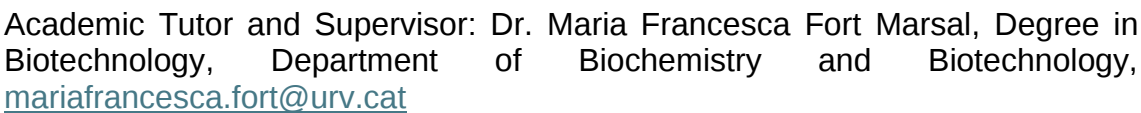




Luis Ricardo Suárez De Abreu

BACHELOR'S THESIS IN BIOTECHNOLOGY



In cooperation with: TECNENOL GROUP

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1 CENTRE INFORMATION

The Research Group in Enological Technology (TECNENOL) is based at the Sescelades Campus of the Universitat Rovira i Virgili (URV) in Tarragona. It is part of the Department of Biochemistry and Biotechnology (DBB). The DBB is home to faculty members involved in various educational programs and encompasses several research groups, including TECNENOL (founded in 2001). In 2005, the group was officially recognized as a quality research group by the Generalitat of Catalonia, as a result of the dedication and work of its researchers and research fellows.

The group has published numerous scientific articles in both international and national peer-reviewed and outreach journals. Additionally, its members regularly give lectures abroad and throughout Spain and participate in national and international conferences.

TECNENOL is composed of two main areas: the Enology Area and the Vine Biology and Viticulture Area, coordinated by Dr. Miquel Canals and Dr. Maria Francesca Fort, respectively. The group coordinator is Dr. Fernando Zamora.

1. Enology Area – Main lines of research:

- Phenolic maturity: influence of grape ripeness and maceration time on wine composition; and the effect of seed removal or addition.
- Wine proteins: analysis of wine proteins and precipitates using size exclusion FPLC (Fast Protein Liquid Chromatography); design of new fining agents and their effect on foam formation.

2. Vine Biology and Viticulture Area – Main lines of research:

- Development of new protocols for DNA and RNA extraction from leaves, canes, seeds, and wine.
- Identification and classification of *Vitis vinifera* L. varieties using microsatellites (Simple Sequence Repeats – SSR).

As an intern at TECNENOL, this project was carried out on the Vine Biology and Viticulture Area.

2 ABSTRACT AND KEYWORDS

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 Lagorhti, 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.

3 INTRODUCTION

Grapevine (*Vitis vinifera* L.) is one of the most important fruit species in the modern world. Native to the Mediterranean Basin and western Asia, it is now cultivated across the globe. Wine, table grape, and raisin sales contribute significantly to the economies of the world's leading grape-producing countries (Wolkovich et al., 2018).

3.1 BOTANICAL CLASSIFICATION OF GRAPEVINE

Grapevine is a sarmentose climbing vine. Until recently, the botanical classification of this species was based on the measurement and comparative observation of its morphological traits under the science of ampelography. The application of this discipline generates confusion since it relies on the observation of phenotypic traits, which are influenced by environmental and nutritional factors. Currently, the development of molecular biology techniques has revolutionized the classical taxonomy and systematics. Accordingly, the most up-to-date classification accepted is: Kingdom: Plantae; Phylum: Magnoliophyte; Class: Magnoliopsida; Order: Vitales; Family: Vitaceae; Genus: *Vitis*; Species: *Vitis vinifera* L.; Subspecies: *Vitis vinifera* subsp. *vinifera* (Marsal, 2015).

3.2 ORIGIN OF THE FAMILY VITACEAE AND THE GENUS *VITIS*

Hitherto, the origin of the Vitaceae family was thought to date from the early Tertiary period (66-2.6 Ma). However, following the publication by Manchester et al. (2013), the scientific community became aware of fossilized seeds belonging to a species described as *Indovitis chitaleyae* gen. et sp. n., a member of the Vitaceae that dates back to the Mesozoic era (145-66 Ma). The earliest specimens of the genus *Vitis* that were discovered consist of fossilized leaves from the Paleocene: 66-56 Ma. Specifically, in Sézanne (France) a specimen named *Vitis sezannensis* was unearthed (Hidalgo and Hidalgo, 2019). From that point onward, a burst of new species of *Vitis* appeared throughout the Miocene (23-5.3 Ma). During the glaciation periods at the end of the Pliocene (5.3-2.6 Ma) and throughout the Pleistocene (2.6 Ma – 11,700 years ago), life on Earth underwent drastic reductions: in Eurasia (Europe and Western Asia), only the two subspecies of *Vitis vinifera* L. (the wild form *Vitis vinifera* subsp. *sylvestris* and the domesticated form *Vitis vinifera* subsp. *vinifera*) persisted in favorable climatic pockets, which we call “refugia”. In other continents, from these refugia, other different species of the genus *Vitis* developed, but only in the Northern Hemisphere (Figure 1) (Wan et al., 2013).



Figure 1. Worldwide vegetation refugia (and thus refugia for *Vitis*) adapted from Alleweldt et al. (1990). Dashed lines indicate the southern limits of the polar ice sheet during the last glaciation; dot-and-dash lines mark the refugia (Wan et al., 2013).

3.3 ORIGIN OF *VITIS VINIFERA* L.

As mentioned above, in Europe and Western Asia (due to its varied topography) a single species would take centre stage: *Vitis vinifera* L. (Wan et al., 2013). The wild form (*Vitis vinifera* subsp. *sylvestris*) colonized all habitats beyond the Caucasus to the Iberian Peninsula (Figure 2) (Zohary and Spiegel-Roy, 1975).



Figure 2. Refugia of *Vitis* in the Mediterranean Basin (enclosed areas) and the Caucasus, showing the colonization of the wild form of *Vitis vinifera* L. (*Vitis vinifera* subsp. *sylvestris*). Light red circle: Iberian Peninsula; blue circle: southern Italy; dark red circle: southern Balkans; green circle: Black Sea; yellow circle: Caucasus. Adapted from Zohary and Spiegel-Roy (1975).

Primitive humans, who appeared 200,000 years ago, gradually evolved, became sedentary, and organized into social structures of varying complexity. The most advanced civilizations (e.g., Mesopotamia and Persia) were the first to domesticate the wild grapevine (*Vitis vinifera* subsp. *sylvestris*) into cultivated vine (*Vitis vinifera* subsp. *vinifera*), around **11,000** years ago. (Dong et al., 2023). At this point, we may ask: how did such an event happened, and how the domesticated grapevine spread?

Currently, Dong et al. (2023) have advanced a **Dual-Origin Theory of grape domestication**, both of the wild ancestor (*Vitis vinifera* subsp. *sylvestris*) and the cultivated form (*Vitis vinifera* subsp. *vinifera*), based on genetic and paleogenomic evidence with 3525 cultivated and wild accessions worldwide (Figure 3).

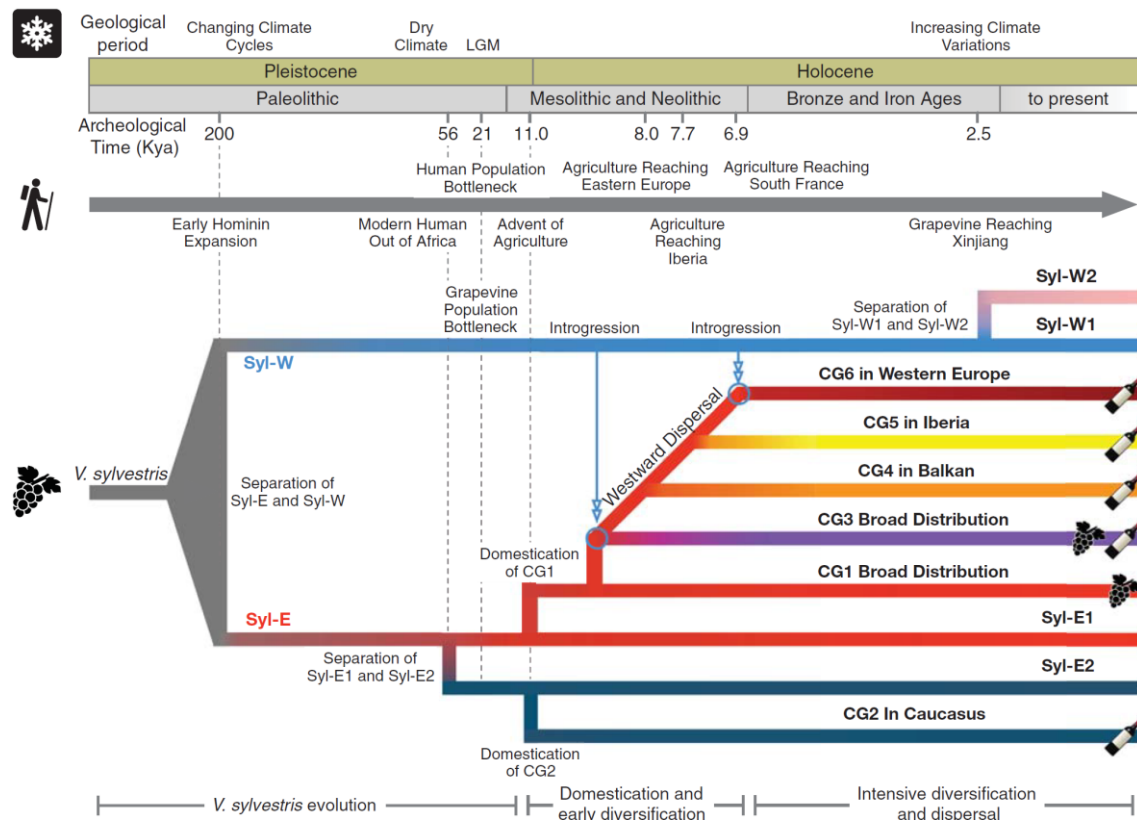


Figure 3. Schematic graph of grapevine evolutionary history (Dong et al., 2023).

According to this theory, after the establishment of climatic refugia during the early glaciations (5.3-2.6 Ma), particularly in Eurasia where only the wild form of *Vitis* persisted (*Vitis vinifera* subsp. *sylvestris*), 200,000 years ago that wild lineage split into two ecotypes: **Syl-E** (eastern ecotype), occupying refugia in the Caucasus; and **Syl-W** (western ecotype), persisting in the northwestern Mediterranean (Iberia, southern France) and northern Mediterranean coast.

The eastern wild grape (Syl-E), about 56,000 years ago split into two populations: **Syl-E1** in the Near East and **Syl-E2** in the Caucasus. Around **11,000** years ago, synchronous with the rise of sedentary human societies and the dawn of agriculture, a dual domestication of grapevine occurred, giving rise to what we now call *Vitis vinifera* subsp. *vinifera*. It is termed “dual” because it took place simultaneously in two primary domestication centres named “Cultivated Grapevine groups” (CG groups) (Figure 4):

1. CG1 (Western Asia Domestication Centre): Derived from Syl-E1, this group comprises the Western Asian table grapes.
2. CG2 (Caucasus Domestication Centre): Derived from Syl-E2, this group comprises the Caucasian wine grapes, including today’s Rkatsiteli, Saperavi, Achilles varieties.

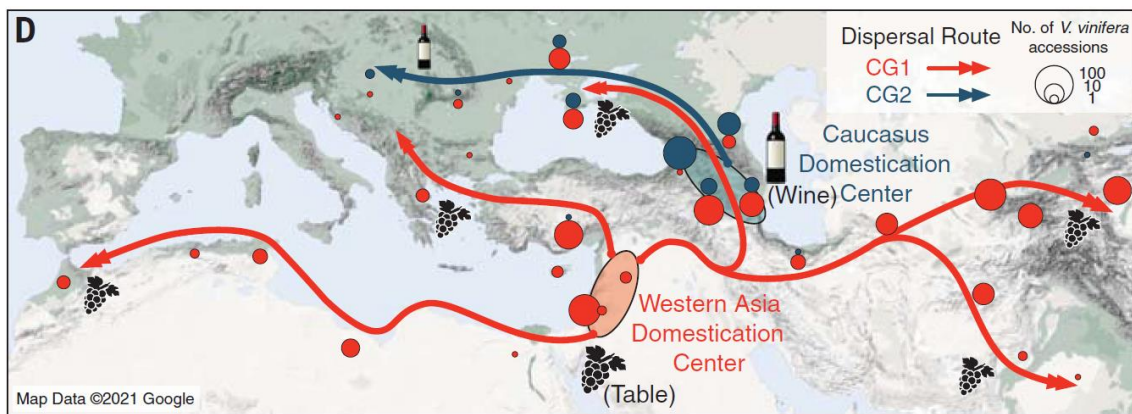


Figure 4. Geographic distribution of CG1 and CG2 in relation to the domestication centres. Human dispersal routes are shown (Dong et al., 2023).

What happens with the most common grapevine varieties? In Figure 4, it can be observed that CG1 from Western Asia expanded through Mesopotamia, Central Asia, India/China, Caucasus, Balkans and Morocco (driven by human migrations and anthropogenic selection pressure). During this dispersal, CG1 came into contact with wild western ecotype populations (Syl-W). The result of this contact is a gene flow (introgression) which sparked the origin of four European wine lineages (four secondary domestication centres), where the vast majority of today’s most famous grapevine varieties arise, including the “Malvasia” Family. These four secondary domestication centres are: CG3 (Muscat varieties, 10,500 years ago); CG4 (Balkan varieties, 8,070 years ago); CG5 (Iberian varieties, 7,740 years ago) and CG6 (Western European varieties: Pinot, Cabernet, Merlot..., 6,910 years ago) (Figure 5). Therefore, introgressions from the

western wild grapevine (Syl-W) definitively marked the emergence of grape cultivars for winemaking across the different regions of the Western Mediterranean Basin.

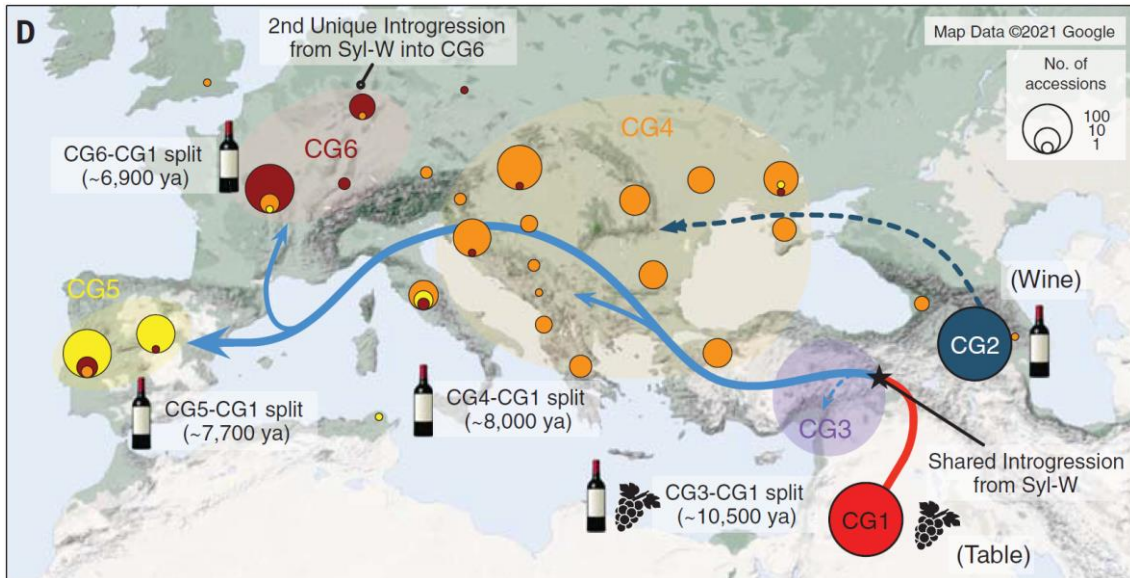


Figure 5. Origination of *Vitis vinifera* subsp. *vinifera* groups (CG3 to CG6). Geographic distributions of CG groups are shown by colored circles (Dong et al., 2023).

Thus, the genesis of *Vitis vinifera* subsp. *vinifera* is the result of human selection (domestication). But why did humans feel the need to transform wild *Vitis vinifera* subsp. *sylvestris* into *Vitis vinifera* subsp. *vinifera*? The differential traits between the two subspecies are the direct consequence of the process of domestication, during which humans selected characteristics of particular interest, changing the biology of the plant whether by sexual reproduction (natural crosses) or by asexual propagation where mutations fixed under anthropogenic selection (Bacilieri et al., 2013; Myles et al., 2011; This et al., 2006). The primary traits selected by humans during domestication were: hermaphroditism, fertility, flower shedding (abscission), productivity, berry size, sugar content and acidity, along with other features such as tolerance to abiotic and biotic stress and ease of grafting (asexual propagation). All of these characteristics underpin a productive, high-quality viticulture (Bacilieri et al., 2013).

3.4 HISTORICAL DISTRIBUTION OF *VITIS VINIFERA* SUBSP. *VINIFERA*

From the earliest domestication centres (located in regions with the most advanced civilizations) grapevines first spread into adjoining areas. Thus, the use and consumption of vine and wine reached Egypt, the Balkan Peninsula, and Lower Mesopotamia. Subsequently, the expansion throughout the Mediterranean Basin was driven by trading

and expansionist peoples such as the Assyrians, Phoenicians, Greeks, Romans, Etruscans and Carthaginians (This et al., 2006). At the same time, the vine-wine complex also traveled eastward into Asia, reaching India, China and Japan (Hidalgo and Hidalgo, 2019). During the Roman Empire, viticulture and wine consumption extended into central and northern Europe along major river trade routes (the Rhine, Rhône, Danube and Garonne) reaching as far north as Germany. The Romans were apparently the first to assign names to grape varieties, although it is now difficult to correlate those ancient names with modern cultivars. Nonetheless, it seems they already distinguished between table and wine grapes, as well as between red and white varieties (This et al., 2006). In the Middle Ages, while Islamic culture held sway over parts of Europe, North Africa and Asia Minor, it was the Christian religious orders that preserved and propagated wine consumption (both through the Crusades to the Levant and the *Reconquista* of the Iberian Peninsula) while also extending viticulture into northern Europe. Recall that wine's liturgical role in the Eucharist cemented its importance in Christian rites, whereas Islam explicitly forbade wine consumption. Therefore, Christianity maintained and expanded viticultural practices for winemaking, while Muslim regions focused on grapes for fresh fruit and raisins (Hidalgo and Hidalgo, 2019). After the discovery of the Americas at the end of the 15th century, colonists and missionaries introduced *Vitis vinifera* L. to the New World (arriving in Mexico in 1525 and Argentina in 1556). Throughout the 17th century, domesticated grapevines continued to spread: they reached Australia in 1606, South Africa in 1640, California in 1697 (brought by Jesuits), and New Zealand in 1819 (From Australia) (Royer, 1988). A corresponding chronology is illustrated in Figure 6.

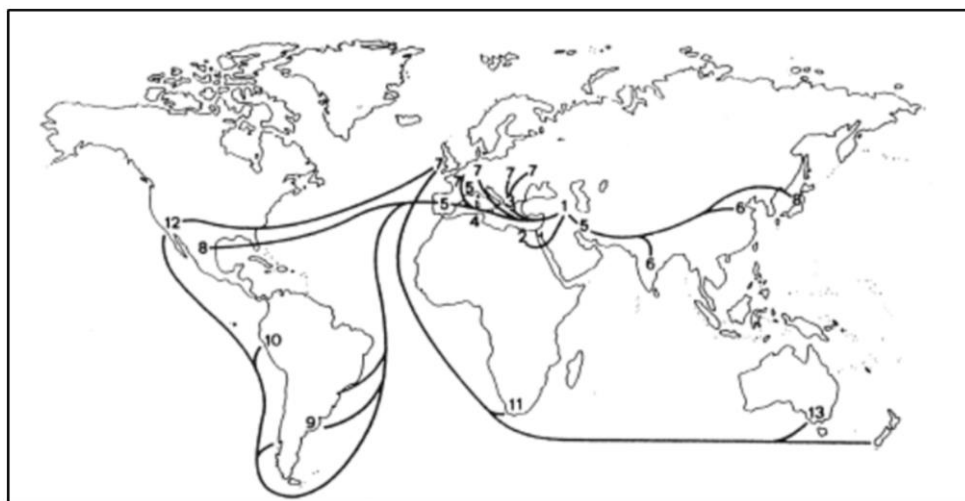


Figure 6. Worldwide spread of *Vitis vinifera* subsp. *vinifera* and its chronology (Hidalgo and Hidalgo, 2019).

In the second half of the 19th century, a two-way exchange of wood between Europe and Americas introduced fungal diseases (powdery and downy mildew) and the phylloxera insect pest, which devastated European vineyards and transformed traditional vine plantings (Royer, 1988). These fungi and insects, co-evolved with American *Vitis* species, parasitized European vines without fatal consequences in their native hosts but severely impacted *Vitis vinifera* L. To withstand this ecological onslaught, European growers adopted grafting, using American species as rootstocks (This et al., 2006).

Today, factors such as globalization, shifting consumer trends, regulatory changes, and climate change continue to influence the biodiversity and vineyard composition of *Vitis vinifera* subsp. *vinifera* (Fort et al., 2023).

3.5 THE “MALVASIA” FAMILY

Having established the historical framework for the origin and global spread of *Vitis vinifera* L., we are ready to address a number of unresolved questions regarding a group of grape varieties: the “Malvasia” family (Crespan et al., 2006). At present, the global wine industry faces various challenges related to 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”. 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 (Maul et al., 2015; Vitis International Variety Catalogue, accessed on 1 March 2025). 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 (Lacôme et al., 2007).

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 (Crespan et al., 2006; Galet, 2000; Calò et al., 2001). An example of the expansion of one of the best-known Malvasias is presented in Figure 7, specifically the case of Malvasia Dubrovacka (Crespan et al., 2010). Moreover, the first written record referencing this variety dates was found to be from 1385 (Archive of the Republic of Dubrovnik, Croatia) (Crespan et al., 2006).



Figure 7. Expansion of the Malvasia dubrovacka variety during the 14th–18th centuries, from the eastern Mediterranean Basin to the Atlantic Ocean (map by Crespan et al., 2010).

Another indication of the renown of Malvasia is the fact that the term has been translated (adapted) into different languages, according to Vitis International Variety Catalogue (VIVC). The grape variety is known by a number of names, including Malvazija in Croatian, Malvasia or Malvagia in Italian, Malvasia 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 (Lacômbé et al., 2007).

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, as it is mentioned above, 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 (CG4). 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)) (Dong et al., 2023). 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 Torrontes, Tinta, Tintilla, Ugni blanc 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, Borrego et al. (2002) published a study titled “Genetic Study of Malvasia and Torrontes Groups through Molecular Markers” and in 2009, a study titled “Synonyms and homonyms of ‘Malvasia’ cultivars (*Vitis vinifera* L.) existing in Spain” by Rodriguez-Torres et al. (2009) was published. 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), Malvasia 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 (Crespan et al., 2006; Galet, 2000).

3.6 PLANT GENOME AND THE CONCEPT OF MOLECULAR MARKER

Genetically, *Vitis vinifera* L. is considered a plant with a small genome, approximately 500 Mbp, which makes it relatively easy to study at the molecular level (This et al., 2006). Since the expansion of the Roman Empire, humans have shown interest in characterizing and identifying different grapevine varieties using strategies based on the study of phenotypic traits. Ampelography consists of subjectively describing the plant's morphological characteristics as seen with the naked eye. This methodology often leads to errors, since each ampelographer may interpret traits differently. As a result, ampelographic characterizations can hinder the exchange of reliable data, even when standardized criteria are applied. Throughout history, these techniques have evolved into more sophisticated approaches: genetic markers. In the mid-1990s, microsatellites, also known as Simple Sequence Repeats (SSR) emerged. These have allowed researchers to differentiate genotypes and identify new varieties. Microsatellites are defined as non-coding DNA sequences in which a specific number of base pairs are repeated consecutively.

SSR markers are widely recognized as a standard tool for the identification and differentiation of grapevine cultivars due to their high reproducibility, codominance, and multiallelic nature. Their global use and comparability make them particularly useful for varietal identification and the detection of synonyms, homonyms, or mislabelled genotypes (Fort et al., 2023). As highlighted by Baránková et al. (2020), SSR analysis not only allows confirmation of cultivar identity but also supports the correction of incorrectly assigned names and the discovery of unique genotypes.

The Vitis International Variety Catalogue (VIVC) serves as a centralized platform where these validated SSR profiles are stored and continuously updated, making it an ideal reference for studies aiming to resolve genetic relationships among cultivars.

4 HYPOTHESIS AND OBJECTIVES

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.

Hypothesis: Not all grapevine varieties that include the term “Malvasia” in their primary or commonly known name are true “Malvasia” varieties.

For the purpose of this study, data were drawn from the VIVC, which is recognized as the world’s most extensive database (Maul et al, 2015; Vitis International Variety Catalogue, accessed on 1 March 2025). 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 Simple Sequence Repeats (SSR) being used. **The following objectives were pursued:**

1. To identify which individuals belong to the “Malvasia” family.
2. To determine which members commonly associated with the “Malvasia” family are not in fact true “Malvasia” varieties.
3. To establish a possible origin on the “Malvasia” family.

5 METHODOLOGY

5.1 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, Fort et al., 2025). 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.

5.2 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, which are among the most reliable and widely used molecular markers in plant genotyping. The 9 internationally recognized SSR markers were used, i.e., those accepted as reference SSR markers by the global scientific community: VVS2 (Thomas et al., 1993), VVMD5, VVMD7, VVMD28 (Bowers et al., 1996), VVMD25, VVMD27, VVMD32 (Bowers et al., 1999), VrZAG62, VrZAG79 (Sefc et al., 1999) (Table S2, Fort et al., 2025). 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 (Maul et al., 2015; Vitis International Variety Catalogue, accessed on 1 March 2025). 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.

5.3 DATA ANALYSIS

The population structure of “Malvasia” was studied using the program Structure 2.3. (Pritchard et al., 2000; Falush et al., 2003), 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. (2005). 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 (Peakall and Smouse, 2012; Paetkau et al., 2012). 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 (Paetkau et al., 2004). Second, based on the standardized covariance of the genetic distances calculated for codominant markers, GenAlEx 6.5 allowed us to generate two-dimensional PCoA graphical representations for a set of populations and for a set of individuals from different populations. The programs Python Data (VanderPlas, 2016) applying the Matplotlib strategy, and MEGA version 7 (Kumar et al., 2016), applying the Neighbor-Joining strategy (Saitou and Nei, 1987), were used to create three-dimensional PCoA plots and phylogenetic trees, respectively.

6 RESULTS

6.1 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 (the most extensive and complete database to date) 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 cultivar names and PNs presenting the 12 derived spellings of the term “Malvasia”.

NAME	CULTIVARS NAME (No. of Accessions)	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 catalogued varieties in the ampelographic section of the VIVC (Table S1, Fort et al., 2025). These, classified by their origin (Table S3, Fort et al., 2025), 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.

6.2 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, Fort et al., 2025) 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 (Fort et al., 2025).

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, Fort et al., 2025). First, “sports” (varieties with color or skin mutations, but same SSR-MP) were eliminated. Thus, 4 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, 4 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 1 to 7 were tested, with the best result being the distribution into 3 populations (K = 3) (Figure S1, Fort et al., 2025). 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 (Žulj Mihaljevic et al., 2020), 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 8 shows the best distribution for the 'Malvasia' group population into 3 populations (POP1, POP2, POP3), with the varieties ordered according to the *q* parameter (Table S5, Fort et al., 2025).

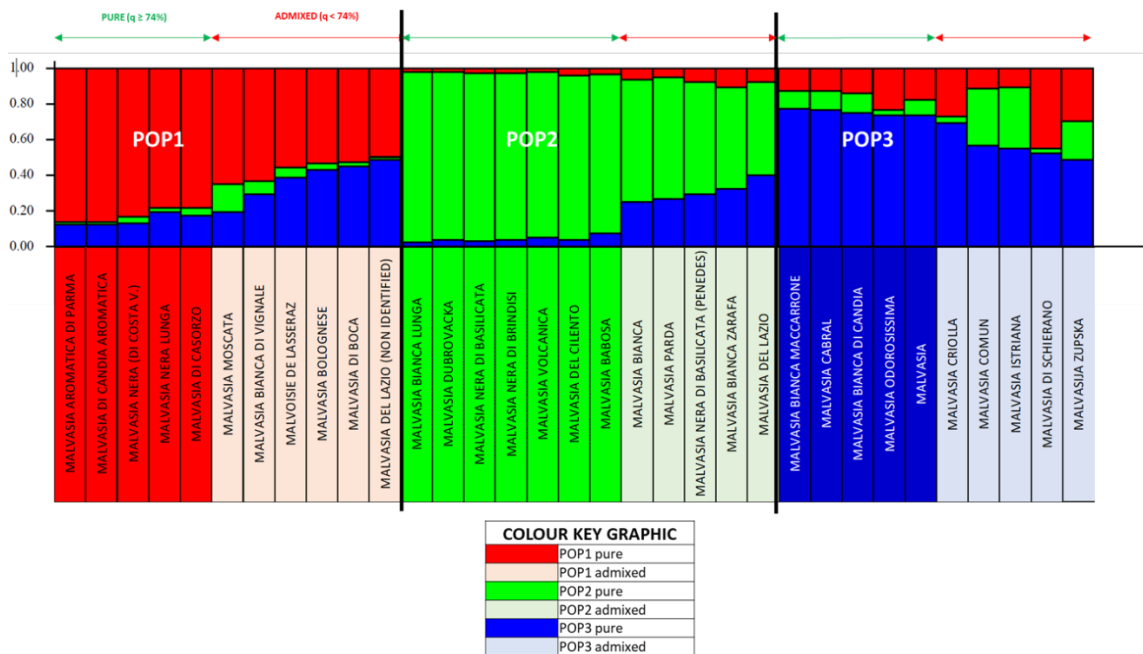


Figure 8. “Malvasia” grapevine varieties population (unique molecular profiles). Structure 2.3. diagram: K=3 distribution for pure and admixed individuals.

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 3 populations and ordered according to the q parameter (Table S5, Fort et al., 2025).

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))	?
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 VISPAPOLA))
MALVASIA VOLCANICA	SPAIN	?	COMPLETE	HERMAFRODITE	OTHER FLAVOR THAN MUSCAT, FOXY OR HERBACEOUS	W	W	MALVASIA DUBROVACKA	BERMEJUELA
MALVASIA DEL CILENTO	ITALY	?	?	?	?	B	W	?	?
MALVASIA BAROSA	PORTUGAL	A	COMPLETE	?	?	W	W	HEBEN	MALVASIA DUBROVACKA
MALVASIA BIANCA	ITALY	?	COMPLETE	HERMAFRODITE	NONE	W	W	SCIACCARELLO	?
MALVASIA PANDA	PORTUGAL	?	COMPLETE	HERMAFRODITE	NONE	W	W	?	?
MALVASIA NERA DI BASILICATA (PENEDÉS)	SPAIN	?	COMPLETE	?	NONE	B	W	?	?
MALVASIA BIANCA ZARAFÁ	ITALY	?	COMPLETE	?	MUSCAT	W	W	?	?
MALVASIA DEL LAZIO	ITALY	?	COMPLETE	HERMAFRODITE	NONE	W	W	?	?
MALVASIA BIANCA MACCARRONE	ITALY	?	COMPLETE	?	MUSCAT	W	W	?	?
MALVASIA CABRAL	PT0501	?	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	?	?
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	?
MALVASIA ZUPSKA	CROATIA	D	COMPLETE	?	?	W	W	HEUNISCH WEISS	?

1. 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.
2. 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.

3. POP3 includes 10 components (30.30%), 50% of which are pure and the remaining 50% admixed. Most are Italian, although there are also 2 varieties from Croatia, 1 Spanish, 1 from Argentina, and 1 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; 3 have flowers of unknown sex, and 1 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 3 populations, with a goodness of fit of 82% for each population (Figure S2, Fort et al., 2025). The members of each population were then reassigned until a goodness of fit of 100% was achieved (Figure S3, Fort et al., 2025). In this process, the distribution of the members of the “Malvasia” group was reduced to 2 populations. Figure 9 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.

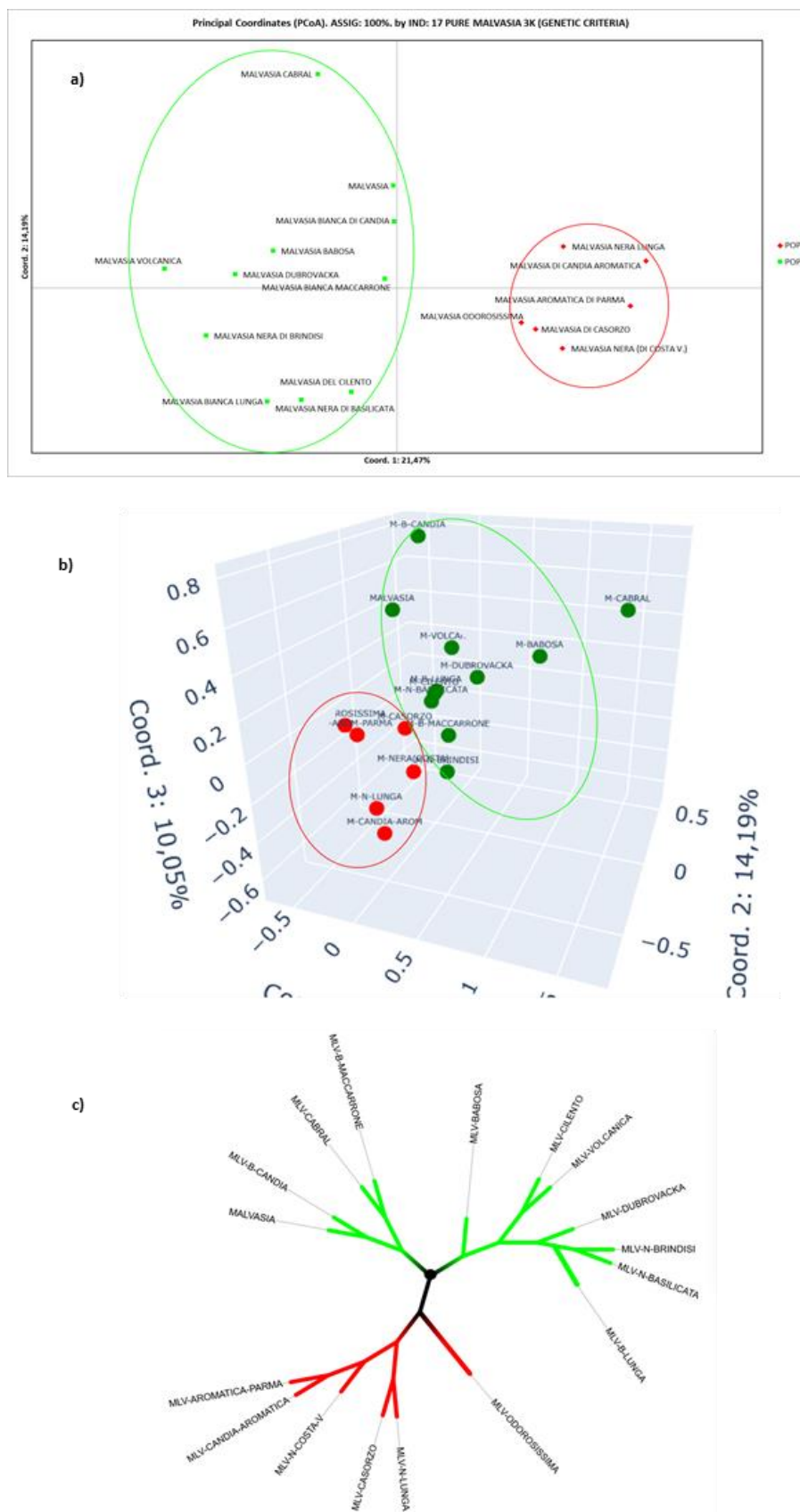


Figure 9. Graphical representation of the distribution of the 17 pure varieties ($q \geq 74\%$), using PCoA of their individuals in 2 (a) and 3 (b) dimensions, and also through the representation of a phylogenetic tree (c).

In Figure 9a, 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 odorisissima* (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 9b). In this plot, with slight variations, the same pattern described above is repeated. Finally, the phylogenetic tree (Figure 9c) 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 odorisissima* (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.

In Figure 10, 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) (Galet, 2000; Italian Vitis Database, accessed on 8 March 2025; Vine to Wine Cercle (Portugal and Spain), accessed on 8 March 2025).

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	CHLOROTYPE	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 ?))
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	?	?
MALVASIA 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	?
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 ZARAFÀ	ITA	?	COMPLETE	?	MUSCAT	W	W	?	?
MALVASIA PARDÀ	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 (PENEDÉS)	ESP	?	COMPLETE	?	NONE	B	W	?	?
MALVASIA DEL LAZIO	ITA	?	COMPLETE	HERMAFRODITE	NONE	W	W	?	?

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 11.

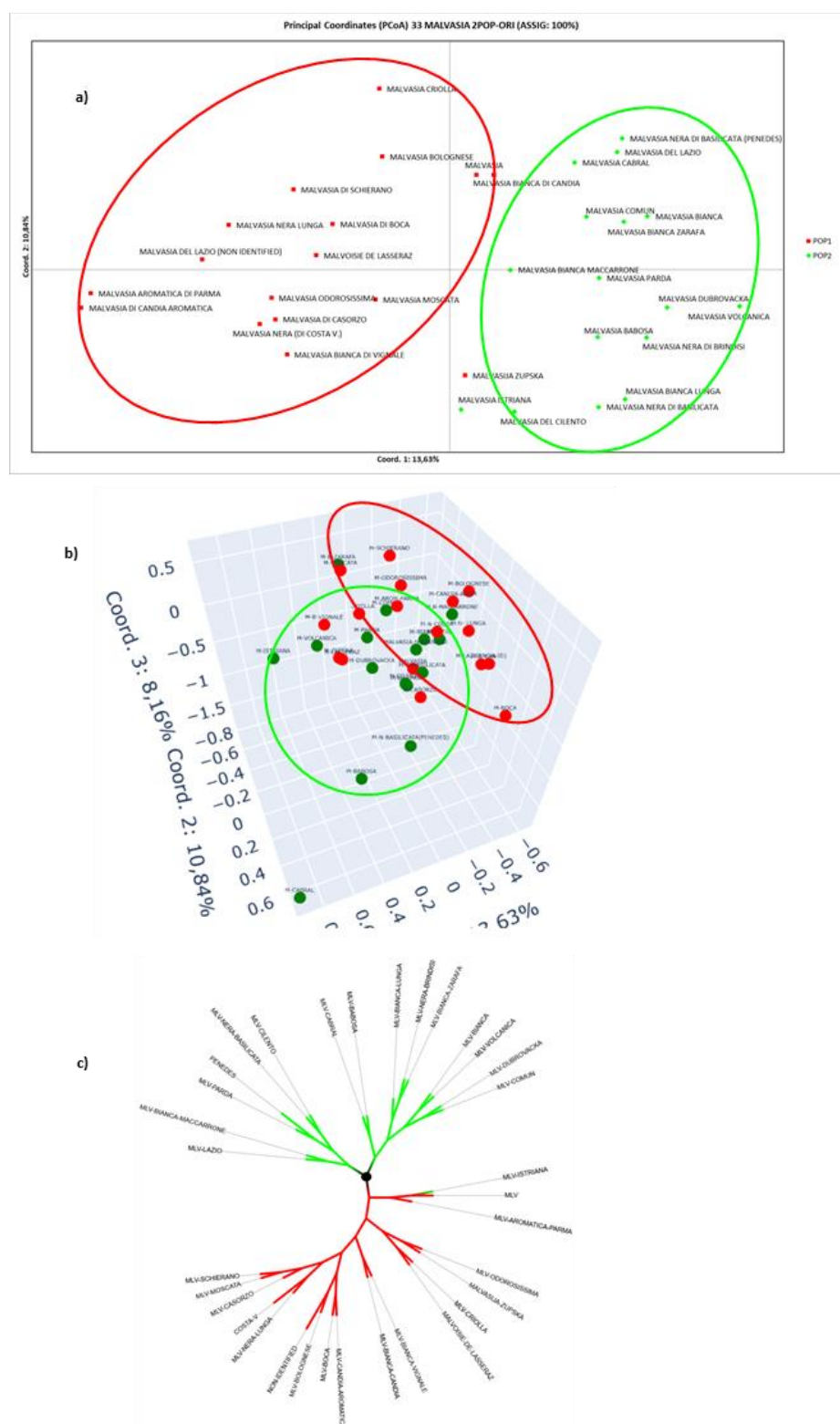


Figure 11. Graphical representation of the distribution of the 33 varieties under the geographical strategy, using PCoA of their individuals in 2D (a) and 3D (b), as well as a phylogenetic tree (c).

In Figure 11a, 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 12). 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 11b), 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 11c, 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.

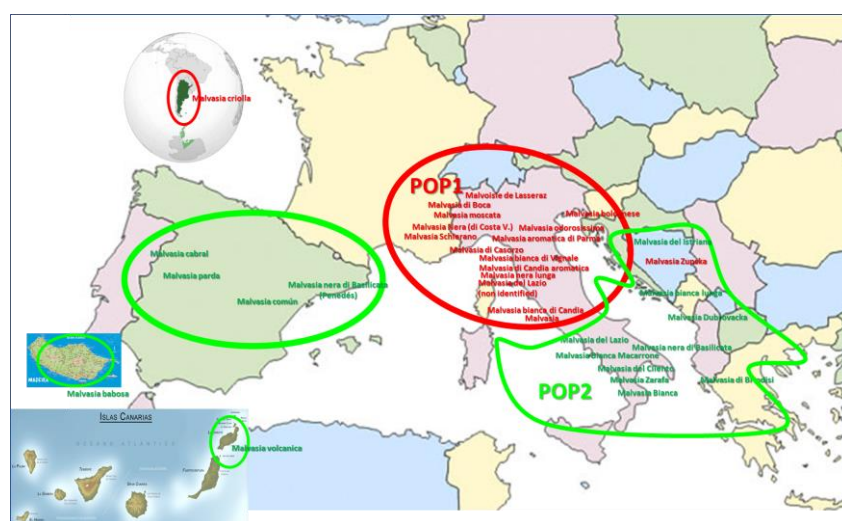


Figure 12. Map of the geographical location (approximate (Galet, 2000; Italian Vitis Database, accessed on 8 March 2025; Rodriguez-Torres, 2018)) of the 33 “Malvasia” varieties under the geographical strategy with 2 populations. Goodness of fit: 100%.

The 33 members of the “Malvasia” group were then distributed into three populations (Figures 9c and 11c) 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%.

Table 4. Final distribution of “Malvasia” varieties based on their origin as described in the VIVC, divided into 3 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	?	?
MALVASIA 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)
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 MARENCO (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 MARENCO (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 OTTOGONDISIMA	ITA	?	COMPLETE	FEMALE	MUSCAT	W	W	?	?
MALVASIA COMUN	ESP	A	COMPLETE	HERMAFRODITE	NONE	W	W	HEBEN	?
MALVASIA BIANCA	ITA	?	COMPLETE	HERMAFRODITE	NONE	W	W	SCIACCARELLO	?
MALVASIA BIANCA ZARAFÀ	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 (PENEDÉS)	ESP	?	COMPLETE	?	NONE	B	W	?	?
MALVASIA DEL LAZIO	ITA	?	COMPLETE	HERMAFRODITE	NONE	W	W	?	?

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.

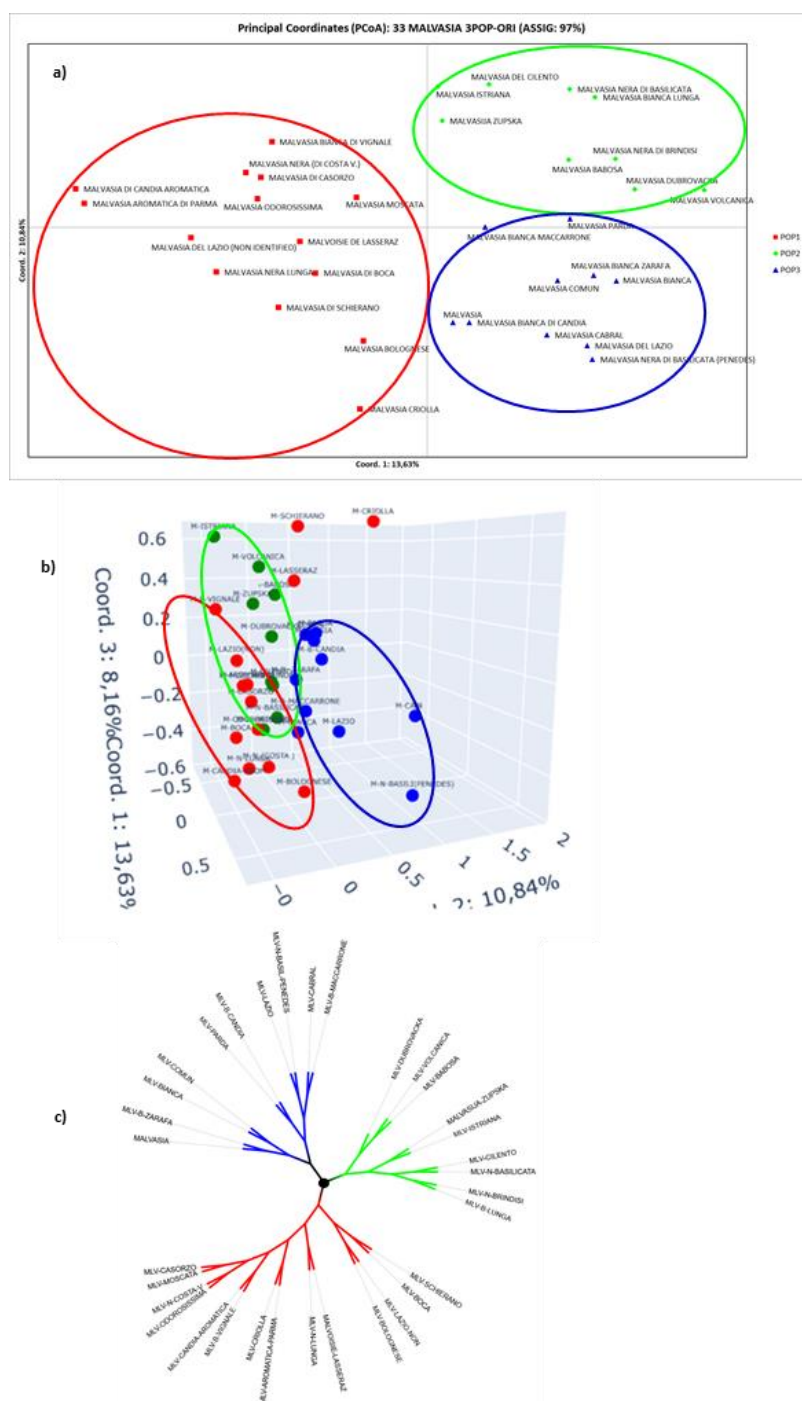


Figure 13. Graphical representation of the distribution of the 33 varieties in 3 populations from the geographical strategy, using PCoA of their individuals in 2 (a) and 3 (b) dimensions, as well as the representation of a phylogenetic tree (c).

7 DISCUSSION

For most authors, the “Malvasia” family is a heterogeneous group of varieties (Lacômbé et al., 2007; Meneghetti et al., 2013). There is no agreement regarding their origin, nor ampelographic (Figure S4, Fort et al., 2025) (Rodriguez-Torres, 2018; Mendez, 2024), nor genetic traits (Crespan et al., 2006; Meneghetti et al., 2013). Today, the quality and prestige of a wine are usually associated with a specific variety (Lacômbé et al., 2007). 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 (Crespan et al., 2006). 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, personal communication). For that reason, its demand increased substantially (Crespan et al., 2006; Lacômbé et al., 2007). Thus, it can be hypothesized that possibly different varieties were used to meet market demands, 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. Now, what we might ask ourselves is how many varieties truly have the potential to be considered “Malvasia” among all those that have incorporated this term into their name. It is a right that society owes to the consumer who seeks to define in their sensory register a distinct and unique profile of aromas and flavors for the “Malvasia” family, and, consequently, a much more reduced number of varieties. For the past two centuries, a number of ampelographers have been calling for this clarification to help establish a more homogeneous classification of this family (Crespan et al., 2006).

Our research group has a database with over 1300 accessions, but it contains only 10 samples of possible “Malvasia” candidates (Fort et al., 2023). 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 (Fort et al., 2025), 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, Fort et al., 2025)). Table S3 (Fort et al., 2025) 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 (Vitis International Variety Catalogue, accessed on 1 March 2025) (Table S1, Fort et al., 2025). 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, Fort et al., 2025). 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 8. The Structure 2.3 software proposes, as the best distribution of the “Malvasia” population, dividing it into three populations (Figure S1, Fort et al., 2025), where varieties are grouped based on their genetic proximity as defined, in this case, by the q parameter (Table S5, Fort et al., 2025). 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, Fort et al., 2025), 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 9). 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, Fort et al., 2025)). 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, Fort et al., 2025). 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 9a) and three dimensions (Figure 9b) 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 9c), demonstrating the distance of POP3 members both from each other and from their adoptive populations. Looking at Figure 10, 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 (Crespan et al., 2010; Rodriguez-Torres, 2018).

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, Fort et al., 2025). 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 (Arroyo-Garcia et al., 2006; Žulj Mihaljevic et al., 2020).

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*) 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 (Mendez et al., 2021).

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 (Massonnet et al., 2020). 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 (Arroyo-Garcia et al., 2006; Žulj Mihaljevic et al., 2020). 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 8) 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 11a,b), in the phylogenetic tree representation (Figure 11c), and in the

approximate geographical distribution presented in Figure 12, 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 8), 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 11a, 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 9c and 11c). 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 13a,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 (Crespan et al., 2010; Garcia-Munoz et al., 2012). These results are consistent with those found by Lacombe et al. (2007). 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. (2013) 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 (D’Onofrio et al., 2021), is often found either distant from the grouping of Balkan varieties or associated with individuals from POP1. The genetic study (Figure 8) 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 12).

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 (D’Onofrio et al., 2021; Maul et al., 2015; Vitis International Variety Catalogue, accessed on 1 March 2025)..

Moreover, at the aromatic level, the differences are also substantial. Several studies have shown that the unique aroma of Muscat-flavored grape varieties is related to the presence of monoterpenoids with a low olfactory perception threshold in the grape. In particular, linalool, geraniol, nerol, citronellol, and α -terpineol have been described as the main aromatic determinants due to their high concentrations in Muscat cultivars (Emanuelli et al., 2010). In fact, the 'floral' perception is strongly correlated with the perception of 'freshness' in these wines (Bordiga et al., 2013). In contrast, *Malvasia Dubrovacka*, the best-known and most studied of the entire 'Malvasia' family, is characterized by fruity aromas. The fruity, apricot, and exotic fruit notes are due to the high content of acetate, ethyl, and isoamyl esters. Additionally, aromas of compote, honey, caramel, and raisins have also been described. These attributes can be mainly correlated with the presence of benzaldehyde and 2-furfural, which have aromas of burnt sugar, caramel, and almond (Scacco et al., 2010). The terpene content in *Malvasia Dubrovacka* was significantly lower compared to those found in the Muscat family (Calò et al., 2000). However, when comparing the content of monoterpenic glycosides between *Malvasia Dubrovacka*, *Malvasia bianca lunga*, and *Malvasia istriana*, the former is shown to be much more aromatic than *Malvasia istriana*, which in turn is more aromatic than *Malvasia bianca lunga* in terms of these terpenic compounds (Flamini et al., 2013). Another relevant observation is that the vast majority of 'Malvasia' candidates descending from crosses with members of the Muscat family are located in the northern (half) of the Italian Peninsula (except for the Argentine *Malvasia criolla*). Moreover, our research group believes that performing the organoleptic profiling of the flower must of each of these varieties would provide a much more reliable basis for drawing conclusions than relying on the organoleptic profile of a wine.

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 8, Table S5, Fort et al., 2025): (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. 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 (Crespan et al., 2006). In the case of *Malvasia bianca lunga*, another candidate to be part of this highly selective group of varieties, D’Onofrio et al. (2021) 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.

Finally, we must also consider the very real possibility that some of the “*Malvasia*” varieties from the Middle Ages or from periods prior to the phylloxera plague may have disappeared and therefore cannot be accounted for in this study.

8 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.

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10 SELF-EVALUATION

At the outset of my bibliographic investigation into the genetic characterization of “Malvasia” grape varieties, I aimed to deepen my understanding of grapevine diversity and develop advanced skills in data mining and bioinformatic analysis. I expected to learn how to formulate a robust hypothesis, identify and access relevant datasets, particularly from the VIVC database, and apply theoretical knowledge from my coursework to a real-world, database-driven research project.

Throughout the project, I mastered several key computational and analytical techniques. I became proficient with software tools such as GenAlEx for population genetics statistics, MEGA for phylogenetic tree construction, and STRUCTURE for inferring genetic clusters. I also learned to navigate and curate large SSR datasets from the VIVC repository, to perform quality control checks, and to troubleshoot unexpected patterns in the data. These skills enabled me to rigorously test my hypothesis and to document each analytical step with clarity and reproducibility.

This experience fostered significant personal and professional growth. I enhanced my critical-scientific mindset by rigorously questioning each assumption in my data-analysis pipeline and by integrating constructive feedback from my supervisor. Collaborating remotely with peers improved my communication skills and taught me to present complex results to both technical and non-technical audiences. I also developed stronger time-management and organizational strategies by balancing literature review, database mining, and report writing. Overall, I feel more confident in my ability to conduct independent, data-driven research and more motivated to pursue a career in bioinformatics and molecular biotechnology.