at highly polymorphic loci. *Ann. Hum. Genet.* **1995**, *59*, 97–105. [CrossRef]
28. Addinsoft. *XLSTAT Statistical and Data Analysis Solution*; Addinsoft: Paris, France, 2022. Available online: https://www.xlstat.com/fr (accessed on 12 July 2022).
29. Perrier, X.; Jacquemoud-Collet, J.P. DARwin Software. 2006. Available online: http://darwin.cirad.fr/darwin (accessed on 12 July 2022).
30. Murray, D.G. *Tableau Your Data!: Fast and Easy Visual Analysis with Tableau Software*; John Wiley & Sons: Hoboken, NJ, USA, 2013.
31. International Plant Genetic Resources Institute. *Descriptors for Coffee (Coffea spp. and Psilanthus spp.)*; IPGRI: Paris, France, 1996. Available online: https://www.bioversityinternational.org/fileadmin/user_upload/online_library/publications/pdfs/365.pdf (accessed on 12 July 2022).
32. Krug, C.A.; Mendes, J.E.T.; Carvalho, A. Taxonomia de *Coffea arabica* L.: II-*Coffea arabica* L. Var. Caturra e sua forma Xanthocarpa. *Bragantia* **1949**, *9*, 157–163.
33. Carvalho, A. Genética de Coffea: IV. Instabilidade do par de alelos Na-na de *Coffea arabica* L. *Bragantia* **1941**, *1*, 453–466.
34. Carvalho, A.; Filho, H.P.M.; Fazuoli, L.C.; Costa, W.M.D. Genética de Coffea: XXVI. Hereditariedade do porte reduzido do cultivar Caturra. *Bragantia* **1984**, *43*, 443–458.
35. Krug, C.A. Mutações em *Coffea arabica* L. *Bragantia* **1949**, *9*, 1–10. [CrossRef]
36. Lécolier, A.; Besse, P.; Charrier, A.; Tchakaloff, T.N.; Noirot, M. Unraveling the origin of *Coffea arabica* 'Bourbon pointu' from La Réunion: A historical and scientific perspective. *Euphytica* **2009**, *168*, 1–10. [CrossRef]
37. Eskes, A.B. *Identification, Description and Collection of Coffee Types in P.D.R. Yemen*; Technical Report of Mission 15 April–7 May 1989; IRCC-CIRAD: Montpellier, France, 1989. Available online: http://agritrop.cirad.fr/359247/1/ID359247.pdf (accessed on 1 July 2022).
38. Benti, T.; Gebre, E.; Tesfaye, K.; Berecha, G.; Lashermes, P.; Kyallo, M.; Yao, N.K. Genetic diversity among commercial arabica coffee (*Coffea arabica* L.) varieties in Ethiopia using simple sequence repeat markers. *J. Crop Improv.* **2021**, *35*, 147–168. [CrossRef]
39. Hill, T.; Bekele, G. *A Reference Guide to Ethiopian Coffee Varieties*; Counter Culture Coffee: Durham, NC, USA, 2018.
40. Tesfaye, K.; Oljira, T.; Govers, K.; Belkele, E.; Borsh, T. Genetic diversity and population structure of wild *Coffea arabica* populations in Ethiopia using molecular markers. In *Coffee Diversity and Knowledge*; Adugna, G., Bellachew, B., Taye, E., Kufa, T., Eds.; Ethiopian Institute of Agricultural Research: Jimma, Ethiopia, 2008; pp. 35–44.
41. Aga, E.; Bekele, E.; Bryngelsson, T. Inter-simple sequence repeat (ISSR) variation in forest coffee trees (*Coffea arabica* L.) populations from Ethiopia. *Genetica* **2005**, *124*, 213–221. [CrossRef]
42. Dida, G.; Bantte, K.; Disasa, T. Molecular characterization of Arabica Coffee (*Coffea arabica* L.) germplasms and their contribution to biodiversity in Ethiopia. *Plant Biotechnol. Rep.* **2021**, *15*, 791–804. [CrossRef]
43. Carvalho, A.; Krug, C.A. Agentes de polinizacao da flor do cafeeiro (*Coffea arabica* L.). *Bragantia* **1949**, *9*, 11–24. [CrossRef]
44. Castillo-Zapata, J. Tasa de polinization cruzada del café arabigo en la region de Chinchina. *Cenicafe* **1976**, *27*, 78–88.
45. Berecha, G.; Aerts, R.; Vandepitte, K.; Van Glabeke, S.; Muys, B.; Roldán-Ruiz, I.; Honnay, O. Effects of forest management on mating patterns, pollen flow and intergenerational transfer of genetic diversity in wild Arabica coffee (*Coffea arabica* L.) from Afromontane rainforests. *Biol. J. Linn. Soc.* **2014**, *112*, 76–88. [CrossRef]
46. Peroni, N.; Kageyama, P.Y.; Begossi, A. Molecular differentiation, diversity, and folk classification of "sweet" and "bitter" cassava (*Manihot esculenta*) in Caiçara and Caboclo management systems (Brazil). *Genet. Resour. Crop Evol.* **2007**, *54*, 1333–1349. [CrossRef]
47. Birmeta, G.; Nybom, H.; Bekele, E. RAPD analysis of genetic diversity among clones of the Ethiopian crop plant *Ensete ventricosum*. *Euphytica* **2002**, *124*, 315–325. [CrossRef]