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Origin and Possible Members of the 'Malvasia' Family: The New Fuencaliente de La Palma Hypothesis on the True 'Malvasia'

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Abstract: The name 'Malvasia' and its various spellings has historically been associated with a type of sweet and/or aromatic wine. However, a definitive association with a specific grape variety remains unconfirmed. In fact, up to 413 different grape variety names (cultivar name (synonym name) and/or first name) are related to the term "Malvasia". The question arises: are all of these truly Malvasia? To answer this question, our research group presents a hypothesis. We worked with 43 genetic profiles that various scientific groups have published over decades and that are stored in the world's largest grape database, the Vitis International Variety Catalogue (VIVC). The known molecular profiles were obtained using the SSR (Simple Sequence Repeats) or microsatellite technique. Various population structure programs were applied, information on the possible origin or area where each of the varieties was mostly grown was used, and historical information was used to explain the results obtained. Therefore, it can be concluded that the current varieties best positioned to define the concept of grape and/or wine variety "Malvasia" would be (1) Malvasia Dubrovacka, Malvasia bianca lunga, and Malvasia del Cilento, by genetic proximity; (2) Malvasia volcanica, Malvasia babosa, Malvasia nera di Basilicata, Malvasia nera di Brindisi, Vitovska, Pelena, Prunesta (false), and Lagorthi, by crosses; and (3) Malvasia di Sardegna Rosada, by mutation. The rest of the candidate varieties to be part of the 'Malvasia' family are dismissed because they result from crosses with members of the Muscat family or crosses with other varieties (known or unknown) that, in any case, are not related historically, genetically, or geographically (with the exception of Malvasia istriana and Malvasia Župska) to the hypothetical members of the 'Malvasia' family.

Keywords: *Vitis vinifera* L.; SSR; microsatellite; true Malvasia; muscat; origin; synonym

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1. Introduction

At present, the global wine industry is confronted with a number of unresolved questions regarding grape varieties that bear the term 'Malvasia' in their names. These aspects range from their unknown geographical origin to whether all the varieties identified with this term are truly 'Malvasia' [1]. Currently, there are hundreds of varieties that use the term 'Malvasia' (or one of its variants in different languages), in either their main or synonym names [2,3]. Conversely, in today's market, the perception of quality is often linked to the prestige of a specific variety, taking into account both its intrinsic attributes and its historical and cultural relevance. For this reason, it would be highly interesting to restrict the term 'Malvasia' to a smaller number of varieties that meet specific conditions [4].

It appears that in 1214, a written document first mentioned a wine called Malvasia (Monovasia or Monemvasias). The term Malvasia derives from 'Monemvasia', an old commercial port in Greece, which at that time belonged to the Serenissima Republic of Venice (10th–18th centuries). Most of the commercial activity of the Mediterranean Basin during this period was controlled by Venetian merchants, who promoted a sweet and aromatic wine called 'Vinum de Malvasias' (in 1278). The success of this wine and its high demand led Venetian merchants to expand the cultivation of its variety/varieties to different areas of the eastern Mediterranean, and later to the rest of the Mediterranean Basin, eventually reaching the Atlantic [1,5,6]. An example of the expansion of one of the best-known Malvasias is presented in Figure 1, specifically the case of Malvasia Dubrovacka [7]. Moreover, the first written record referencing this variety dates was found to be from 1385 (Archive of the Republic of Dubrovnik, Croatia) [1].

Figure 1. Expansion of the Malvasia Dubrovacka variety during the 14th–18th centuries, from the eastern Mediterranean Basin to the Atlantic Ocean (map created by Crespan M., 2010) [7].

Another indication of the renown of Malvasia is the fact that the term has been translated (adapted) into different languages, according Vitis International Variety Catalogue (VIVC). The grape variety is known by a number of names, including Malvazija in Croatian, Malvasia or Mal-vagia in Italian, Malvasía in Spanish, Malvoisie or Malvasie in French, Malmsey in English-speaking countries, and Malvasier in German-speaking countries, along with other spellings like Malvagia, Malvasika, and Malvasiya [4].

It is widely accepted among experts in the field that the name 'Malvasia' derives from a port city in present-day Greece, and that the origin of the Malvasia variety or varieties lies in the eastern Mediterranean Basin. Nevertheless, the precise geographical origin of this variety, and indeed of any varieties, remains to be ascertained. The location of the site is uncertain, but it may be along the Balkan coasts of the Adriatic Sea, in today's Greece, or in both. It is also known that grapevines of Balkan origin (including present-day Greece) emerged about 8070 years ago from a wild vine that colonized the eastern Mediterranean Basin (with an introgression from the western wild grapevine), and that these were small-berried vines intended for winemaking. Before them (around 10,500 years ago), also originating from the same wild grapevine, the Muscat family emerged, with large berries more suitable for fresh consumption. The Muscat family's origin is in Anatolia (modern-day Turkey) and nearby areas of Asia Minor (northern Mesopotamia (Iraq) and northern Persia (Iran)) [8]. These regions were inhabited by more advanced civilizations that had already initiated viticulture.

Other major mysteries include knowing (1) how many 'Malvasia' varieties exist and (2) whether all the varieties bearing the name 'Malvasia' are truly 'Malvasia'. A major problem with the term Malvasia is its frequent use alongside the names of other cultivars, such as Torrontés, Tinta, Tintilla, Ugni blac etc., which constitutes a clear case of homonymy. A homonym is a name used, knowingly or not, to refer to different grapevine varieties. This obviously leads to errors and confusion. In the case of Spanish 'Malvasia', different research groups were already raising this problem in 2002. Thus, J. Borrego et al. published a study titled 'Genetic Study of Malvasia and Torrontes Groups through Molecular Markers' [9] and in 2009, a study titled 'Synonyms and homonyms of 'Malvasía' cultivars (*Vitis vinifera* L.) existing in Spain' by I. Rodríguez-Torres et al. was published [10]. In any case, these authors highlighted that the term 'Malvasia' was a homonym, i.e., there were varieties called 'Malvasia' that were actually different varieties, such as the Spanish Alarije or Cayetana blanca or the French Chasselas blanc, among others. Another conclusion from this study is that Spain grows two true 'Malvasia' varieties—Malvasia aromatica (Prime Name (PN): Malvasia Dubrovacka), Malvasía de Lanzarote (PN: Malvasia volcanica)—as well as a pink mutation of Malvasia Dubrovacka, known as Malvasia rosada. Therefore, according to this study, the remaining Spanish 'Malvasia' varieties would not be considered true 'Malvasia' by these authors.

At present, several Mediterranean countries and their outermost regions produce 'Malvasia' wines (especially Croatia, Greece, Italy, Spain, and Portugal. In addition there are two Russian 'Malvasia' varieties, as well as one Argentine and one French. In reality, due to the fame and popularity associated with the name 'Malvasia', the term has been used throughout history and in various parts of the world to name very different varieties [1,4].

The present theoretical–bibliographic study on the subject of 'Malvasia' worldwide is intended to identify any potential evidence that may assist in resolving the aforementioned uncertainties concerning the global 'Malvasia' group. For the purpose of this study, data were drawn from the Vitis International Variety Catalogue (VIVC), which is recognized as the world's most extensive database [2,3]. In order to achieve the objectives of the study, both the ampelographic section and the molecular profiles section were consulted, with the relevant microsatellites or SSR (Simple Sequence Repeats) being used.

2. Materials and Methods

2.1. The Term 'Malvasia' in the Cultivar and Prime Names

The study of the term 'Malvasia' and its derived spellings began by consulting these terms in the ampelographic section of the VIVC (Table S1). The different names by which this family is known in various languages were entered. The "Cultivar Name" tab was used first, and then the operation was repeated in the "Prime Name" tab.

2.2. SSR or Microsatellites Used

The molecular study on the genetic profiles of the varieties that make up the 'Malvasia' was based on the SSR or microsatellite technique. The 9 internationally recognized SSR markers were used, i.e., those accepted as reference SSR markers by the global scientific community: VVS2 [11] VVMD5, VVMD7, VVMD28 [12], VVMD25, VVMD27, VVMD32 [13], VrZAG62, VrZAG79 [14] (Table S2).

The genetic profiles of these 9 SSRs were obtained from the VIVC database, as it holds the largest number of genetic profiles for 'Malvasia' varieties [2,3]. The study started with all the Molecular Profiles (SSR-MPs) of 'Malvasia' stored in this database, although not all accessions found in the ampelographic section had SSR-MPs.

2.3. Data Analysis

The population structure of 'Malvasia' was studied using the program Structure 2.3 [15,16], a clustering method based on Bayesian models. In this model, it is assumed that several ancestral populations (K) are present, each characterized by a set of allele frequencies at each locus. The individuals in the sample are assigned to specific populations (clusters), or to multiple populations if their genotypes suggest admixture. All loci are assumed to be independent, and each population K is in Hardy–Weinberg equilibrium. Posterior probabilities were estimated using the Markov Chain Monte Carlo (MCMC) method. The MCMC chains were run with a burn-in period of 100,000 iterations, followed by 1,000,000 iterations, using a model that allows for admixture and correlated allele frequencies. Structure was run at least ten times, configuring K from 1 to 7, and a mean likelihood value, L(K), was calculated across all runs for each K. The mean log-likelihood of the data was calculated for each K to determine the most appropriate number of clusters and the K value for which this probability was highest. Then, ΔK was calculated using the method described by Evanno et al. [17]. ΔK is a quantity based on the rate of change and in the log probability of the data between successive K values. The parameter q defines what proportion of an individual's genome belongs to each predefined cluster (K). Membership in a cluster was accepted for mean q values ≥ 0.74.

The program GenAlEx 6.5 was used for two purposes [18,19]. First, it allowed the performance of assignment tests to evaluate the goodness of fit of a given sample distribution into different populations. GenAlEx 6.5 bases this strategy on the allele frequency of each accession. It calculates a log-likelihood value for this accession for each subpopulation using the allele frequencies of the respective subpopulations. An individual is assigned to the subpopulation with the highest log-likelihood value [20]. Second, based on the standardized covariance of the genetic distances calculated for codominant markers, GenAlEx 6.5 allowed us to generate two-dimensional Principal Coordinate (PCoA) graphical representations for a set of populations and for a set of individuals from different populations.

The programs Python Data [21], applying the Matplotlib strategy, and MEGA version 7 [22], using the Neighbor-Joining strategy [23], were used to create three-dimensional PCoA plots and phylogenetic trees, respectively.

3. Results

3.1. The Names of the Term 'Malvasia'

To begin this study, it was first necessary to determine how many varieties used the term 'Malvasia' and/or its derived spellings in their primary names or synonyms. Twelve different terms appeared (Table 1). For this, the ampelographic section of the VIVC was consulted. Specifically, each of the spellings was entered into the "Cultivar Name" field (where all accession names of a given variety that include the entered spelling are stored): (1) MALVASIA (Spanish), with 290 items; (2) MALVOISIE (French), with 52 items; (3) MALVASIER (English), with 15 items; (4) MALVAZIYA (Russian), with 14 items; (5) MALVAZIJA (Croatian), with 13 items; (6) MALVAZIA (English), with 11 items; (7) MALMSEY (English), with 6 items; (8) MALVAGIA (Italian), with 4 items; (9) MALVASIJA (Latvian), with 4 items; (10) MALVASIE (French), with 2 items; (11) MALVASIKA (Croatian), with 1 item; and (12) MALVASIYA (?), with 1 item. In total, 413 accession names were found that included the term 'Malvasia' or its derived spellings, in all possible combinations (a single name or combination of several names).

Table 1. No. of cultivars names and PNs presenting the 12 derived spellings of the term 'Malvasia'.

NAME	CULTIVARS NAME (No. of Accesions)	PRINCIPAL NAME (No. of Accessions)
MALVASIA	290	203
MALVOISIE	52	13
MALVASIER	15	3
MALVAZIYA	14	8
MALVAZIJA	13	9
MALVAZIA	11	2
MALMSEY	6	3
MALVAGIA	4	4
MALVASIJA	4	4
MALVASIE	2	0
MALVASIKA	1	1
MALVASIYA	1	0
TOTAL No. OF NAMES	413	250

Then, the next step was to enter the previously used spellings into the "Prime Name" field in order to select only those terms where the word "Malvasia" or its derived spellings appeared. Thus, the following results were obtained: (1) MALVASIA was reduced to 203 prime names; (2) MALVOISIE showed only 13 items; (3) MALVASIER had 3 items; (4) MALVAZIYA had 7 items; (5) MALVAZIJA had 9 items; (6) MALVAZIA had 2 items; (7) MALMSEY had 3 items; (8) MALVAGIA had 4 items; (9) MALVASIJA had 4 items; (10) MALVASIE had 0 items; (11) MALVASIKA had 1 item; and (12) MALVASIYA had 0 items. The final count of PNs including the term "Malvasia" was reduced to 250.

Finally, the number of unique PNs including the term "Malvasia" or one of its derived spellings was narrowed down, definitively, to 68 unique and cataloged varieties in the ampelographic section of the VIVC (Supplementary Material 1 (Table S1)). These, classified by their origin (Table S3), correspond to (a) 14 without an assigned country of origin (although the institution that holds the sample described in the ampelographic section of the VIVC is reported); (b) 1 Argentinian; (c) 1 French; (d) 2 Croatian; (e) 2 Russian; (f) 9 Spanish; (g) 11 Portuguese; and (h) 28 Italian.

3.2. Genetic Structure of the Population of the "Malvasia" Group Varieties (Genetic Strategy)

Once the 68 unique varieties that included the term 'Malvasia' in their prime name were identified, their molecular profiles (SSR-MPs) were obtained from the SSR or Microsatellite section of the VIVC. Only 43 SSR-MPs (Table S4) out of the 68 described varieties were available, leaving 25 varieties excluded. The main characteristics and genetic profiles for the 9 published SSRs of these 43 SSR-MPs are shown in Table S1.

To carry out the study of the population structure of the group formed by the unique SSR-MP 'Malvasia' varieties efficiently and effectively, data normalization was performed (Table S1). First, 'sports' were eliminated. Thus, four prime names and their corresponding

SSR-MPs were excluded from this study: Malvasia di Sardegna rosada, Malvasia fina roxa, Malvasia preta roxa, and Malvasia rosa. Then, varieties resulting from directed crosses by a breeder were excluded; this was the case of the varieties Malvasia branca de Sao Jorge and Malvasia moscatel Fonte grande. Finally, four varieties were excluded whose natural crosses were known and whose parents (and their crosses) corresponded to known varieties with no relevant aroma and unrelated to either the 'Malvasia' group or the Muscat group. These were (1) Malvasia (Malvasia de Colares); (2) Malvasia fina; (3) Malvasia preta; and (4) Malvoisie de madeira. Therefore, the population structure study of the 'Malvasia' group used 33 SSR-MPs. Varieties for which the cross or one of the parents was unknown were not excluded.

To achieve the best distribution of this population of 33 individuals into different ancestral populations (K), the program Structure 2.3 was used. Population distributions from one to seven were tested, with the best result being the distribution into three populations (K = 3) (Figure S1). Each individual in the 'Malvasia' group population was assigned to one of these three proposed populations based on a statistical parameter q (which indicates the percentage of its inferred genome that belongs to one of these populations). In our study, an arbitrary threshold of 74% was chosen [24], such that values of $q \geq 74\%$ corresponded to pure individuals belonging to a given population, while those with $q < 74\%$ were considered admixed individuals for that population and were excluded from further analysis. Figure 2 shows the best distribution for the 'Malvasia' group population into three populations (POP1, POP2, POP3), with the varieties ordered according to the q parameter (Table S5).

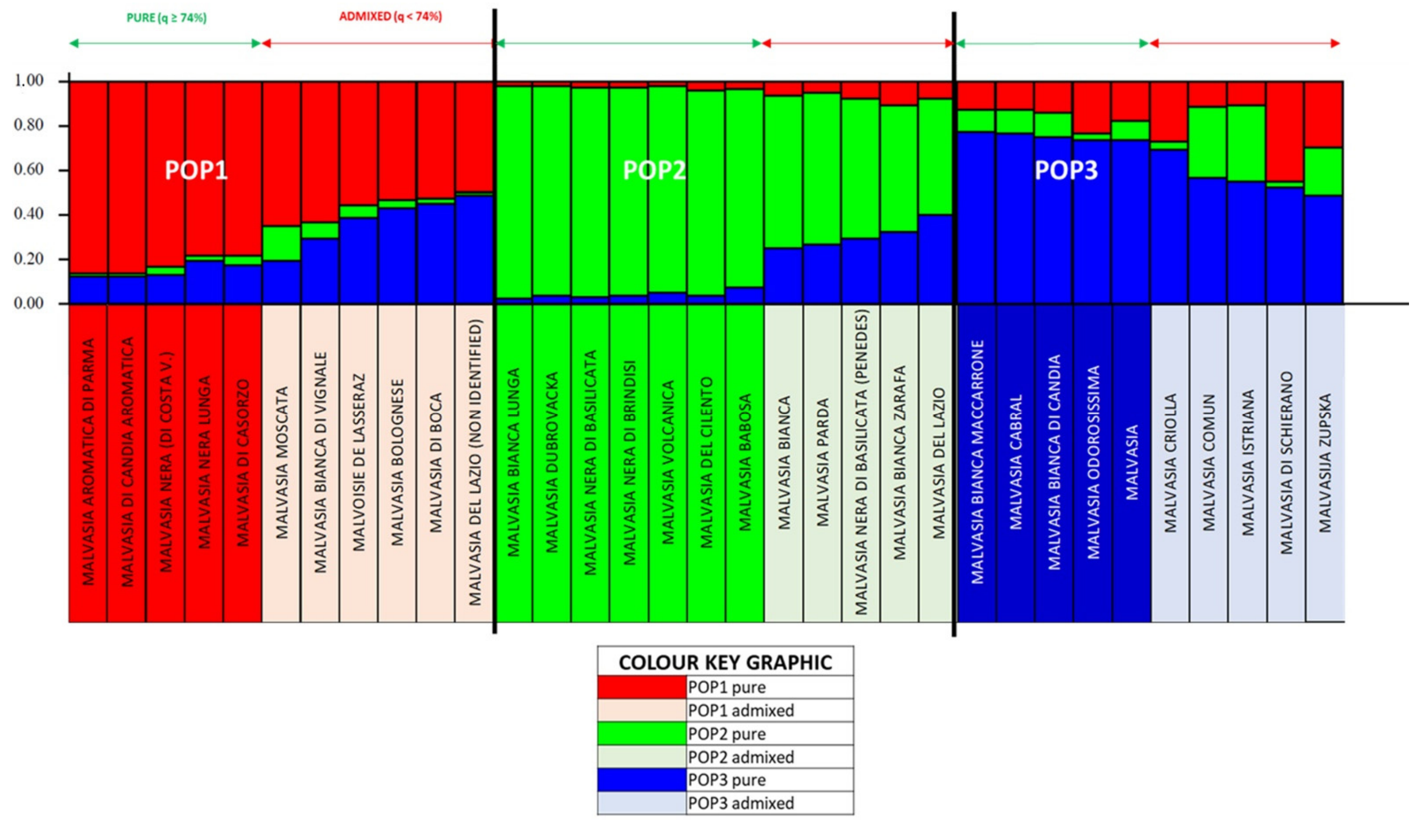

Figure 2. 'Malvasia' grapevine varieties population (unique molecular profiles). Structure 2.3. diagram: K = 3 distribution for pure and admixed individuals.

Table 2 shows the most relevant information for each of the 33 members of this group, following the same classification criteria defined by the Structure 2.3 program.

Table 2. Relevant information (VIVC) on the main characteristics of each of the 33 members of the "Malvasia" group analyzed in this study, distributed into three populations and ordered according to the *q* parameter (Table S5).

GENERAL INFORMATION								PEDIGREE	
PRIME NAME	COUNTRY ORIGIN	CHLOROTYPE	SEED FORMATION	SEX	TASTE	COLOR	USE	PARENT 1	PARENT 2
MALVASIA AROMATICA DI PARMA	FRA139 /MEX062/USA 06/USA028	D	COMPLETE	FEMALE	MUSCAT	W	W	MUSCAT A PETITS GRAINS BLANCS	NEBBIOLO x BOTTAGERA (FALSE)
MALVASIA DI CANDIA AROMATICA	ITALY	D	COMPLETE	HERMAFRODITE	MUSCAT	W	T/W	MALVASIA AROMATICA DI PARMA (MUSCAT A PETITS GRAINS BLANCS x NEBBIOLO X BOTTAGERA (FALSE))	?
MALVASIA NERA (DI COSTA V.)	ITALY	D	COMPLETE	HERMAFRODITE	MUSCAT	B	?	MALVASIA AROMATICA DI PARMA (MUSCAT A PETITS GRAINS BLANCS x NEBBIOLO X BOTTAGERA (FALSE))	LAMBRUSCA DI ALESSANDRIA (CROVIN x NERETTO DI MARENGO (LAMBRUSCA DI ALESSANDRIA x ?))
MALVASIA NERA LUNGA	ITALY	D	COMPLETE	HERMAFRODITE	ARMATIC	B	W	MALVASIA AROMATICA DI PARMA (MUSCAT A PETITS GRAINS BLANCS x NEBBIOLO X BOTTAGERA (FALSE))	FREISA (NEBBIOLO x ?)
MALVASIA DI CASORZO	ITALY	D	COMPLETE	HERMAFRODITE	AROMATIC	B	W	MALVASIA AROMATICA DI PARMA (MUSCAT A PETITS GRAINS BLANCS x NEBBIOLO X BOTTAGERA (FALSE))	LAMBRUSCA DI ALESSANDRIA (CROVIN x NERETTO DI MARENGO (LAMBRUSCA DI ALESSANDRIA x ?))
MALVASIA MOSCATA	ITALY	D	COMPLETE	HERMAFRODITE	MUSCAT	W	W	MALVASIA AROMATICA DI PARMA (MUSCAT A PETITS GRAINS BLANCS x NEBBIOLO X BOTTAGERA (FALSE))	?

Table 2. *Cont.*

GENERAL INFORMATION								PEDIGREE	
PRIME NAME	**COUNTRY ORIGIN**	**CHLOROTYPE**	**SEED FORMATION**	**SEX**	**TASTE**	**COLOR**	**USE**	**PARENT 1**	**PARENT 2**
MALVASIA BIANCA DI VIGNALE	ITALY	D	COMPLETE	HERMAFRODITE	AROMATIC	W	W	MALVASIA AROMATICA DI PARMA (MUSCAT A PETITS GRAINS BLANCS x NEBBIOLO X BOTTAGERA (FALSE))	COCCALONA BIANCA
MALVOISIE DE LASSERAZ	FRANCE	?	COMPLETE	FEMALE	NONE	W	W	?	?
MALVASIA BOLOGNESE	ITALY	?	COMPLETE	?	?	W	W	?	?
MALVASIA DI BOCA	ITALY	?	COMPLETE	HERMAFRODITE	AROMATIC	W	W	?	?
MALVASIA DEL LAZIO (NON-IDENTIFIED)	ITALY	?	COMPLETE	HERMAFRODITE	MUSCAT	W	W	MUSCAT OF ALEXANDRIA (MUSCAT A PETITS GRAINS BLANCS x HEPTALIKO)	SCHIAVA GROSSA
MALVASIA BIANCA LUNGA	ITALY	D	COMPLETE	HERMAFRODITE	NONE	W	W	?	?
MALVASIA DUBROVACKA	SPAIN	A	COMPLETE	HERMAFRODITE	AROMATIC	W	W	?	?
MALVASIA NERA DI BASILICATA	ITALY	?	COMPLETE	HERMAFRODITE	ARMATIC	B	W	MALVASIA BIANCA LUNGA	SOMARELLO NERO (UVA SACRA (ACHLADI x ?) x GARGANEGA)
MALVASIA NERA DI BRINDISI	ITALY	?	COMPLETE	HERMAFRODITE	NONE	B	T/W	MALVASIA BIANCA LUNGA	NEGRO AMARO (? x MAIOLICA (? x VISPAROLA))
MALVASIA VOLCANICA	SPAIN	?	COMPLETE	HERMAFRODITE	OTHER FLAVOR THAN MUSCAT, FOXY OR HERBACEOUS	W	W	MALVASIA DUBROVACKA	BERMEJUELA

Table 2. *Cont.*

GENERAL INFORMATION								PEDIGREE	
PRIME NAME	COUNTRY ORIGIN	CHLOROTYPE	SEED FORMATION	SEX	TASTE	COLOR	USE	PARENT 1	PARENT 2
MALVASIA DEL CILENTO	ITALY	?	?	?	?	B	W	?	?
MALVASIA BABOSA	PORTUGAL	A	COMPLETE	?	?	W	W	HEBEN	MALVASIA DUBROVACKA
MALVASIA BIANCA	ITALY	?	COMPLETE	HERMAFRODITE	NONE	W	W	SCIACCARELLO	?
MALVASIA PARDA	PORTUGAL	?	COMPLETE	HERMAFRODITE	NONE	W	W	?	?
MALVASIA NERA DI BASILICATA (PENEDES)	SPAIN	?	COMPLETE	?	NONE	B	W	?	?
MALVASIA BIANCA ZARAFA	ITALY	?	COMPLETE	?	MUSCAT	W	W	?	?
MALVASIA DEL LAZIO	ITALY	?	COMPLETE	HERMAFRODITE	NONE	W	W	?	?
MALVASIA BIANCA MACCARRONE	ITALY	?	COMPLETE	?	MUSCAT	W	W	?	?
MALVASIA CABRAL	PRT051	?	COMPLETE	HERMAFRODITE	NONE	Rs	W	?	?
MALVASIA BIANCA DI CANDIA	ITALY	D	COMPLETE	HERMAFRODITE	NONE	W	W	GARGANEGA	?
MALVASIA ODOROSISSIMA	ITALY	?	COMPLETE	FEMALE	MUSCAT	W	W	?	?
MALVASIA	ITALY	?	COMPLETE	?	?	B	W	?	?

Table 2. *Cont.*

GENERAL INFORMATION								PEDIGREE	
PRIME NAME	COUNTRY ORIGIN	CHLOROTYPE	SEED FORMATION	SEX	TASTE	COLOR	USE	PARENT 1	PARENT 2
MALVASIA CRIOLLA	ARGENTINA	?	COMPLETE	HERMAFRODITE	MUSCAT	W	W	LISTAN PRIETO	MUSCAT OF ALEXANDRIA (MUSCAT A PETITS GRAINS BLANCS x HEPTALIKO)
MALVASIA COMUN	SPAIN	A	COMPLETE	HERMAFRODITE	NONE	W	W	HEBEN	?
MALVASIA ISTRIANA	CROATIA	D	COMPLETE	HERMAFRODITE	NONE	W	W	?	?
MALVASIA DI SCHIERANO	ITALY	D	COMPLETE	HERMAFRODITE	MUSCAT	B	W	MUSCAT A PETITS GRAINS BLANCS	?
MALVASIJA ZUPSKA	CROATIA	D	COMPLETE	?	?	W	W	HEUNISCH WEISS	?

1: Red; POP1 pure; light red: POP1 admixed; green: POP2 pure; light green: POP2 admixed; blue: POP3 pure; light blue: POP3 admixed. 2: x is the crossing (pedigree).

POP1 is composed of 11 varieties (33.33%), of which 5 are pure and the remaining 6 are admixed. Virtually all members of this cluster population are Italian varieties (except for Malvasia aromatica di Parma (of unknown origin) and Malvasia Lasseraz (French)), white (except for Malvasia nera lunga, which is pure), and intended for winemaking (except for Malvasia di Candia aromatica, which is assigned a dual purpose). Most have hermaphroditic flowers (except for Malvasia aromatica di Parma (Italian) and Malvasia Lasseraz (French) which are female). All known chlorotypes are either D or unknown, and all known crosses involve a member of the Muscat family. Most of its components exhibit a muscat or aromatic aroma.

POP2 consists of 12 components (36.36%), of which 7 are considered pure varieties and 5 are admixed, originating from the Italian and Iberian Peninsulas (7 Italian, 3 Spanish, and 2 Portuguese). This group is characterized by having most individuals with an unknown chlorotype, except for 2 chlorotype A (Malvasia Dubrovacka and Malvasia Babosa) and 1 chlorotype D (Malvasia bianca lunga). Among its 12 components, 4 are red varieties, and only Malvasia nera di Brindisi (also widely known as Malvasia di Lecce) is intended for dual use (table/winemaking); the rest are for winemaking. Most are hermaphroditic, and for the remaining ones, the floral sex has not been described. There are representatives with aromatic, non-aromatic, and unknown aroma profiles, and one with a muscat aroma (Malvasia Zarafa). Four complete crosses are known in which either Malvasia Dubrovacka or Malvasia bianca lunga is involved, and one incomplete cross: Malvasia bianca (with only one known parent, Sciaccarello). The parentage of the remaining varieties is unknown.

POP3 includes 10 components (30.30%), 50% of which are pure and the remaining 50% admixed. Most are Italian, although there are also two varieties from Croatia, one Spanish, one from Argentina, and one of unknown origin. Chlorotype D predominates, although there are also members with unknown chlorotypes and one specimen with chlorotype A (Malvasia común). Most are hermaphroditic; three have flowers of unknown sex, and one variety, Malvasia odorosissima, has female flowers. Four members have been described as having a muscat aroma, four more are non-aromatic, and for the remaining two, no information on this trait is available. All are intended for winemaking and are white, except for Malvasia and Malvasia di Schierano, which are red, and Malvasia Cabral, which is pink. Regarding their crosses, it is worth noting that only one complete cross is known, that of Malvasia criolla; for four crosses, only one parent is known; and for the remaining five, both parents are unknown. Two of the crosses involve Muscat varieties, and three incomplete crosses involve two Italian varieties and one Spanish.

As previously mentioned, the admixed members were removed, and the 'Malvasia' population was reduced to 17 components, distributed across three populations, with a goodness of fit of 82% for each population (Figure S2). The members of each population were then reassigned until a goodness of fit of 100% was achieved (Figure S3). In this process, the distribution of the members of the 'Malvasia' group was reduced to two populations. Figure 3 shows the distribution of the 'Malvasia' population through Principal Coordinates Analysis (PCoA) in two and three dimensions, in addition to the phylogenetic tree derived from this distribution. In Figure 3a, corresponding to the two-dimensional PCoA plot (with a goodness of fit of 35.66%), it can be seen that Coordinate 1, with a goodness of fit of 21.47%, separates the two populations, placing POP1 in the right quadrants and POP2 in the left quadrants. Looking at both populations as a whole, it can be observed that they are mostly arranged around the axis of Coordinate 2 (with some exceptions). This coordinate, which has a goodness of fit of 14.19%, slightly divides both POP1 and POP2 into two subpopulations each. In the upper quadrant of POP1 (right side), the varieties Malvasia nera lunga and Malvasia di Candia aromatica are located, while in the lower quadrant, the remaining four varieties are found (Malvasia aromatica di Parma, Malvasia odorosissima (originating from POP3), Malvasia nera (di Costa v.), and Malvasia di Casorzo). In the upper left quadrant of POP2, the most distant variety is Malvasia Cabral; closer to the center and near the axis of Coordinate 1, we find Malvasia, Malvasia bianca di Candia, and further down, Malvasia bianca Maccarrone, all of them coming from POP3. In the more central and lower part of this quadrant, Malvasia Dubrovacka and its progeny (Malvasia volcánica and Malvasia Babosa) can be observed. In contrast, Malvasia bianca lunga and its progeny, along with Malvasia del Cilento, are located in the lower left quadrant. The three-dimensional PCoA plot shows an explanatory goodness of fit of 45.71% (Figure 3b). In this plot, with slight variations, the same pattern described above is repeated. Finally, the phylogenetic tree (Figure 3c) clearly shows three branches emerging from the root. In red, the branch corresponding to POP1 includes the five previously described components, highlighting the split of Malvasia odorosissima (originating from POP3). POP2 (in lime green) and its initial components remain grouped on another branch (on the right side of the tree), and with the same color, but now located on the left branch of the phylogenetic tree, the four 'Malvasia' varieties from the former POP3 are grouped together.

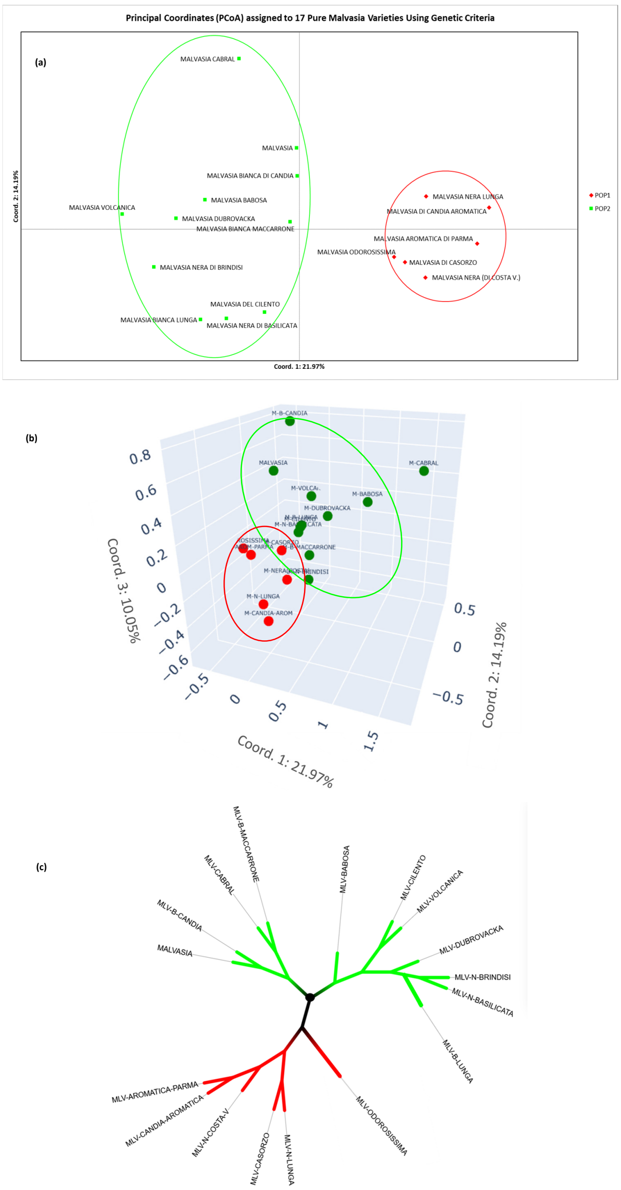

Figure 3. Graphical representation of the distribution of the 17 pure varieties ($q \geq 74\%$), using PCoA of their individuals in two (**a**) and three (**b**) dimensions, and also through the representation of a phylogenetic tree (**c**).

In Figure 4, a map is shown depicting the approximate geographical locations assigned to the 17 pure varieties analyzed in this genetic study. It can be observed that POP1 is located in the northern regions of the Italian Peninsula. In contrast, POP2 encompasses the Balkan areas bordering the Adriatic Sea, as well as the southern half of Italy, parts of Portugal, and the outermost regions of Spain and Portugal (Canary Islands and Madeira Archipelago) [5,25,26].

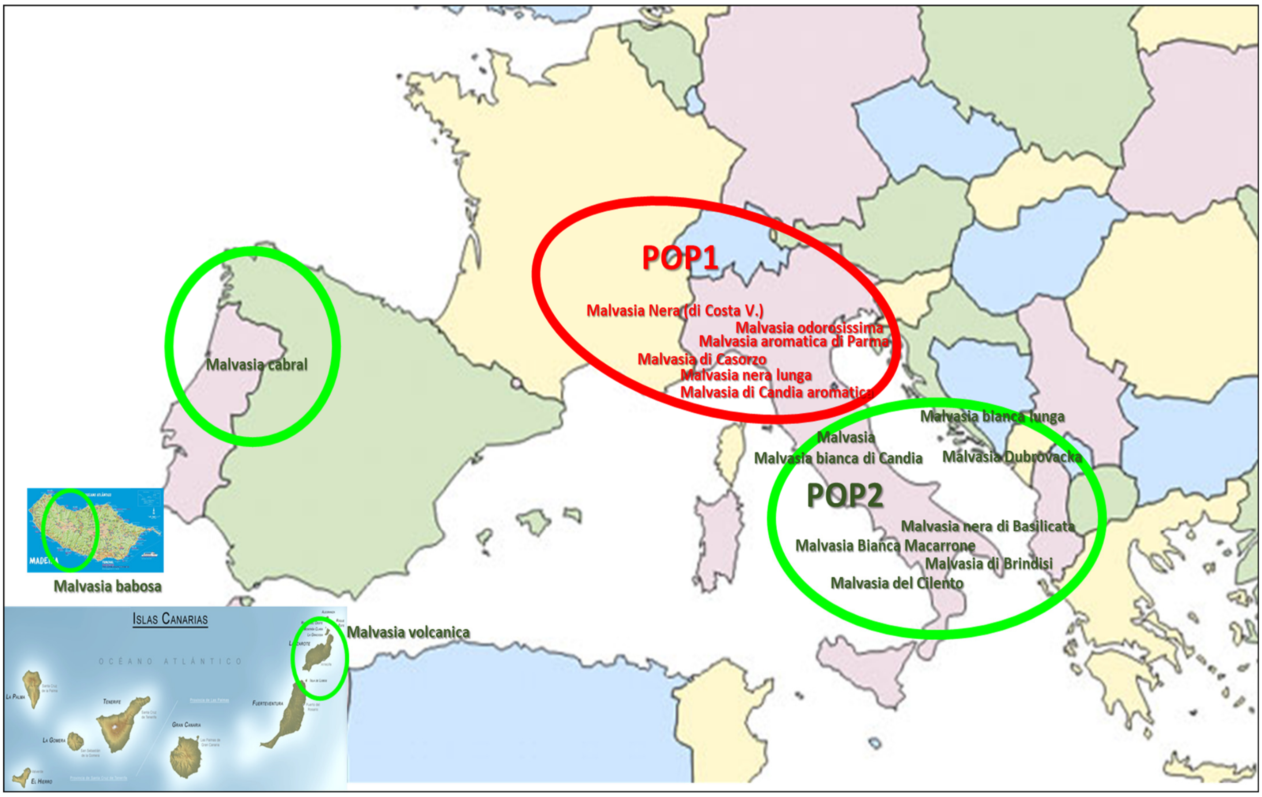

Figure 4. Map of the approximate geographical location ([5,25–27]) of the 17 pure 'Malvasia' varieties. Genetic strategy. Goodness of fit: 100%.

3.3. Distribution of the 'Malvasia' Variety Group Population According to Geographical Criteria

In this section, a geographical criterion was applied in order to observe the composition of the populations and the membership of the groups in question. Evidently, a genetic element could not be disregarded, as it would contribute to the final organization of the populations resulting from this new arrangement.

The process was initiated with the 33 unique and non-redundant profiles of varieties that could potentially be candidates to form part of the 'Malvasia' group. Initially, two populations were created based on whether the variety originated from the Italian Peninsula (POP1) or its surroundings, or from the Iberian Peninsula (POP2) and its areas of influence. Table S6 presents this initial distribution according to geographical criteria (origin as described in the VIVC), and some important trends were already observable. For instance, when the chlorotype of a variety was known, it was type D in POP1, while in POP2, it was type A. Another noteworthy detail was the presence of Muscat family members as progenitors in most of the crosses of varieties from the POP1 area (for this reason, the Argentine variety Malvasia criolla was placed in this group). This distribution showed a goodness of fit of 76%. No misassigned individuals were excluded, as the goal was to observe their behavior; instead, they were reassigned until a 100% goodness of fit was achieved. Table 3 shows the final distribution obtained. In the 'Prime Name' column, the final distribution of the 'Malvasia' group is presented, with varieties assigned to POP1 in red and those assigned to POP2 in green. In the 'Country Origin' column, the initial distribution is shown (with a goodness of fit of 76%). POP1, which previously had 26 components, now has 17, and POP2 increases by 9 components, reaching 16 members. Regarding chlorotypes, in POP1, the known chlorotypes remain D, while in POP2, which has seen a significant incorporation of varieties from POP1 (Italy and nearby areas), there are three A-type chlorotypes (those initially present) and two D-type chlorotypes. The crosses follow the same distribution pattern; varieties whose progenitors belong to the Muscat family are in POP1, and in POP2 there is no evidence of Muscat parentage. However, two distinct lineages can be observed in POP2: one related to Malvasia Dubrovacka and the other to Malvasia bianca lunga and their respective progenies. Regarding aromas, POP1 includes both muscat-flavored varieties (which are the most abundant) and varieties defined as aromatic. In POP2, aromatic varieties are also observed, along with two muscat-flavored ones, while the rest are either neutral or of unknown aroma.

The graphical representation of the PCoA in two and three dimensions, along with the corresponding phylogenetic tree, is presented in Figure 5. In Figure 5a, the distribution of the "Malvasia" population by individuals in two dimensions is shown using PCoA. This representation has a goodness of fit of 24.47%. Once again, Coordinate 1, with 13.63% of goodness of fit, separates most individuals whose crosses involve a member of the Muscat family (group of 'Malvasia' from northern Italy) from the group led by the 'Malvasia' varieties from the Iberian Peninsula, the southern half of the Italian Peninsula, and the Balkan coasts of the Adriatic Sea (Figure 6). Coordinate 2, with 10.84% of goodness of fit, does not play a very defined role in the distribution of the two populations. In this representation, it is worth highlighting how Malvasia, Malvasia bianca di Candia, and Malvasia Zupska, which belong to POP1 (red), are positioned on the right quadrant (near the axis), together with members of POP2. The three-dimensional representation, with a goodness of fit of 32.63% (Figure 5b), does not bring major new insights either. However, it does show that POP1 is positioned above POP2, which appears in the lower part of the graph. It also highlights the ' Malvasia' varieties that show a more distant SSR profile compared to the rest. These include Malvasia cabral, Malvasia babosa, Malvasia istriana, Malvasia nera di Basilicata (from Penedès), Malvasia di Boca, Malvasia di Schierano, Malvasia de Zarafa, and Malvasia moscata. In Figure 5c, we present the distribution adopted by the 'Malvasia' population for the two initial populations with a 100% goodness of fit. This tree is divided into three branches from the point of origin, as POP2 splits into two sub-branches. Another noteworthy aspect is the transfer of Malvasia istriana (originally from Croatia) into POP1.

Table 3. Final distribution of 'Malvasia' varieties based on their origin as described in the VIVC. Goodness of fit of 100% (Prime Name column). No misassigned varieties were eliminated; they were reassigned.

GENERAL INFORMATION								PEDIGREE	
PRIME NAME	COUNTRY ORIGIN	CHLOROTYP	SEED FORMATION	SEX	TASTE	COLOR	USE	PARENT 1	PARENT 2
MALVASIA AROMATICA DI PARMA	ITA	D	COMPLETE	FEMALE	MUSCAT	W	W	MUSCAT A PETITS GRAINS BLANCS	NEBBIOLO x BOTTAGERA (FALSE)
MALVASIA DI CANDIA AROMATICA	ITA	D	COMPLETE	HERMAFRODITE	MUSCAT	W	T/W	MALVASIA AROMATICA DI PARMA (MUSCAT A PETITS GRAINS BLANCS x NEBBIOLO X BOTTAGERA (FALSE))	?
MALVASIA NERA LUNGA	ITA	D	COMPLETE	HERMAFRODITE	ARMATIC	B	W	MALVASIA AROMATICA DI PARMA (MUSCAT A PETITS GRAINS BLANCS x NEBBIOLO X BOTTAGERA (FALSE))	FREISA (NEBBIOLO x ?)
MALVASIA BIANCA DI VIGNALE	ITA	D	COMPLETE	HERMAFRODITE	AROMATIC	W	W	MALVASIA AROMATICA DI PARMA (MUSCAT A PETITS GRAINS BLANCS x NEBBIOLO X BOTTAGERA (FALSE))	COCCALONA BIANCA
MALVASIA DI CASORZO	ITA	D	COMPLETE	HERMAFRODITE	AROMATIC	B	W	MALVASIA AROMATICA DI PARMA (MUSCAT A PETITS GRAINS BLANCS x NEBBIOLO X BOTTAGERA (FALSE))	LAMBRUSCA DI ALESSANDRIA (CROVIN x NERETTO DI MARENGO (LAMBRUSCA DI ALESSANDRIA x ?))
MALVASIA NERA (DI COSTA V.)	ITA	D	COMPLETE	HERMAFRODITE	MUSCAT	W	?	MALVASIA AROMATICA DI PARMA (MUSCAT A PETITS GRAINS BLANCS x NEBBIOLO X BOTTAGERA (FALSE))	LAMBRUSCA DI ALESSANDRIA (CROVIN x NERETTO DI MARENGO (LAMBRUSCA DI ALESSANDRIA x ?))

Table 3. *Cont.*

GENERAL INFORMATION								PEDIGREE	
PRIME NAME	COUNTRY ORIGIN	CHLOROTYP	SEED FORMATION	SEX	TASTE	COLOR	USE	PARENT 1	PARENT 2
MALVASIA MOSCATA	ITA	D	COMPLETE	HERMAFRODITE	MUSCAT	W	W	MALVASIA AROMATICA DI PARMA (MUSCAT A PETITS GRAINS BLANCS x NEBBIOLO X BOTTAGERA (FALSE))	?
MALVASIA DI SCHIERANO	ITA	D	COMPLETE	HERMAFRODITE	MUSCAT	B	W	MUSCAT A PETITS GRAINS BLANCS	?
MALVASIA DEL LAZIO (NON-IDENTIFIED)	ITA	?	COMPLETE	HERMAFRODITE	MUSCAT	W	W	MUSCAT OF ALEXANDRIA (MUSCAT A PETITS GRAINS BLANCS x HEPTALIKO)	SCHIAVA GROSSA
MALVASIA CRIOLLA	ARG	?	COMPLETE	HERMAFRODITE	MUSCAT	W	W	LISTAN PRIETO	MUSCAT OF ALEXANDRIA (MUSCAT A PETITS GRAINS BLANCS x HEPTALIKO)
MALVASIA BOLOGNESE	ITA	?	COMPLETE	?	?	W	W	?	?
MALVASIA DI BOCA	ITA	?	COMPLETE	HERMAFRODITE	AROMATIC	W	W	?	?
MALVOISIE DE LASSERAZ	FRA	?	COMPLETE	FEMALE	NONE	W	W	?	?
MALVASIA ODOROSISSIMA	ITA	?	COMPLETE	FEMALE	MUSCAT	W	W	?	?
MALVASIJA ZUPSKA	HRV	D	COMPLETE	?	?	W	W	HEUNISCH WEISS	?
MALVASIA	ITA	?	COMPLETE	?	?	B	W	?	?
MALVASIA BIANCA DI CANDIA	ITA	D	COMPLETE	HERMAFRODITE	NONE	W	W	GARGANEGA	?

Table 3. *Cont.*

GENERAL INFORMATION								PEDIGREE	
PRIME NAME	COUNTRY ORIGIN	CHLOROTYP	SEED FORMATION	SEX	TASTE	COLOR	USE	PARENT 1	PARENT 2
MALVASIA DUBROVACKA	ESP	A	COMPLETE	HERMAFRODITE	AROMATIC	W	W	?	?
MALVASIA BABOSA	PRT	A	COMPLETE	?	?	W	W	HEBEN	MALVASIA DUBROVACKA
MALVASIA VOLCANICA	ESP	?	COMPLETE	HERMAFRODITE	OTHER FLAVOR THAN MUSCAT, FOXY OR HERBACEOUS	W	W	MALVASIA DUBROVACKA	BERMEJUELA
MALVASIA BIANCA LUNGA	ITA	D	COMPLETE	HERMAFRODITE	NONE	W	W	?	?
MALVASIA NERA DI BRINDISI	ITA	?	COMPLETE	HERMAFRODITE	NONE	B	T/W	MALVASIA BIANCA LUNGA	NEGRO AMARO (? x MAIOLICA (? x VISPAROLA))
MALVASIA NERA DI BASILICATA	ITA	?	COMPLETE	HERMAFRODITE	ARMATIC	B	W	MALVASIA BIANCA LUNGA	SOMARELLO NERO (UVA SACRA (ACHLADI x ?) x GARGANEGA)
MALVASIA DEL CILENTO	ITA	?	?	?	?	B	W	?	?
MALVASIA ISTRIANA	HRV	D	COMPLETE	HERMAFRODITE	NONE	W	W	?	?
MALVASIA COMUN	ESP	A	COMPLETE	HERMAFRODITE	NONE	W	W	HEBEN	?
MALVASIA BIANCA	ITA	?	COMPLETE		NONE	W	W	SCIACCARELLO	?
MALVASIA BIANCA ZARAFA	ITA	?	COMPLETE	?	MUSCAT	W	W	?	?
MALVASIA PARDA	PRT	?	COMPLETE	HERMAFRODITE	NONE	W	W	?	?
MALVASIA BIANCA MACCARRONE	ITA	?	COMPLETE	?	MUSCAT	W	W	?	?
MALVASIA CABRAL	PRT051	?	COMPLETE	HERMAFRODITE	NONE	Rs	W	?	?
MALVASIA NERA DI BASILICATA (PENEDES)	ESP	?	COMPLETE	?	NONE	B	W	?	?
MALVASIA DEL LAZIO	ITA	?	COMPLETE	HERMAFRODITE	NONE	W	W	?	?

1: Red; POP1 pure; light red: POP1 admixed; green: POP2 pure; light green: POP2 admixed; blue: POP3 pure; light blue: POP3 admixed. 2 x is the crossing (pedigree).

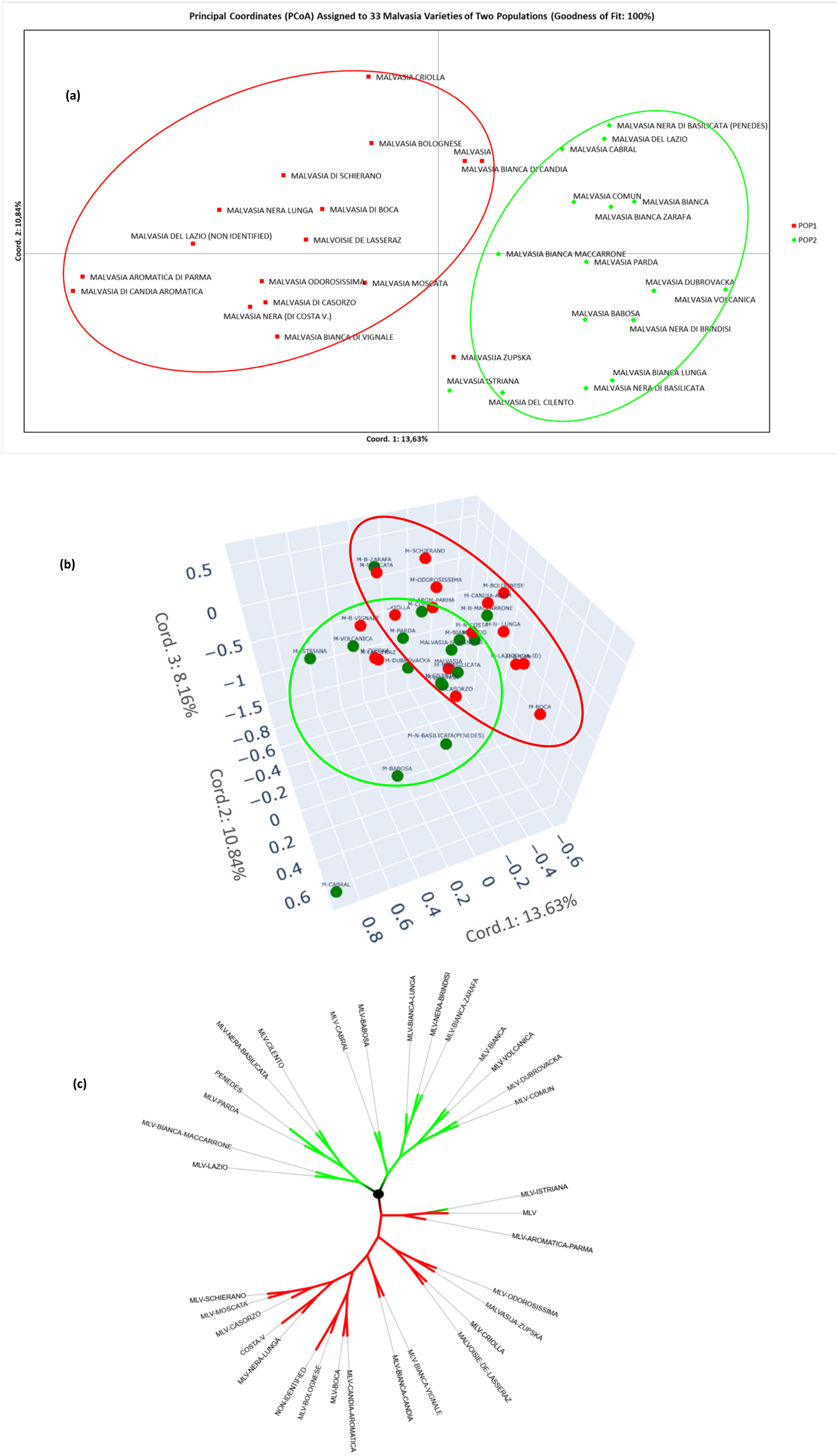

Figure 5. Graphical representation of the distribution of the 33 varieties under the geographical strategy, using PCoA of their individuals in 2D (**a**) and 3D (**b**), as well as a phylogenetic tree (**c**).

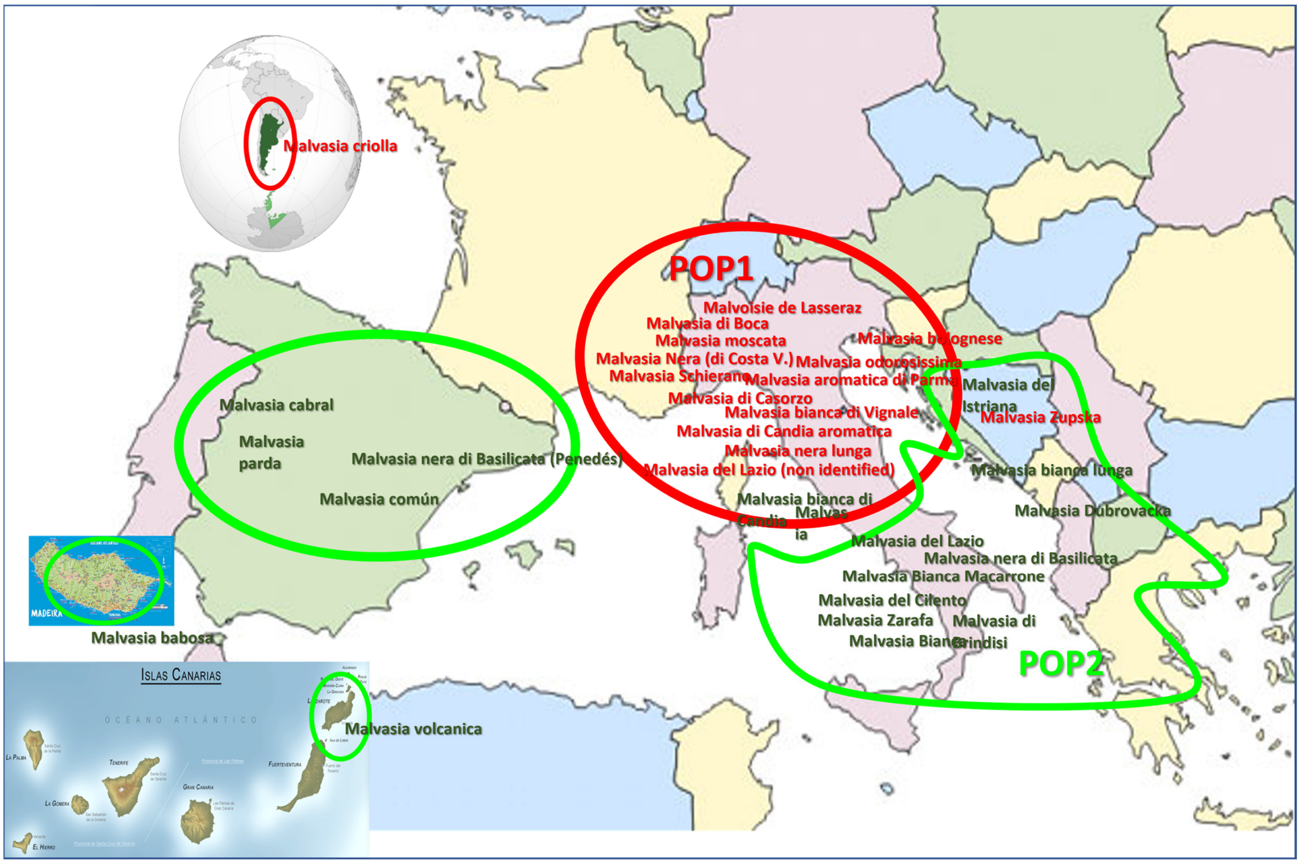

Figure 6. Map of the geographical location (approximate [5,25–27]) of the 33 'Malvasia' varieties under the geographical strategy with two populations. Goodness of fit: 100%.

The 33 members of the 'Malvasia' group were then distributed into three populations (Figures 3c and 5c) to observe the results obtained. In this way, POP2 was split into (1) the group of 'Malvasia' varieties led by Malvasia Dubrovacka and Malvasia bianca lunga and their descendants, along with Malvasia del Cilento, which often appeared close to the latter, as well as the Croatian 'Malvasia' varieties Malvasia istriana and Malvasia Zupska, and (2) the remaining 'Malvasia' group. Table 4 shows the main characteristics of this new distribution following the geographical origin strategy. This distribution achieved a goodness of fit of 97.5%.

The only misassigned variety is the Argentinian Malvasia criolla, which oscillates between POP1 and POP3, meaning this distribution never reaches a 100% goodness of fit. Thus, this misassigned (admixed) variety was left in POP1, where the progenies of the Muscat family are located. POP1 mostly includes 'Malvasia' varieties resulting from crosses with the Muscat family, and in POP2 and POP3 this pattern is not observed. POP1 contains 14 members, mostly Italian (with the exception of one French and one Argentinian variety), and with chlorotype D. POP2 includes individuals (nine varieties) from the Iberian, Italian, and Balkan Peninsulas, with chlorotypes A and D. Finally, POP3, with 10 members, is also characterized by having chlorotypes A and D, and includes members from the Iberian and Italian Peninsulas. It should be noted that this last population results from the division of POP2.

Table 4. Final distribution of 'Malvasia' varieties based on their origin as described in the VIVC, divided into three populations. Goodness of fit: 97.5%. Misassigned varieties were not eliminated, but reassigned.

GENERAL INFORMATION								PEDIGREE	
PRIME NAME	COUNTRY ORIGIN	CHLOROTYPE	SEED FORMATION	SEX	TASTE	COLOR	USE	PARENT 1	PARENT 2
MALVASIA DUBROVACKA	ESP	A	COMPLETE	HERMAFRODITE	AROMATIC	W	W	?	?
MALVASIA BABOSA	PRT	A	COMPLETE	?	?	W	W	HEBEN	MALVASIA DUBROVACKA
MALVASIA VOLCANICA	ESP	?	COMPLETE	HERMAFRODITE	OTHER FLAVOR THAN MUSCAT, FOXY OR HERBACEOUS	W	W	MALVASIA DUBROVACKA	BERMEJUELA
MALVASIA BIANCA LUNGA	ITA	D	COMPLETE	HERMAFRODITE	NONE	W	W	?	?
MALVASIA NERA DI BRINDISI	ITA	?	COMPLETE	HERMAFRODITE	NONE	B	T/W	MALVASIA BIANCA LUNGA	NEGRO AMARO (? x MAIOLICA (? x VISPAROLA))
MALVASIA NERA DI BASILICATA	ITA	?	COMPLETE	HERMAFRODITE	ARMATIC	B	W	MALVASIA BIANCA LUNGA	SOMARELLO NERO (UVA SACRA (ACHLADI x ?) x GARGANEGA)
MALVASIA DEL CILENTO	ITA	?	?	?	?	B	W	?	?
MALVASIA ISTRIANA	HRV	D	COMPLETE	HERMAFRODITE	NONE	W	W	?	?
MALVASIJA ZUPSKA	HRV	D	COMPLETE	?	?	W	W	HEUNISCH WEISS	?
MALVASIA AROMATICA DI PARMA	ITA	D	COMPLETE	FEMALE	MUSCAT	W	W	MUSCAT A PETITS GRAINS BLANCS	NEBBIOLO x BOTTAGERA (FALSE)

Table 4. *Cont.*

GENERAL INFORMATION								PEDIGREE	
PRIME NAME	COUNTRY ORIGIN	CHLOROTYPE	SEED FORMATION	SEX	TASTE	COLOR	USE	PARENT 1	PARENT 2
MALVASIA DI CANDIA AROMATICA	ITA	D	COMPLETE	HERMAFRODITE	MUSCAT	W	T/W	MALVASIA AROMATICA DI PARMA (MUSCAT A PETITS GRAINS BLANCS x NEBBIOLO X BOTTAGERA (FALSE))	?
MALVASIA NERA LUNGA	ITA	D	COMPLETE	HERMAFRODITE	ARMATIC	B	W	MALVASIA AROMATICA DI PARMA (MUSCAT A PETITS GRAINS BLANCS x NEBBIOLO X BOTTAGERA (FALSE))	FREISA (NEBBIOLO x ?)
MALVASIA BIANCA DI VIGNALE	ITA	D	COMPLETE	HERMAFRODITE	AROMATIC	W	W	MALVASIA AROMATICA DI PARMA (MUSCAT A PETITS GRAINS BLANCS x NEBBIOLO X BOTTAGERA (FALSE))	COCCALONA BIANCA
MALVASIA DI CASORZO	ITA	D	COMPLETE	HERMAFRODITE	AROMATIC	N	W	MALVASIA AROMATICA DI PARMA (MUSCAT A PETITS GRAINS BLANCS x NEBBIOLO X BOTTAGERA (FALSE))	LAMBRUSCA DI ALESSANDRIA (CROVIN x NERETTO DI MARENGO (LAMBRUSCA DI ALESSANDRIA x ?))

Table 4. *Cont.*

GENERAL INFORMATION								PEDIGREE	
PRIME NAME	COUNTRY ORIGIN	CHLOROTYPE	SEED FORMATION	SEX	TASTE	COLOR	USE	PARENT 1	PARENT 2
MALVASIA NERA (DI COSTA V.)	ITA	D	COMPLETE	HERMAFRODITE	MUSCAT	W	?	MALVASIA AROMATICA DI PARMA (MUSCAT A PETITS GRAINS BLANCS x NEBBIOLO X BOTTAGERA (FALSE))	LAMBRUSCA DI ALESSANDRIA (CROVIN x NERETTO DI MARENGO (LAMBRUSCA DI ALESSANDRIA x ?))
MALVASIA MOSCATA	ITA	D	COMPLETE	HERMAFRODITE	MUSCAT	W	W	MALVASIA AROMATICA DI PARMA (MUSCAT A PETITS GRAINS BLANCS x NEBBIOLO X BOTTAGERA (FALSE))	?
MALVASIA DI SCHIERANO	ITA	D	COMPLETE	HERMAFRODITE	MUSCAT	B	W	MUSCAT A PETITS GRAINS BLANCS	?
MALVASIA DEL LAZIO (NON-IDENTIFIED)	ITA	?	COMPLETE	HERMAFRODITE	MUSCAT	W	W	MUSCAT OF ALEXANDRIA (MUSCAT A PETITS GRAINS BLANCS x HEPTALIKO)	SCHIAVA GROSSA
MALVASIA CRIOLLA	ARG	?	COMPLETE	HERMAFRODITE	MUSCAT	W	W	LISTAN PRIETO	MUSCAT OF ALEXANDRIA (MUSCAT A PETITS GRAINS BLANCS x HEPTALIKO)
MALVASIA BOLOGNESE	ITA	?	COMPLETE	?	?	W	W	?	?
MALVASIA DI BOCA	ITA	?	COMPLETE	HERMAFRODITE	AROMATIC	W	W	?	?
MALVOISIE DE LASSERAZ	FRA	?	COMPLETE	FEMALE	NONE	W	W	?	?
MALVASIA ODOROSISSIMA	ITA	?	COMPLETE	FEMALE	MUSCAT	W	W	?	?

Table 4. *Cont.*

GENERAL INFORMATION								PEDIGREE	
PRIME NAME	COUNTRY ORIGIN	CHLOROTYPE	SEED FORMATION	SEX	TASTE	COLOR	USE	PARENT 1	PARENT 2
MALVASIA COMUN	ESP	A	COMPLETE	HERMAFRODITE	NONE	W	W	HEBEN	?
MALVASIA BIANCA	ITA	?	COMPLETE	HERMAFRODITE	NONE	W	W	SCIACCARELLO	?
MALVASIA BIANCA ZARAFA	ITA	?	COMPLETE	?	MUSCAT	W	W	?	?
MALVASIA	ITA	?	COMPLETE	?	?	B	W	?	?
MALVASIA BIANCA DI CANDIA	ITA	D	COMPLETE	HERMAFRODITE	NONE	W	W	GARGANEGA	?
MALVASIA PARDA	PRT	?	COMPLETE	HERMAFRODITE	NONE	W	W	?	?
MALVASIA BIANCA MACCARRONE	ITA	?	COMPLETE	?	MUSCAT	W	W	?	?
MALVASIA CABRAL	PRT051	?	COMPLETE	HERMAFRODITE	NONE	Rs	W	?	?
MALVASIA NERA DI BASILICATA (PENEDES)	ESP	?	COMPLETE	?	NONE	B	W	?	?
MALVASIA DEL LAZIO	ITA	?	COMPLETE	HERMAFRODITE	NONE	W	W	?	?

1: Red; POP1 pure; light red: POP1 admixed; green: POP2 pure; light green: POP2 admixed; blue: POP3 pure; light blue: POP3 admixed. 2 x is the crossing (pedigree).

Figure 7, following the same approach as in the previous cases, presents the results of the graphical representations using PCoA in two and three dimensions, along with the corresponding phylogenetic tree. In Figure 7a, corresponding to the 2D PCoA representation (with a goodness of fit of 24.47%), the three populations are clearly distinguished: POP1 is located in the left quadrants, POP2 in the upper right quadrant, and POP3 in the lower right quadrant. The addition of one more dimension (Figure 7b) and the corresponding increase in the PCoA representation's goodness of fit (32.63%) show the same pattern, with POP1 and POP3 appearing in the front upper part of the graph and POP2 in the inner part, behind POP1 and POP3. The corresponding phylogenetic tree (Figure 7c), with three branches, one for each population, again defines the distribution into three populations.

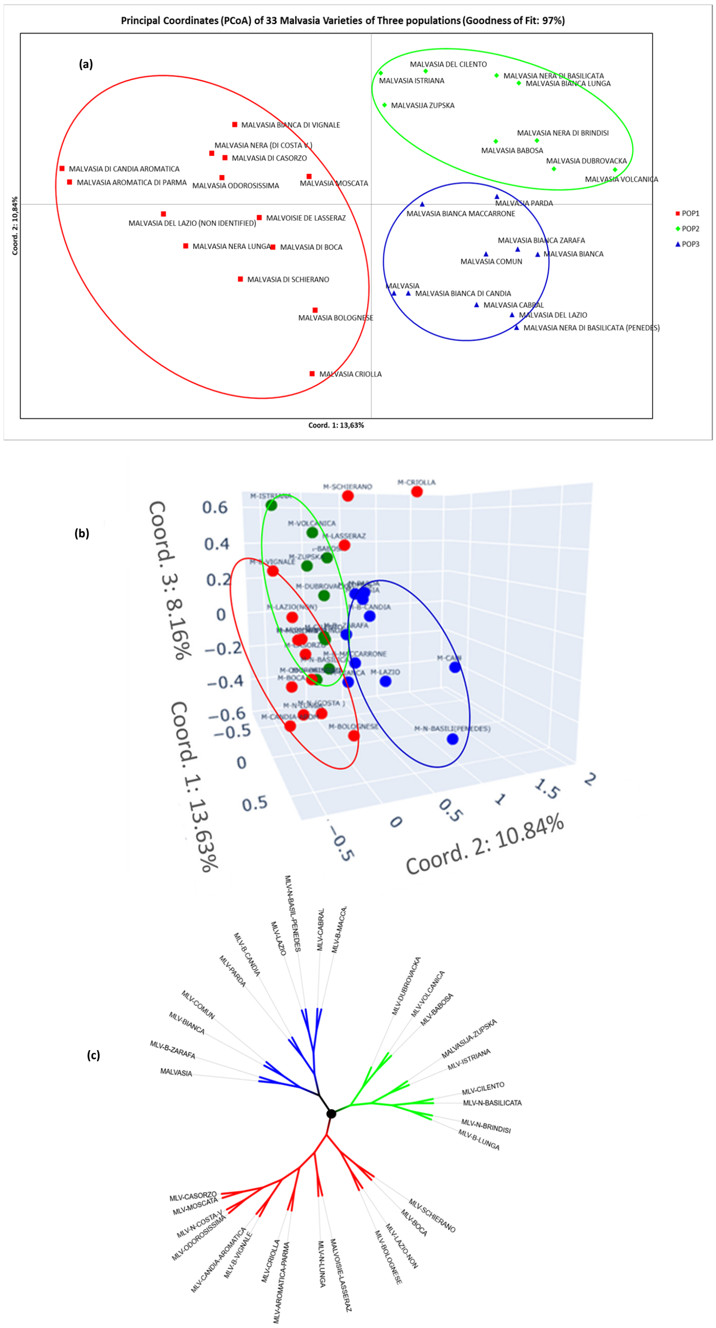

Figure 7. Graphical representation of the distribution of the 33 varieties in three populations from the geographical strategy, using PCoA of their individuals in two (**a**) and three (**b**) dimensions, as well as the representation of a phylogenetic tree (**c**).

The map showing the geographical location corresponding to this distribution is presented in Figure 8. In this image, POP1 covers the entire northern half of the Italian Peninsula, while POP2 is located in the Balkan Peninsula, ultraperipheral regions of the Iberian Peninsula, and the southern half of the Italian Peninsula bordering the Adriatic Sea. Finally, POP3 would be located in the southern half bordering the Mediterranean Sea and in the Iberian Peninsula.

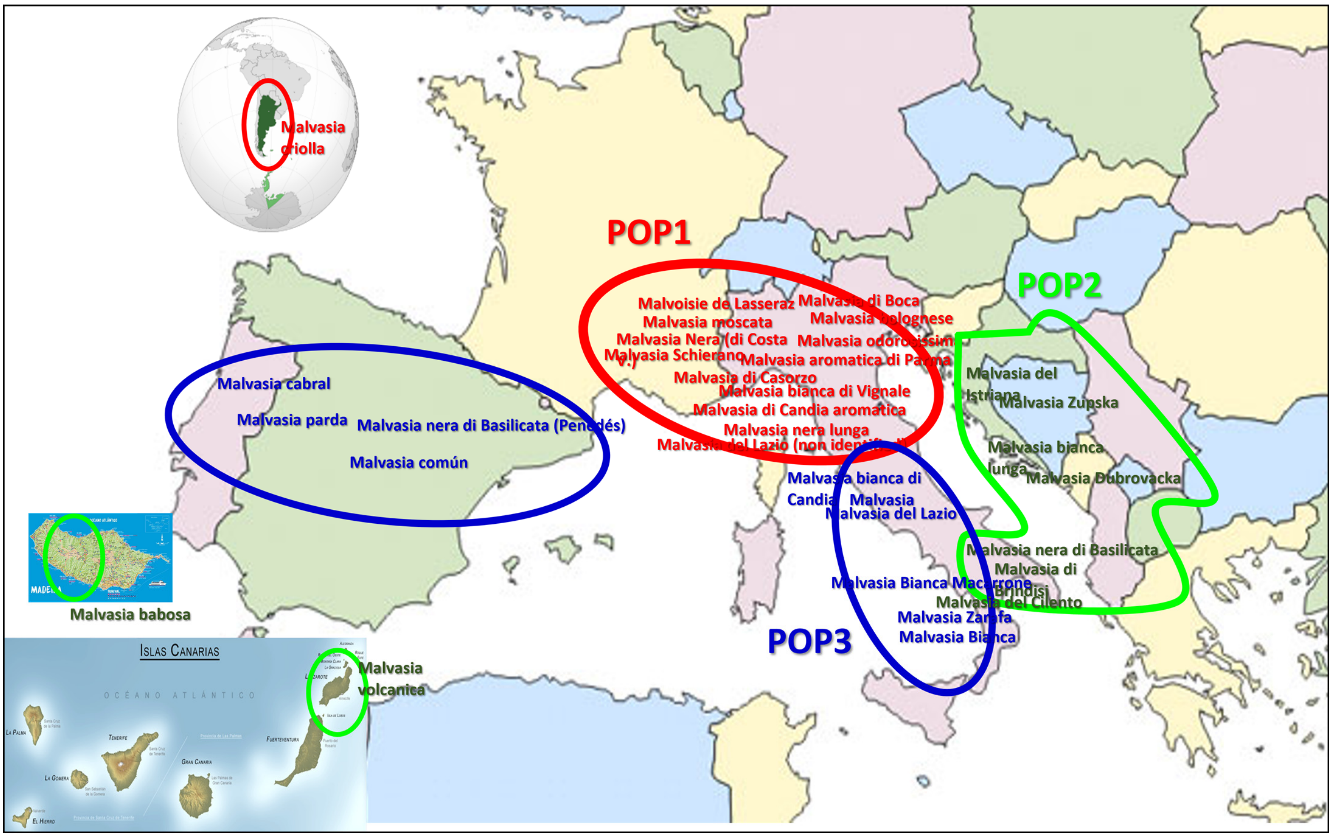

Figure 8. Map of the geographical location (approximate [5,25–27]) of the 33 'Malvasia' varieties from the geographical strategy in three populations. Goodness of fit of 97.5%.

4. Discussion

For most authors, the 'Malvasia' family is a heterogeneous group of varieties [4,28]. There is no agreement regarding their origin, nor ampelographic (Figure S4) [27,29], nor genetic traits [1,28].

Today, the quality and prestige of a wine are usually associated with a specific variety [4]. That is why we find it somewhat unusual when the opposite occurs. 'Malvasia' is a wine that gives its name to many varieties and is characterized by being sweet, aromatic, and alcoholic, although other versions exist in today's market [1].

The merchants of the Most Serene Republic of Venice successfully marketed this type of wine, which reached its peak splendor during the Middle Ages and lasted until the 18th century. They positioned it as one of the great treasures of the trade at the time due to its exquisite quality and the value it acquired among the most discerning consumers (Asenjo, J., personal communication). For that reason, its demand increased substantially [1,4].

Thus, it can be hypothesized that different varieties were possibly used to meet market requirements, always characterized by being more or less aromatic. This has surely been the main reason why so many varieties have incorporated the term "Malvasia" in their names, and why this diversity of organoleptic and ampelographic profiles has been generated for the "Malvasia" family [1].

Our research group has a database with over 1300 accessions, but it contains only 10 samples of possible 'Malvasia' candidates [30–36]. Therefore, to carry out a study of these characteristics, the most extensive and complete database to date was used. In the VIVC, 413 accessions were found that include the term 'Malvasia' or its corresponding spellings in different languages in their names (either as the main name or as a synonym) (Table 1). These accessions correspond to 250 prime names, many of them repeated, since if a prime name has various synonymous names, it will appear as many times as synonyms it has. After correcting this redundancy, the number of unique prime names was reduced to 68. In this way, the ampelographic section of the VIVC contains the description of 68 'Malvasia' varieties, of which 14 have an unknown origin. For this reason, in Table S1, where the main characteristics of these 68 'Malvasia' candidates are presented, an alternative indication is also provided of the grapevine collection (Institution) that hosts the given sample. This helps to form a hypothesis regarding its possible area of origin, although it is not always indicative (Tables S1 and S3). Table S3 shows that the country currently contributing the highest number of 'Malvasia' candidates is Italy, with 28 candidates, followed by Portugal with 11 accessions, Spain with 9 entries, and then Russia (2), Croatia (2), France (1), and Argentina (1). Out of all these, only 43 MP-SSRs are stored in the SSR section of the same database, which will therefore be the starting point of this study.

To carry out the study of population structure, the initial data were normalized to avoid redundant profiles and other artifacts that could bias and therefore interfere with the final statistical results. Thus, four varieties that turned out to be color 'sports' were excluded (variations or mutations in color and/or hairiness that have an identical genetic profile to the main variety). In this population, they were pink mutations (Malvasia di Sardegna rosada, Malvasia fina roxa, Malvasia preta roxa, and Malvasia rosa). The SSR-MPs of varieties resulting from non-natural crosses were also excluded, as they would bias the final result due to being directed crosses. This was the case for Malvasia branca de Sao Jorge and Malvasia moscatel Fonte grande, both Portuguese and designed by the breeders J. L. Ferreira de Almeida and A.P. Soares Franco, respectively in Vitis International Variety Catalogue [3] (Table S1). The varieties Malvasia (Malvasia de Colares), Malvasia fina, Malvasia preta, and Malvoisie de madera were also excluded. These four varieties were the result of natural crosses with varieties from the Iberian Peninsula, France, or Turkey, and thus presumably had no relationship with aromatic varieties (presumed 'Malvasia') or with Muscats (Table S1). This led to the exclusion of 10 varieties, leaving a final study population of 33 SSR-MPs corresponding to their respective varieties.

It is also important to note an aspect concerning the graphical representations of PCoA. Considering that we are working with 9 SSRs and that each SSR has 2 alleles, we will use 18 numerical values (measuring the length of each microsatellite in base pairs (bp)) to define the profile of an individual. Its accurate graphical representation would require the use of 18 dimensions, and that, at present and with our resources, is impossible. Normally, we work in two dimensions and, exceptionally, in three dimensions. This dimensional reduction involves an error that the scientific community must accept, and does accept, which is why we often refer to trends.

In this work, two strategies have been addressed. The first, known as the genetic strategy, consists of distributing the varieties into several populations based on the parameter q, which indicates the percentage of their inferred genome that belongs to one of these populations (Structure 2.3. software). The second is the geographic strategy, in which the distribution of varieties into different populations according to their allelic frequency is conditioned by their geographical origin (GenAlEx 6.5 software (assignment)). Observing the results of these two strategies will allow us to refine the hypothesis that is the subject of this study.

The result obtained in the genetic strategy is presented in Figure 2. The Structure 2.3 software proposes, as the best distribution of the 'Malvasia' population, dividing it into three populations (Figure S1), where varieties are grouped based on their genetic proximity as defined, in this case, by the q parameter (Table S5). A color has been assigned to each population, and at a glance, one can distinguish the so-called 'pure' varieties ($q \geq 74\%$) in which the corresponding color predominates, and the varieties referred to as 'admixed' ($q < 74\%$), where the primary color of the population is shared with the other two colors corresponding to the other populations. Thus, the admixed varieties were eliminated, and the analysis continued with the 17 pure varieties. In this distribution, with a goodness of fit of 82%, POP2 was the most consistent and closely related group (Table S5), with a range of q values for pure varieties between 95.9% and 89.2% and represented by the color green. This was because this cluster was composed of two main varieties (Malvasia Dubrovacka and Malvasia bianca lunga) and their respective progeny, in addition to Malvasia del Cilento, which was always very close to these families (Figure 3). This group was characterized by not having any members related to the Muscat family (only Malvasia bianca Zarafa, which was removed for being admixed, had a Muscat aroma). Interestingly, almost all the 'Malvasia' candidates with one or two Muscat family progenitors were located in POP1 (Table 2). These were not as closely related to one another as those in POP2, and their group color was red (the range of group membership for pure varieties was between 86.2% and 78% (Table S5)). In POP3, the most genetically distant varieties were grouped, with a range for pure varieties between 77.7% and 74.1%, and this population was represented by the color blue (Table S5). When reassignment was performed to reach 100% goodness of fit, POP3, the most distant group, was split between the other two. Malvasia odorosissima ended up in POP1, and Malvasia Maccarrone, Malvasia cabral, Malvasia bianca di Candia, and Malvasia were assigned to POP2. The PCoA graphical representations in two (Figure 3a) and three dimensions (Figure 3b) supported this new redistribution into two populations clearly, with a noticeable distance observed for Malvasia cabral, Malvasia bianca di Candia, and Malvasia from the rest of POP2. However, Malvasia Maccarrone (despite having a Muscat aroma (Table 2)) appeared well integrated into group POP2, and Malvasia odorosissima into POP1. Thus, in the phylogenetic tree, the former POP3 members appeared distant from their respective new groupings to the extent that the four varieties integrated into POP2 formed a main branch on their own (Figure 3c), demonstrating the distance of POP3 members both from each other and from their adoptive populations. Looking at Figure 4, the approximate geographical distribution of these two populations (after reassignment) shows POP1 located in the northern regions of the Italian Peninsula, while POP2 is spread across the southern zone of the Italian Peninsula and the Adriatic area of the Balkan Peninsula (also in its southern part), in addition to overseas areas and the Iberian Peninsula. This distribution of POP2 could have a historical explanation, due to human movements across the Mediterranean Basin and the conquest of the Atlantic Ocean [7,37].

In the geographic strategy, we chose not to eliminate the misassigned varieties (corresponding to the admixed ones), knowing that the behavior of the graphical representations might not be as clear and strong as in the previous case. However, this approach was expected to allow the monitoring of all candidates. Curiously, it turned out that when the 33 varieties were grouped according to the geographic area listed in the VIVC and their related and/or nearby zones, two populations were also formed (Table S6). POP1 included 26 varieties corresponding to the Italian Peninsula and nearby areas, plus the exception of Malvasia criolla (from Argentina). This Argentinean variety was included in POP1 since all the varieties with natural crosses involving members of the Muscat family were found here. Thus, most of the varieties in this cluster had Muscat-like aromas or were classified as aromatic. Likewise, it could be observed that the known chlorotypes of their components were D, a chlorotype widely spread in the Italian and Balkan Peninsulas [24,38].

In addition, when examining the flower sex column, it was found that three 'Malvasia' varieties exhibited female sex, while the vast majority of cultivated grapevine varieties were hermaphroditic. These were the northern Italian varieties, Malvasia aromatica di Parma, Malvasia odorosissima, and the French Alpine variety Malvoisie de Lasseraz. Wild grapevine (*Vitis vinifera* L. ssp. *sylvestris* (C.C. Gmel.) Beger & Hegi) is dioecious, meaning it has either male or female individuals, a strategy that was selected for being favorable to colonizing new territories once this subspecies began expanding from Mediterranean refugia [39].

In contrast, during the domestication process of wild grapevine for cultivation, the selected flower type was hermaphroditic, significantly reducing dioecy. Currently, there are very few grapevine varieties that exhibit female flowers [40]. POP2, with seven members corresponding to the Iberian Peninsula (and outermost territories), presented crosses without members of the Muscat family, and therefore without Muscat aromas, with any variety having female flowers and with known chlorotypes of type A, which is very common in varieties from the Iberian Peninsula and much less present in the Italian and Balkan Peninsulas [24,38]. This distribution had a goodness of fit of 76%. The misassigned varieties were reassigned until reaching a goodness of fit of 100%. Interestingly, as expected, the varieties that in the genetic strategy had constituted POP3 (Figure 2) were divided between POP1 and POP2 in the geographic strategy. The pure varieties Malvasia odorosissima, Malvasia, and Malvasia bianca di Candia were placed in POP1, along with the admixed varieties Malvasia di Schierano, Malvasia criolla, and Malvasija Zupska. In POP2, the pure varieties Malvasia Maccarrone and Malvasia cabral were assigned, as well as the admixed varieties Malvasia istriana and Malvasia comun. It can be observed that the presence of the admixed candidates changed the previous placement of some of the pure varieties from POP3. In the PCoA representations in two and three dimensions (Figure 5a,b), in the phylogenetic tree representation (Figure 5c), and in the approximate geographical distribution presented in Figure 6, it can be stated that, globally and generally, the behavior observed in the genetic strategy for two populations is repeated. Once again, the phylogenetic tree suggests a third population formed by the individuals from POP3 of the genetic strategy (Figure 2), which are mostly now located in POP2 of this new geographic distribution.

Based on all the observations up to this point, we decided to configure a new population within the geographic strategy, composed of all the varieties located in the upper right quadrant of Figure 5a, along with two varieties located along the axis of Coordinate 2 within this quadrant (most of which corresponded to POP3 from the previous distribution under the genetic strategy). The objective was to divide POP2, as suggested by the two phylogenetic trees from the two strategies studied so far (Figures 3c and 5c). Now, POP3 would be composed of the following 10 members: Malvasia comun, Malvasia bianca, Malvasia, Malvasia Zarafa, Malvasia bianca di Candia, Malvasia parda, Malvasia Maccarrone, Malvasia cabral, Malvasia nera de Basilicata (Penedès), and Malvasia del Lazio. Once this new geographic distribution into three populations was carried out (Table 4), the corresponding assignment test was conducted, which resulted in a goodness of fit of 97.5%. A full 100% was never reached because the Argentine variety Malvasia criolla, which shifted back and forth between POP1 and POP3, was ultimately placed in POP1, since one of its parents belonged to the Muscat family. Figure 7a,b show the graphical representations using PCoA in two and three dimensions, respectively. In them, the three populations are clearly distinguishable. As has consistently occurred, POP1 includes the varieties related to the Muscat family, POP2 includes varieties with a possible origin in the Balkan Peninsula, and POP3 contains a group without an apparent relationship, possibly composed of varieties whose crosses involve Italian and Iberian representatives with some ancestral link resulting from human migrations that we cannot determine [7,37]. These results are consistent with those found by Lacombe et al. [4]. In their study, a clear dichotomy is also established between the varieties whose name includes the term 'Malvasia' and descend from crosses with members of the Muscat family, in contrast to another group composed of varieties whose origin is possibly the Balkan Peninsula, along with some groups of varieties without apparent connection. Meneghetti et al. [28] also studied a group of varieties belonging to the 'Malvasia' family, with only 10 representatives. Their results would also be in line with this. From their work, it is worth highlighting that the Malvasia Istriana alone formed a significant sub-branch of the dendrogram they presented, underscoring a trend that is also observed in the present study. Malvasia Istriana, although of Balkan origin [41], is often found either distant from the grouping of Balkan varieties or associated with individuals from POP1. The genetic study (Figure 2) identified it as an admixed individual from POP3, just like the other Balkan variety, Malvasia Zubska, which also appeared as a member of POP1 on some occasions (Figure 6).

Before moving on to the conclusions from the previous paragraphs, the authors of this work would like to make one final observation regarding the Muscat family. If one consults the ampelographic section of the VIVC and enters the term 'Moscatel' in the 'Prime Name' field, a list of Muscats appears. In this list, it can be seen that the variety Muscat d'Istanbul is a natural cross between the Spanish variety Beba and Muscat of Alexandria (Muscat à petits grains blancs x Heptaliko) and that the variety Muscat fleur d'oranger is a natural cross between Muscat à petits grains blancs and the French variety Chasselas. It is logical to think that the offspring of crosses between members of the Muscat family would also carry the term 'Muscat' in their compound names, since they may retain the characteristic aromas of this family. From this reflection arises the question: why, when a cross is made between a member of the Muscat family and another variety, be it Spanish, Italian, Portuguese, etc., is the term 'Malvasia' included in the name and not 'Muscat'? (see, for example, the crosses in Table 2).

For the authors of this work, such a practice is illogical, and the results of these crosses cannot be considered members of the 'Malvasia' family. Therefore, all varieties that are descendants of the Muscat family would be excluded from being part of the 'Malvasia' family. On the other hand, candidates that could be considered part of this family would be the progeny of Malvasia Dubrovacka and Malvasia bianca lunga. In the case of Malvasia Dubrovacka, the crosses in which it is involved, as described in the VIVC, correspond to Malvasia volcanica and Malvasia babosa. Both are daughter varieties that already include the term 'Malvasia' in their names and can thus be considered members of this family. In the case of Malvasia bianca lunga, its progeny includes a mix. There are varieties that have retained the term 'Malvasia' in their names, such as Malvasia nera di Basilicata and Malvasia nera di Brindisi. However, the Slovenian variety Vitovska and the Italian variety Pelena (Glera (Vulpea (Visparola x ?) x ?) x Malvasia bianca lunga), the Italian variety Prunesta (false) (Malvasia bianca lunga x ?), and the Greek variety Lagorthi (known in Italy as Verdeca) (Malvasia bianca lunga x ?), all descendants of Malvasia bianca lunga, have not retained the term 'Malvasia' in their names, yet in our opinion they would still be members of the 'Malvasia' family [2,3,41].

Based on everything discussed so far, it is clear that POP2 (the green population) contains the strongest candidates to belong to the 'Malvasia' family, both in the genetic and the geographical strategies, and in all their combinations. That said, it can be hypothesized that the leading candidates to represent the 'Malvasia' family would be the following seven varieties (Figure 2, Table S5): (a) Malvasia Dubrovacka (with q = 94.2%) and its progeny, Malvasia volcanica (q = 93.2%) and Malvasia Babosa (q = 89.2%); (b) Malvasia bianca lunga

(q = 95.9%) and its progeny, Malvasia nera di Basilicata (q = 94.2%) and Malvasia nera di Brindisi (q = 93.6%); (c) Malvasia del Cilento (q = 92%). Let us not forget either that the 'sport' Malvasia di Sardegna rosada (pink Malvasia), with an identical MP-SSR to Malvasia Dubrovacka, would also be a notable member of the 'Malvasia' family.

As for hypothesizing about the origin of this or these varieties, it can be said that they most likely originated in the Balkan Peninsula (including present-day Greece), even though it has been stated that, for example, the genotype of Malvasia Dubrovacka (one of the strongest candidates to be a true 'Malvasia') showed no connection with individuals in Greek databases, nor could its allele frequencies be related to Croatian, Greek, Italian, Spanish, or Portuguese varieties [1]. The fact remains that a record of Malvasia Dubrovacka exists in the Archives of the Republic of Dubrovnik (Croatia) as early as the year 1385 [1]. In the case of Malvasia bianca lunga, another candidate to be part of this highly selective group of varieties, D'Onofrio et al. [41] proposed its origin in the Balkan Peninsula. These clues, along with the origin of the term that defines 'Malvasia', as discussed previously in the Introduction to this work, reinforce the possibility of a Balkan origin for the varieties used to produce 'Malvasia' wine.

5. Conclusions

It is a fact that the term "Malvasia" and its versions in different languages have been associated throughout history with grape varieties and high-quality wines. It is probably for this very reason that it has even been used to name varieties that have nothing to do with those that are very possibly the true members of this family. Of the 413 variety names containing the term "Malvasia", only 68 remained as candidates to form part of this family. In the MP-SSR section of the VIVC, the genetic profiles of only 43 of them were found. After data normalization, the study was reduced to 33 MP-SSRs. Finally, using different genetic and geographical population structure strategies, it can be concluded that a small group of seven varieties and a color mutation of one of them were chosen as candidates to constitute the "Malvasia" family. In other published works, a small group of four varieties is also proposed as true "Malvasia", although their names do not include this term.

Essentially, this would be a starting group composed of two "reference" varieties genetically linked to each other and their derived strains, either through crosses or mutations. These would be Malvasia Dubrovacka and Malvasia bianca lunga. Another variety that is also very genetically similar to the previous varieties, Malvasia del Cilento, would also be included in this family. Through crossing Malvasia Dubrovacka with other varieties, the varieties Malvasia volcanica (ESP) and Malvasia babosa (PRT) are considered "Malvasia", and through mutation, Malvasia di Sardegna rosé (ESP). If the cross in question involved Malvasia bianca lunga, the varieties to be incorporated into this family would be Malvasia nera di Basilicata (ITA) and Malvasia nera di Brindisi (ITA). Furthermore, the following varieties would also be part of the offspring of Malvasia bianca lunga and therefore also considered "Malvasia" the varieties Vitovska (SVN), Pelena (ITA), Prunesta (false) (ITA), and Lagorthi (GRC). The remaining varieties studied as candidates for "Malvasia" status were rejected, either because they originated from crosses with Muscats or because they derived from crosses with other local varieties from each geographical area in question.

Substantially reducing the number of candidates for this family ensures, on the one hand, the family prestige, and on the other, ensures that consumers associate unique organoleptic characteristics with the varieties proposed as candidates for the "Malvasia" family.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/horticulturae11060561/s1, Table S1. General information on the 68 unique varieties which include the term 'Malvasia' in their PNs and are registered in the ampelographic section of the VIVC; Table S2. List of "international" primers used by different authors for the amplification of the selected satellite regions. Main characteristics; Table S3. Information on the origin of the 68 unique varieties that include the term 'Malvasia' in their prime name and are registered in the ampelographic section of the VIVC; Table S4. Summary of the general information on the 43 unique varieties with published SSR-MP (Table S1) that include the term 'Malvasia' in their prime name; Figure S1. The four steps of the graphical method of Evanno et al. (2005) [17], allowing the estimation of the true number of ancestral K groups for a population with 33 individuals from 'Malvasia' group; Table S5. Details of the distribution into three populations of the 33 unique varieties and the proportion of pure and admixed individuals based on the q value (pure: $q \geq 74\%$; admixed: $q < 74\%$), as proposed by the Structure 2.3 program; Figure S2. Result of the assignment test for the genetic strategy with K = 3, that is, for three populations; Figure S3. Result of the assignment test for the geographical strategy with two populations; Table S6. Initial distribution of 'Malvasia' varieties based on their origin as described in the VIVC. Goodness of fit: 76%. POP1 (in red) corresponds to the population from the Italian Peninsula and surrounding areas, and POP2 (in green) corresponds to the population from the Iberian Peninsula and areas of influence (with the exception of the Argentine variety Malvasia criolla); Figure S4. Examples of leaves and bunches of different varieties of the "Malvasia" family, corresponding to "true" components. Leaf and bunch shape polymorphism exhibited by genetically related varieties.

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