


RESEARCH ARTICLE

Genetic fingerprinting reveals how traditional farming practices aided to preserve ancient table grape varieties in Almería (southeastern Spain)

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Societal Impact Statement

Table grape production is a traditional practice in southeastern Spain, where locals have produced fresh grapes and raisins for centuries. Many of these vines are now centenary, and they represent a useful source of diversity for developing future table grape varieties with improved traits. Genetic analysis showed that many of the local varieties identified in this study were traditional varieties from Western Mediterranean countries. Others were not identified, and they might be old grape varieties of previous importance in the region. The conservation and characterization of these varieties could be key to ensuring current and future vineyard sustainability.

Summary

- Current worldwide table grape production focuses on a reduced number of *Vitis vinifera* L. varieties. However, traditional farmers have grown many table grape varieties for centuries, as they provided a steady source of fresh fruit and raisins. These ancient living genotypes potentially store a genetic diversity that can be used now to ensure future grape production.
- Here we focused on the study of grapevines found across Almería, one of the Spanish regions with longer tradition in table grape production. After an exhaustive inspection, we located 220 old (some centenary) vines producing grapes consumed by owners or in abandoned areas no longer devoted to agriculture.
- Some of these vines were identified by comparing their simple sequence repeat (SSR) and single nucleotide polymorphism (SNP) genetic profiles with available data from international databases. We found that, while grape growers' efforts focused on the cultivation of traditional grape varieties from Western Mediterranean regions, they also cultivated few exogenous varieties if they provided additional fruit features. Other vines were found to have genetic profiles that did not match reference datasets. Interestingly, some of them were found in multiple locations, suggesting they are endangered varieties with some previous relevance in the region. Besides, first-degree relationships support the autochthonous origin of many of these unidentified genotypes.

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- Locals kept a high number of different grapevine varieties, now considered reservoirs of genetic diversity. Traditional farming practices have been useful to prevent the loss of this diversity, which now needs to be preserved and further studied to contribute to the sustainability of viticultural systems.

KEYWORDS

conservation, genetic diversity, simple sequence repeat (SSR), single nucleotide polymorphism (SNP), sustainability, table grapes, vineyard, *Vitis vinifera* L

1 | INTRODUCTION

Grape cultivation has been historically linked to the development of some of the most relevant societies around the Mediterranean basin. Archeological findings indicate that the first grape varieties were introduced into the Iberian Peninsula by Phoenicians, with some of the oldest evidences of grape cultivation and winemaking found in Southern Spain dating back to the ninth to eighth centuries BCE (Peña-Cervantes, 2018). Grape production was prompted under Roman dominance, who intensified production systems to satisfy their growing need of wine and fresh grapes for their ceremonies and events (Bouby et al., 2013). In the Middle Ages, Catholics maintained the cultivation of grapes for winemaking, while the later arrival and spread of the Islamic civilization boosted the cultivation of table grapes (This et al., 2006). The use of different genetic pools along the primary and secondary processes of *V. vinifera* L. domestication, and the different selection and breeding targets followed for the development of wine and table grapes, resulted in an incredibly wide genetic diversity within cultivated grapevines, producing varieties that have been maintained for centuries through vegetative reproduction (Migicovsky et al., 2017; Myles et al., 2011; Wolkovich et al., 2018). However, the arrival of disease-causing agents from North America at the end of the 19th century decimated *V. vinifera* diversity after centuries of genetic diversification (This et al., 2006). European grape production was particularly affected by the destructive effect of grape phylloxera (*Daktulosphaira vitifoliae*) (Tello et al., 2019), whose feeding behavior on *V. vinifera* roots (either from wine or table grape varieties) creates wounds that ends in vine decline by the infection of secondary agents (Forneck & Huber, 2009). This pest appeared in Southern Spain in 1878 (Piqueras-Haba, 2005), and in few decades, it devastated most of local wine and table grape vineyards (Barke, 1997), with an irreversible loss of local grapevine varieties. In addition, later market globalization led to another drastic reduction of genetic diversity when many local varieties were replaced by few renowned ones (Wolkovich et al., 2018). In the case of table grapes, it implied the replacement of traditional seeded varieties by others with seedless grapes, mainly ‘Sultanina’ and ‘Sultanina’-derived obtentions (FAO and OIV, 2016) which took place in the second half of the 20th century. As a result, today, diversity is a reduced portion of what existed in the first half of the 19th century (This et al., 2006).

The drastic loss of grapevine genetic resources is clearly evidenced when comparing current available varieties with those

reported before the arrival of phylloxera. For example, the work of the botanist Simón de Rojas Clemente y Rubio includes the description of 119 wine and table grapevine varieties commonly cultivated in Andalucía (Southern Spain) at the beginning of the 19th century, and cites up to 124 additional minority grapevine varieties (Clemente y Rubio, 1807). This high diversity contrasts with the low number of varieties used at the end of the 20th century for commercial grape production in the same region: 17 for winemaking (García de Luján et al., 1990) and 29 for fresh fruit or raisins (García de Luján & Lara, 1998). Recent studies in traditional winemaking areas indicate that old and abandoned vineyards preserve numerous unknown grapevine genotypes of likely local historical relevance (Balda et al., 2014; Barrias et al., 2023; Maraš et al., 2020; Zombardo et al., 2021). These genotypes are known to be adapted to different biotic and abiotic stressing factors, as they were likely steadily selected by local farmers to fit specific habitats to produce high yield stability under low technification levels and input requirements (water, fertilizers, and pesticides) (Biasi & Brunori, 2015). There is now a strong interest in recovering these varieties, as they can be key to face current viticulture challenges while being a novel source of innovation and diversification for the grape and wine industries (Maraš et al., 2020; Zombardo et al., 2021). In addition, they can be used in modern breeding programs as a source of beneficial traits (Sargolzaei et al., 2021). Finally, yet importantly, the identification of these varieties is highly relevant from a historical perspective, as they represent an important part of rural heritage, culture, and landscapes.

In contrast to the numerous works aimed to detect and preserve wine grapevine genotypes in the edge of extinction, few works have focused on the identification of endangered table grape genetic resources. Table grape production has been a common practice in southeastern Spain, where climate and soil conditions favor grape cultivation (García de Luján & Lara, 1998). In this region, grapevines for table grape production are cultivated through extended training systems (arbor vines, or “parral” in Spanish). Grapevines are trained up to a series of arbor posts to form a permanent structure of the aerial canopy, which captures the most sunlight. Consequently, this system encourages high grape production, and it protects grape clusters from excessive direct sun irradiation by the leaf canopy and eases fruit collection at harvest time (Alonso et al., 2006). This traditional production system has provided fresh fruit and raisins to farms and homesteads for centuries, and a steady income from sales to local communities. Likewise, export of table grapes to different countries

constituted for several decades an economically important activity in the region (Alonso et al., 2006). Interestingly, grapevines have been also grown by locals in country houses mimicking this training system to provide fruit, shadow, and for their ornamental value. These plants have been cared for decades by different generations of the same family, resulting in some centenary vines that can be found today growing as isolated individuals. In Almería province (Andalucía region, southeastern Spain), the conservation group “Grupo Ecologista Mediterráneo, GEM” recognized the need of preserving these surviving centenary individuals. Supported by local community organizations, it has coordinated efforts for more than 25 years to locate and, in some cases, multiply these singular vines before they are lost. In order to value these unique genetic resources, it is necessary to achieve an accurate description to identify the variety that each isolated plant represent. In grapevine, this task is specially complicated, given that some varieties are known under different names (synonyms), some names are used to name different varieties (homonyms), and the great amount of misnomers (This et al., 2006). Grapevine variety identification can be performed by means of ampelographic methods, which is based on the visual description of multiple morphological traits. However, it needs of a high level of expertise to ensure efficacy. Alternatively, it can be performed by genetic profiling, an approach that commonly implies the use of standard sets of microsatellite (SSR) and/or single nucleotide polymorphism (SNP) genetic markers (Cabezas et al., 2011; Maul et al., 2012; This et al., 2004). These genetic systems have proved to be highly efficient for the molecular identification of grapevine varieties of different use and origin when combined with the availability of wide genotype databases (Balda et al., 2014; Barrias et al., 2023; Cunha et al., 2020; Maraš et al., 2020; Nebish et al., 2021; Zombardo et al., 2021).

This work aimed to sample, identify, and preserve from extinction local table grape varieties maintained under traditional farming practices in one of the Spanish regions with longer tradition in table grape production, Almería (Sánchez-Escolano & Ruíz-Moya, 2018). After multiple inspections, many centenary vines of possible interest were sampled from different municipalities. The explored sites included old clay tile potteries, olive and grain mills (to obtain oil and flour, respectively), and water mills (or “water norias”), as well as some private farms, orchards, and house backyards. The detected living vines (non-grafted in many cases) were found to still produce grapes, commonly consumed by the owners as fresh fruit or dried to obtain raisins. In addition, some other old vines were found in abandoned areas no

longer devoted to agriculture. In total, we studied 220 old vines, which were genotyped for identification and pedigree analyses. The location and study of these genetic resources added information on the genetic origin of some putatively old table grape varieties from southeastern Spain, and revealed how traditional farming practices allowed the preservation of some presumably lost table grape varieties.

2 | MATERIAL AND METHODS

2.1 | Plant material

A total of 220 vines were sampled from 48 municipalities of Almería province (Andalucía, southeastern Spain), focusing on old (many centenary) plants growing for table grape production (Figures 1 and 2 and Dataset S1). When a vine of this type was detected, the vine owner was interviewed (when it was possible) to obtain information on its likely origin, its approximate age, and its name. This name was used for its designation if it did not match any cataloged variety after genetic profiling. In addition, we sampled some abandoned vines found in areas no longer devoted to agriculture (Figure 2). In the absence of a local name, they have been designated according to plant characteristics and place of collection. Young leaves were collected on site for each sample and once in the laboratory were store at -80°C until DNA extraction.

2.2 | DNA extraction and genotyping

DNA was isolated from ~ 100 mg of ground leaves using the NZY Plant/Fungi gDNA Isolation Kit (NZYTech, Lisbon, Portugal), following manufacturer indications. DNA quality and quantity was evaluated using a NanoDrop spectrophotometer (Thermo Scientific, Wilmington, USA). DNAs were genotyped at 13 SSR loci using two multiplex polymerase chain reaction (PCR) (M7 and M6). M7 includes VVMD27, VVMD32, VVMD5, VVMD7, VVS2, VrZAG62, and VrZAG79. M6 includes VVMD25, VVMD28, VrZAG112, VrZAG29, VrZAG67, and VrZAG83 (Bowers et al., 1996, 1999; Sefc et al., 1999; Thomas & Scott, 1993). This set compiles the nine markers agreed in the framework of the European project GrapeGen06 for the efficient identification of *V. vinifera* varieties

FIGURE 1 (a) Location of the Spanish region of Almería (dark green) in Andalucía (light green), and (b) location of the sites where the old grapevines studied in this work were found.

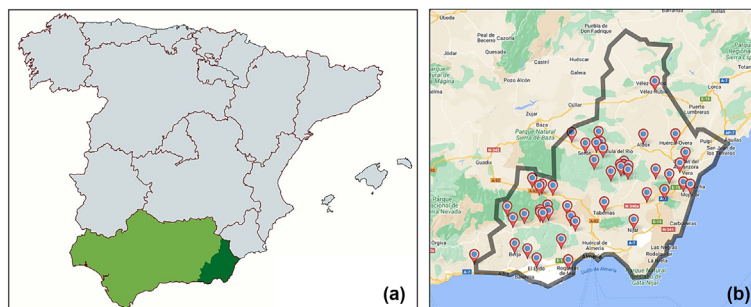




FIGURE 2 Examples of some of the old grapevines found in Almería (Andalucía, Spain) found in (a–e) house backyards or in (f) abandoned sites. In some cases, they were found as free-standing growing grapevines, coiled in (c, e) neighboring trees used as tutors. Images are reproduced from <https://www.gem.es/biodiversidad.html>.

(Maul et al., 2012), which includes a standard set of six microsatellite markers for grapevine genotyping (This et al., 2004). The forward primer of each pair was fluorescently labeled with 6-FAM (VVMD27, VVMD5, VVMD25, and VrZAG67), VIC (VrZAG62, VVMD32, VrZAG29, and VrZAG112), NED (VVS2, VVMD7, VrZAG83, and VVMD28), or PET (VrZAG79) for multiplexing purposes. M7 mix is described in Nebish et al. (2021). M6 mix included 5.0 ng of DNA, 0.15 μ M of VVMD25, 0.25 μ M of VVMD28, 0.12 μ M of VrZAG112, 0.05 μ M of VrZAG29, 0.15 μ M of VrZAG67, and 0.08 μ M of VrZAG83 primers, using QIAGEN multiplex PCR kit (Qiagen, Hilden, Germany). Both M7 and M6 multiplex reactions were performed in a Thermal Cycler T100 (Bio-Rad, Hercules, USA) as detailed in Nebish et al. (2021), and PCR products were visualized in 2.0% agarose gels stained with Green Safe Premium (NZYTech, Lisbon, Portugal). The NZYDNA Ladder VII molecular weight marker (NZYTech, Lisbon, Portugal) was used to confirm the approximate size of the amplified products. PCR products were then subjected to capillary electrophoresis in an ABI 3130XL genetic

analyzer (Applied Biosystems, Foster City, CA, USA) at the Centro de Investigación Biomédica de La Rioja (CIBIR). Prior to it, PCR products were mixed with 20 μ L of highly deionized (Hi-Di) formamide and 0.2 μ L of GeneScan-500 LIZ size standards (both from Applied Biosystems), and denaturalized at 95°C for 5 min. Fragment sizes were rated using GeneMapper v.4.1 (Applied Biosystems, Darmstadt, Germany). Each analysis included a ‘Tempranillo Tinto’ DNA as positive control and a non-template as negative control.

In parallel, DNAs were genotyped at 240 nuclear SNP loci, using Fluidigm technology, through the genotyping services provided by the Sequencing and Genotyping Unit of the Universidad del País Vasco (UPV/EHU). This set includes a subset of 48 SNPs for variety identification (Cabezas et al., 2011) and another subset of 192 SNPs for parentage and diversity analyses (Lijavetzky et al., 2007; Zinelabidine et al., 2012). This set contains a set of chloroplast SNPs for the determination of the most common grapevine chloroplast haplotypes (Maraš et al., 2020), following the classification system of Arroyo-García et al. (2006).

2.3 | Variety identification and parentage analyses

Genetic profiles based on the subset of 48 SNPs for genetic identification were pairwise-compared with those stored at the ICVV-DNA database (3574 non-redundant genotypes in November 2023). Similarly, genetic profiles based on SSR data were compared to those stored at the *Vitis* International Variety Catalogue (VIVC), which stores the genetic profiles of 6354 grapevine varieties (accessed in November 2023) (Maul, 2022).

Non-redundant grapevine genotypes (240 SNPs) were merged with those of the ICVV-DNA database to detect all possible parentage relationships (trios and duos) involving one of the genotypes identified in this work. This analysis was performed using the likelihood-based method implemented in Cervus v.3.071 (Kalinowski et al., 2007) as previously detailed (Cunha et al., 2020). The overall likelihood ratio (LOD) score of all detected trios and duos was used to test their robustness. For duos, only those with a LOD value above 25 were considered. We allowed a maximum number of two and one mismatching SNPs before discarding a trio and a duo, respectively. All parentage relationships were confirmed using SSR data. For each trio, the putative variety acting as mother in the cross was set considering experimental chloroplast haplotype data, given the maternal transmission of chloroplasts in grapevine (Arroyo-García et al., 2006).

2.4 | Grapevine descriptions and comparison with historical data

The names of the 243 varieties described by Clemente y Rubio (1807) were compared with the designations given by local grape growers to the vines analyzed in this study. In the case of a coincidence or reasonable similarity between both terms, local grapevines were described for the same traits described by Clemente y Rubio (1807), using objective descriptors when possible (O.I.V., 2009). Then, both descriptions were compared to suggest or discard a connection between both varieties. The botanical illustrations available in the same work were also used for comparative purposes.

3 | RESULTS

After multiple inspections, 220 old vines were located growing across 48 municipalities of Almería. These vines were found to produce fruits with highly diverse phenotypic features, regarding berry color, shape, and size. Likewise, grape clusters also presented high phenotypic diversity, with most of them having the typical features of table grape varieties (long and loose clusters, with large and fleshy berries) (Figure 3). The genotyping of these plants at 13 SSR and 240 SNP markers revealed 71 different genetic profiles (Dataset S2). These profiles were pair-wise compared to those stored at the ICVV-DNA and VIVC databases for variety identification. This approach led to the identification of 37 of these genetic profiles as referenced grapevine

varieties, most of them table grape varieties from, according to the VIVC, the Western Mediterranean basin (Table 1). After crossing genetic data with available phenotypic data (mainly berry color), the number of identified varieties increased to 39 since we identified two known berry color somatic variants pairs: ‘Beba’/‘Beba Roja’ and ‘Ahmeur Bou Ahmeur’/‘Teta de Vaca Blanca’. The most abundantly found genetic profile corresponded to ‘Beba’/‘Beba Roja’ (found 31 times), followed by ‘Ahmeur Bou Ahmeur’/‘Teta de Vaca Blanca’, ‘Negra Rayada’, ‘De Cilindro’, ‘Dominga’, and ‘Molinera’ (found 26, 15, 12, 9 and 8 times, respectively). In addition to these western table grape varieties, we found some other table grape varieties from other Mediterranean regions, like Greece (‘Muscat of Alexandria’) or Lebanon (‘Afus Ali’, ‘Beitamouni’). Likewise, we found some examples of varieties obtained in table grape breeding programs, like ‘Cardinal’ (bred in the USA in 1939), ‘Italia’ (bred in Italy in 1911), and ‘Autumn Black’ (bred in the USA in 1960). Lastly, we identified some varieties commonly used in the Iberian Peninsula nowadays for winemaking, like ‘Alfrocheiro’, ‘Graciano’, or ‘Monastrell’.

However, we obtained 34 genetic profiles that could not be assigned to a true-to-type variety, although four of them matched the genetic profile of several samples previously analyzed in the ICVV laboratories (Table 1). Interestingly, 13 of these 34 unknown genetic profiles were found at least twice in Almería, indicating that they have been subjected to vegetative propagation. The two most commonly unknown genotypes were “*Corazón de Gallo*” and “*Uva Blanca del Sánchez Cid*” (double quotes and italics are used for the names of unknown genotypes), which were found seven times each in different municipalities of Almería. The next most abundant unidentified genotype was “*Uva Negra del Molino Zenete*,” which was found six times in Almería and matched the genetic profile of one unidentified sample from Aragón (Northern Spain), previously analyzed in our facilities. Similarly, the genotype “*Durilla*”/“*Albilla Negra*” was found four times within the studied vines, three of them with white berries and one with black berries (Dataset S1). Interestingly, this genetic profile matched that of the accession “*Blanca Temprana de Almería*” from the INTA grapevine collection of Mendoza (Argentina). “*Flor de Baladre*” was also found four times, and “*Abeaci de los Vélez*,” “*Blanca de los Ríos*,” “*Imperial*,” “*Uva Negra del Castillo de Benizalón*,” and “*Uva Blanca de Real de Antas*” were found three times. Interestingly, the latter was found to match the genetic profile of the accession “*Rosaki × Almería*” of the IMIDRA (Spanish National Grapevine collection, Finca El Encín, Madrid, Spain). Lastly, the genotype named “*Uva Chinche de Tijola*” was found only once in Almería, as an isolated plant in Tijola. However, it matched the genetic profile of another unidentified old vine collected from an old house in Ayabarrena, a small village from La Rioja (Northern Spain), at 550 km from Tijola.

Parentage analyses uncovered the full pedigree of 17 grapevine varieties, as well as 15 additional duos (Figure 4 and Datasets S3 and S4). All the full pedigrees detected are highly reliable, given their high LOD values (> 60) and the null or very low number of mismatching SNPs and SSRs (Dataset S3). We found a relevant role for the female-flowered variety ‘Ohanes’, involved in eight full pedigrees and three

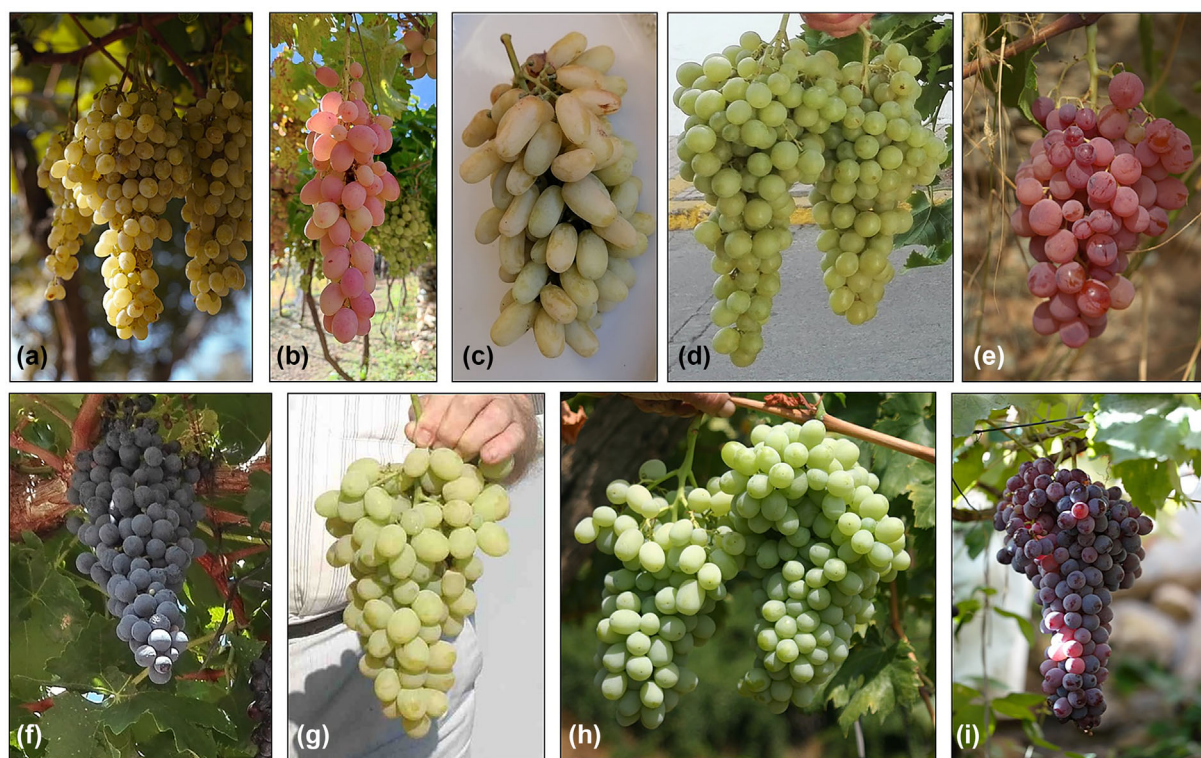


FIGURE 3 Grapevine clusters of nine of the unidentified varieties found in this work (a) “*Blanca de los Ríos*,” (b) “*Corazón de Gallo*,” (c) “*de Datilillo Largo*,” (d) “*de Pan*,” (e) “*Flor de Baladre*,” (f) “*Uva Negra del Castillo de Benizalón*,” (g) “*Uva Blanca de Real de Antas*,” (h) “*Santa Paula del Marchalejo*,” (i) “*Uva Negra del Molino Zenete*.”

parent-offspring relationships (Figure 4). Thus, we found it to be involved in the origin of “*Uva Rosa de Venta Torre*” (‘Ohanes’ × ‘Afus Ali’), “*Quina*” (‘Ohanes’ × ‘Negra Rayada’), and ‘Colgar Roja’, ‘Ciruela Roja’, ‘Imperial Roja’, “*de Datilillo Largo*,” “*Santa Paula del Marchalejo*,” and “*Uva de Diego Ros*,” all full-siblings (‘Ohanes’ × ‘Rágol’). According to chloroplast information, ‘Ohanes’ was the mother in all these crosses, as expected considering that it bears functionally female flowers. In addition, ‘Ohanes’ was also found to be genetically connected to the varieties “*Uva Rosa del Puente de Bocharalla*,” “*Aramon falso*,” and “*Uva Negra del Molino de Doña María*.”

Besides, ‘Beba’ was found to be involved in the origin of four local varieties, namely “*Blanca de los Ríos*” (‘Beba’ × “*Uva Negra del Molino Zenete*”), “*Parra asilvestrada de la Cerrá*” (‘Beba’ selfed), and the full-siblings “*Uva Rosa de Tahal*” and “*Corazón de Gallo*” (‘Náparo’ × ‘Beba’). Both ‘Beba’ and ‘Náparo’ are relatives (probably, descendants) of ‘Hebén’, another variety with an important role in the region, as progenitor of “*de la Gitana*” (‘Hebén’ × ‘Zurieles’) and “*de Lanjarón*” (‘Hebén’ × ‘Ahmeur Bou Ahmeur’). ‘Hebén’ was also found to be linked to two additional varieties, “*Abeací de los Vélez*” and “*Ojo de Liebre*.” ‘Huevo de Gato’ was identified as progenitor of “*Uva Chinche de Tijola*” (‘Huevo de Gato’ × ‘Muscat of Alexandria’) and “*Albilla Real*” (‘Huevo de Gato’ × ‘Palomino’). Interestingly, ‘Hebén’, ‘Huevo de Gato’, and ‘Náparo’ have functionally female flowers, which agrees with the transmission of their chloroplast type (A, C, and A, respectively) to their offspring (Figure 4). Lastly, the

unidentified variety “*Uva Negra del Molino Zenete*” was identified as the male parent of ‘Dominga’ (‘Heptakilo’ × “*Uva Negra del Molino Zenete*”) and “*Blanca de los Ríos*.” It also had a parent-offspring link with two unidentified varieties: “*Uva Blanca del Real de Antas*” and “*Uva Negra de la Noria de Lisardo*” (Figure 4).

Furthermore, we compared the available morphological and agro-nomical descriptions of 243 varieties grown in Andalucía at the beginning of the 19th century (Clemente y Rubio, 1807) and those obtained for vines sampled in this work with similar names (Dataset S5). These pairwise comparisons allowed us to suggest a coincidence for 14 cases. For example, the morphological and agro-nomical attributes of the vines sampled under the local names “*Jaén Blanca*” and “*Ohanes*” matched those described by Clemente y Rubio (1807) of the synonym varieties “*Jaén Blanco*” and “*Casta de Ohanez*”, respectively. In fact, these two vines were genetically identified as ‘Cayetana Blanca’ (synonym of ‘Jaén Blanco’) and ‘Ohanes’ (synonym of ‘Casta de Ohanez’), respectively (Dataset S1), supporting this link and indicating their uninterrupted cultivation in the region for more than two centuries. The coincidence of these cultivars was also observed when comparing the botanical illustrations available in Clemente y Rubio (1807) (Figure 5). Similarly, we observed that the descriptions given by Clemente y Rubio (1807) to the varieties “*Flor de Baladre*” and “*Santa Paula*” (syn. “*Verdal*”) matched to those obtained for the vines in this work named “*Flor de Baladre*” and “*Santa Paula*,” respectively, whose genetic profile did

TABLE 1 List of the 71 grapevine genetic profiles identified in this study after the genetic characterization of 220 old vines found in Almería, southeastern Spain.

Name ^a	ICVV ^b genotype	N	Variety number (VVC) ^c	Country of origin ^c	Use ^c
Beba–Beba Roja	2088	31	22,710–2008	Spain	Wine; table
Ahmeur Bou Ahmeur–Teta de Vaca Blanca	473	26	140–22,713	Algeria	Wine; table
Negra Rayada	650	15	1494	Spain	Wine
De Cilindro	1284	12	3470	Spain	<i>n.a.</i>
Dominga	2114	9	4985	Spain	Wine; table
Molinera	1214	8	7900	Spain	Table
Corazón de Gallo	4316	7	<i>n.a.</i>	<i>n.a.</i>	<i>n.a.</i>
Uva Blanca del Sánchez Cid	4324	7	<i>n.a.</i>	<i>n.a.</i>	<i>n.a.</i>
Uva Negra del Molino Zenete ^d	4124	6	<i>n.a.</i>	<i>n.a.</i>	<i>n.a.</i>
Cayetana	1089	5	5648	Spain	Wine; table
Durilla–Albilla Negra ^d	2516	4	<i>n.a.</i>	<i>n.a.</i>	<i>n.a.</i>
Flor de Baladre	4387	4	<i>n.a.</i>	<i>n.a.</i>	<i>n.a.</i>
Listán Prieto	1274	4	6860	Spain	Wine; table
Ohanes	608	4	8716	Spain	Wine; table
Abeaci de los Vélez	4313	3	<i>n.a.</i>	<i>n.a.</i>	<i>n.a.</i>
Blanca de los Ríos	4315	3	<i>n.a.</i>	<i>n.a.</i>	<i>n.a.</i>
Ciruela Roja	1260	3	2686	Spain	Table
Imperial	1125	3	<i>n.a.</i>	<i>n.a.</i>	<i>n.a.</i>
Imperial Roja	1220	3	22,740	Spain	Table
Uva Negra del Castillo de Benizalón	4325	3	<i>n.a.</i>	<i>n.a.</i>	<i>n.a.</i>
Uva Blanca de real de Antas ^d	453	3	<i>n.a.</i>	<i>n.a.</i>	<i>n.a.</i>
Cardinal	343	2	2091	USA	Wine; table
Colgar Roja	1202	2	2761	Spain	Table
Cornichon blanc	2007	2	16,448	Turkey	Wine; table
Quina	4392	2	<i>n.a.</i>	<i>n.a.</i>	<i>n.a.</i>
De La Gitana	4388	2	<i>n.a.</i>	<i>n.a.</i>	<i>n.a.</i>
Monastrell	2183	2	7915	Spain	Wine; table
Muscat d'Istambul	2736	2	17,493	Tunisia	Wine
Náparo	1187	2	8345	Spain	Wine; table
Ojo de Liebre	4318	2	<i>n.a.</i>	<i>n.a.</i>	<i>n.a.</i>
Afus Ali	2036	1	122	Lebanon	Wine; table
Albilla real	4314	1	<i>n.a.</i>	<i>n.a.</i>	<i>n.a.</i>
Alfrocheiro	2173	1	277	Portugal	Wine
Alphonse Lavallee	1032	1	349	France	Wine; table; raisin
Aramón falso	4320	1	<i>n.a.</i>	<i>n.a.</i>	<i>n.a.</i>
Autumn black	2470	1	14,166	USA	Table; rootstock
Beitamouni	21	1	14,790	Lebanon	Table
Uva Negra de la Noria de Lisardo	4495	1	<i>n.a.</i>	<i>n.a.</i>	<i>n.a.</i>
Cresta de Gallo	4500	1	<i>n.a.</i>	<i>n.a.</i>	<i>n.a.</i>
Uva Chinche de Tijola ^d	4494	1	<i>n.a.</i>	<i>n.a.</i>	<i>n.a.</i>
De Datilillo largo	4386	1	<i>n.a.</i>	<i>n.a.</i>	<i>n.a.</i>
De Lanjarón	4389	1	<i>n.a.</i>	<i>n.a.</i>	<i>n.a.</i>
De Lejía	4390	1	<i>n.a.</i>	<i>n.a.</i>	<i>n.a.</i>
De Pan	4391	1	<i>n.a.</i>	<i>n.a.</i>	<i>n.a.</i>
Doña María	174	1	3641	Portugal	Wine; table
Garnacha	1456	1	4461	Spain	Wine

(Continues)

TABLE 1 (Continued)

Name ^a	ICVV ^b genotype	N	Variety number (VIVC) ^c	Country of origin ^c	Use ^c
Graciano	1321	1	4935	Spain	Wine
Imperial Napoleón	2166	1	5517	Spain	Table
Italia	264	1	5582	Italy	Wine; table
Jacquez	9045	1	5627	USA	Wine
Jaén Negra	4317	1	<i>n.a.</i>	<i>n.a.</i>	<i>n.a.</i>
Jaén Tinto	1105	1	5652	Spain	Wine; table
<i>Uva Negra del Barranco de Benizalón</i>	4499	1	<i>n.a.</i>	<i>n.a.</i>	<i>n.a.</i>
Muscat of Alexandria	2153	1	8241	Greece	Wine; table; raisin
Palomino	1063	1	8888	Spain	Wine; table
Pardillo	2380	1	8934	Spain	Wine
<i>Uva Rosa del Cortijo del Calvo</i>	4498	1	<i>n.a.</i>	<i>n.a.</i>	<i>n.a.</i>
<i>Uva Negra del Molino de Doña María</i>	4497	1	<i>n.a.</i>	<i>n.a.</i>	<i>n.a.</i>
<i>Uva Rosa del Puente de Bocharalla</i>	4319	1	<i>n.a.</i>	<i>n.a.</i>	<i>n.a.</i>
Pizzutello Nero	529	1	9524	Spain	Table
Rágol	1104	1	22,739	Spain	Table
<i>Uva Rosa de Venta Torre</i>	4322	1	<i>n.a.</i>	<i>n.a.</i>	<i>n.a.</i>
<i>Santa Paula del Marchalejo</i>	4395	1	<i>n.a.</i>	<i>n.a.</i>	<i>n.a.</i>
<i>Sora</i>	4393	1	<i>n.a.</i>	<i>n.a.</i>	<i>n.a.</i>
Sultanina	2126	1	12,051	Central Asia	Wine; table; raisin
<i>Uva Rosa de Tahal</i>	4323	1	<i>n.a.</i>	<i>n.a.</i>	<i>n.a.</i>
Tinto Velasco	1017	1	17,353	Spain	Wine
<i>Uva de Cherín</i>	4496	1	<i>n.a.</i>	<i>n.a.</i>	<i>n.a.</i>
<i>Uva de Diego Ros</i>	4394	1	<i>n.a.</i>	<i>n.a.</i>	<i>n.a.</i>
Verijadiego	2606	1	25,695	Spain	Wine
<i>Parra Asilvestrada de la Cerrá</i>	8035	1	<i>n.a.</i>	<i>n.a.</i>	<i>n.a.</i>

Note: When possible, information of the *Vitis* international variety catalogue (VIVC) matching variety is provided.

^aIn italics, local name.

^bICVV: Instituto de Ciencias de la Vid y del Vino.

^cInformation retrieved from the *Vitis* International Variety Catalogue (VIVC) database.

^dGenetic profile available at the ICVV-DNA database, from the previous genetic characterization of unidentified grape samples. *n.a.*: not applicable.

not match any referenced variety. Nevertheless, in other 15 cases, these historical descriptions did not match those of the vines with similar names sampled in this work. For example, “Ojo de Buey” was described as a late variety with small and loose clusters of very large berries, while the homonym vine collected in this work was found to be an early variety with medium-sized clusters of medium-sized berries. Similarly, “Corazón de Gallo” was succinctly described as a black-berried variety (Clemente y Rubio, 1807), but the homonym vine that we analyzed in this work produces red/pink berries (Figure 3), as do the other vines that were found to have the same genetic profile. Lastly, the vine named “*de Lanjarón*” does not correspond to the homonym variety “Lanxaron” described by Clemente y Rubio (1807). Thus, this variety was described as one with non-lobed leaves that produces large and loose clusters of early-ripening berries, while we found that the living vine named “*de Lanjarón*” found in Almería has lobed leaves and medium-sized and compact clusters of late-ripening berries.

4 | DISCUSSION

Grapevine genetic diversity is essential for the evolution of tomorrow's viticulture. Many traditional European *V. vinifera* varieties vanished after the arrival of disease-causing agents from North America and many short-term market decisions (This et al., 2006; Wolkovich et al., 2018). Fortunately, some exceptionally dedicated generations of local farmers treasured some unique genotypes for decades, preserving them from their total disappearance. Now, there is a growing interest to locate and study these genetic resources, as the traits they hold can be a powerful tool to face current viticulture challenges (Biasi & Brunori, 2015; Morales-Castilla et al., 2020). Localization of these singular vines is complicated, and it mostly relies on the knowledge and memories stored by locals, who know where these surviving vines are. In addition, they can provide valuable information regarding their origin, age, use, and historical relevance. Here, we used the information collected by a conservation organization aimed to locate historical vines growing in Almería,

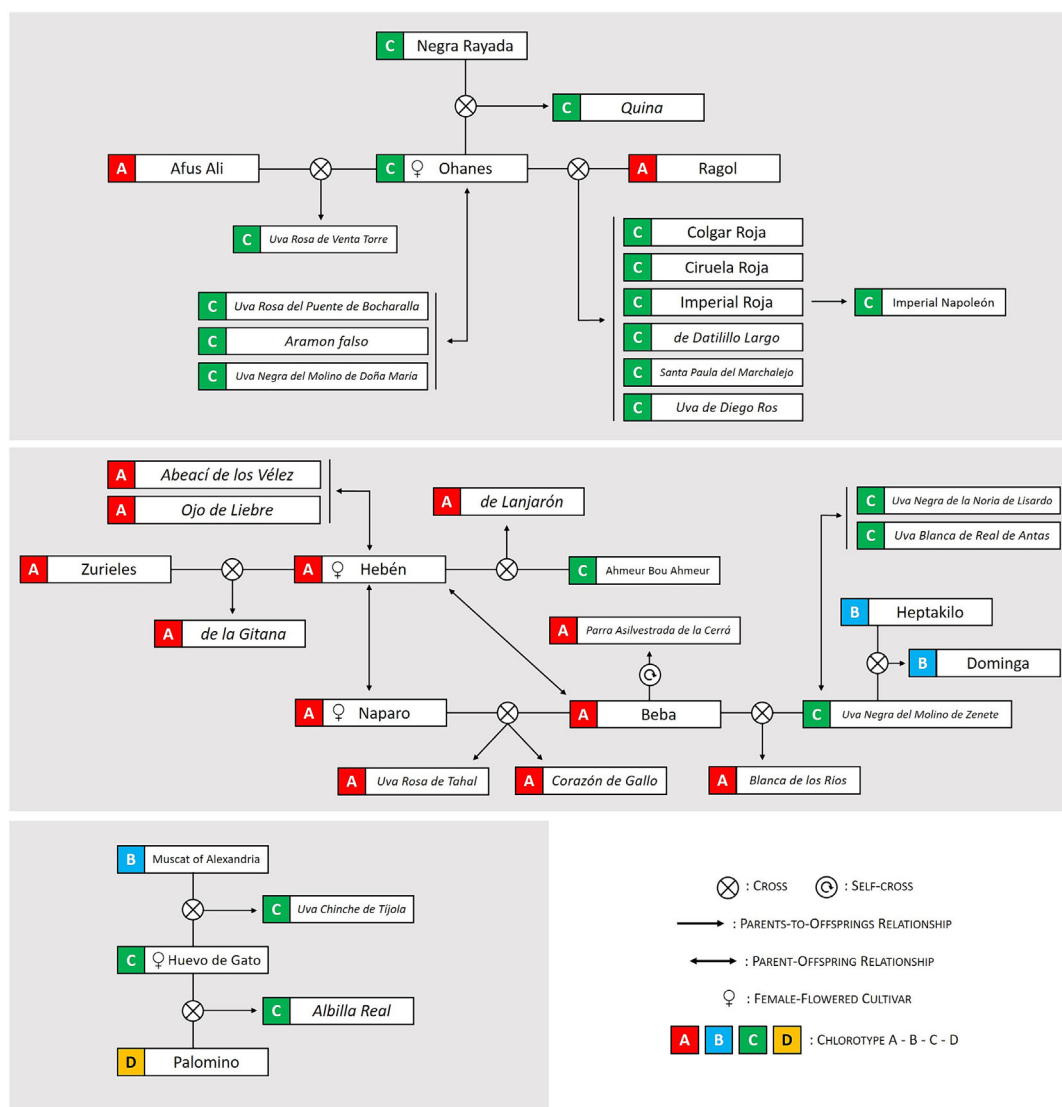


FIGURE 4 Schematic representation of the main parentage relationships identified between the grapevine varieties from Almería (Andalucía, Spain) studied in this work. Unidentified genotypes are indicated in italics.

one of the Spanish regions with longer tradition in table grape production (Sánchez-Escolano & Ruíz-Moya, 2018). As a result, we were able to detect many old vines nearby traditional constructions like old tile potteries, olive and grain mills, and water mills, as well as in house backyards and different sites previously devoted to viticulture. We identified and collected 220 old vines from these sites, which were found to correspond to 71 different genetic profiles after SSR and SNP profiling. These figures reflect the historical relevance of the area under investigation for grape production, which was part of some of the most important trading routes of table grapes in the 19th and 20th centuries (Alonso et al., 2006; Haro-Gil & Sánchez-Picón, 2020). Consequently, the explored sites can be considered as local reservoirs of table grape diversity, where the combination of climate and soil conditions, and traditional farming practices, succeeded in conserving a high number of different genotypes. The analyses of these genetic profiles allowed us to dig deep into the origin of those local genetic resources, as well as to identify a remarkable number of new putative old varieties.

4.1 | Local farmers mainly cultivated traditional and local grape varieties

The present work shows that grapevine varieties from the Western Mediterranean basin were the basis to develop a traditional and profitable viticulture system in Almería. Numerous old vines were identified as ‘Ahmeur Bou Ahmeur’, ‘Beba’, and ‘Dominga’ (Table 1), three ubiquitous varieties found in multiple Mediterranean countries for table grape production. For example, ‘Beba’ has been (and still is) widely grown in Algeria (known as ‘Aïn el Kelb’), Morocco (‘Muscat Sefrou’), Spain (‘Calop Blanco’ and ‘Uva Rey’), and Tunisia (‘Tebourbi’) (Zinelabidine et al., 2010), and ‘Ahmeur Bou Ahmeur’ is grown in Algeria (‘Ahmar de Mascara’), Croatia (‘Flame Tokay’), (‘Barbarossa’), Spain (‘Botó de Gall’, ‘Royal Gordo’ and ‘Teta de Vaca’), and Tunisia (‘Ahmar Bou Ahmar’), to cite some (De Michele et al., 2019; García et al., 2020; Ghaffari et al., 2014; Laiadi et al., 2009; Zinelabidine et al., 2015). ‘Beba’ is a variety of suggested

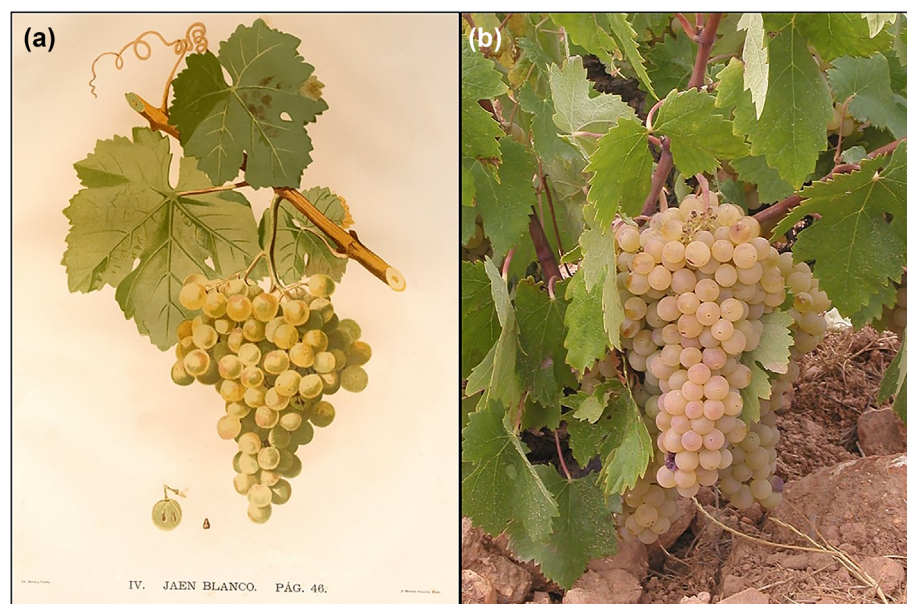


FIGURE 5 Botanical illustration of grape variety (a) “Jaén Blanco” and (b) representative cluster of “Jaén Blanca” (sample: ICVV_20651), identified as var. ‘Cayetana Blanca’ (syn. ‘Jaén Blanco’). The illustration shown Figure 5a is reproduced from Clemente y Rubio (1807).

Spanish origin, while ‘Ahmeur Bou Ahmeur’ is thought to have originated in Algeria. The finding of putative Maghrebian varieties in the Iberian Peninsula and of Iberian varieties in the Maghreb is widely reported (Ghaffari et al., 2014; Laiadi et al., 2009; Zinelabidine et al., 2010), and it reflects the long common history between both regions, which includes the exchange of plant material. However, this ubiquity hinders setting a definitive origin for these varieties, and, in the lack of reliable complete pedigree data, it is difficult to find where they first appeared and where they were spread to. Interestingly, we found that ‘Dominga’, a variety commonly grown both in Algeria (‘Bouni’) and Spain (‘Gloria’ and ‘Uva verde de Alhama’) (Laiadi et al., 2009), derives from the cross between ‘Heptakilo’ and the unidentified local variety “*Uva Negra del Molino Zenete*” (Figure 4). The high presence of “*Uva Negra del Molino Zenete*” in Almería supports that ‘Dominga’ is a variety likely generated in southeastern Spain, which solves previous controversy regarding its origin (Laiadi et al., 2009).

However, numerous identified old vines belong to varieties that, to our knowledge, have not been found outside the Iberian Peninsula, like ‘Aledo’, ‘de Cilindro’, ‘Molinera’, ‘Náparo’, and ‘Negra Rayada’ (Table 1). Little is known about the genetic origin of these varieties, except from some scarce genetic relationships with other putative Iberian varieties (Lacombe et al., 2013; Zinelabidine et al., 2015). Consequently, these varieties can be considered as true Iberian grape varieties. Interestingly, ‘Molinera’ has been recently identified in old vineyards of Málaga (Jiménez-Cantizano et al., 2020), a Spanish province close to Almería, and there are 13 known synonyms for ‘Molinera’ that include the term “Málaga” in its name (<https://www.vivc.de/>). Altogether, these evidences suggest that this variety might have originated in Southern Spain. Likewise, many old vines were identified as ‘Cayetana Blanca’ and ‘Ohanes’. These two varieties are widely spread in the Iberian Peninsula, being progenitors of many Spanish and Portuguese varieties (Vargas et al., 2009; Zinelabidine

et al., 2012). Although the geographical origin of ‘Cayetana Blanca’ has been placed in the southwestern border region between Portugal and Spain (Zinelabidine et al., 2012), Almería is suggested to be the place of origin of ‘Ohanes’ (Alonso et al., 2006). In fact, Ohanes is the name of a village in the Almería region, and this variety is also known as ‘Uva de Almería’, which means “grape from Almería.” The cultivation of ‘Ohanes’ in Almería can be traced back to the beginning of the 19th century (Clemente y Rubio, 1807), when the commercial production and exportation of ‘Ohanes’ grapes became one of the most profitable agricultural activities in the region (Alonso et al., 2006; Haro-Gil & Sánchez-Picón, 2020; Zambrana-Pineda, 2006). As a consequence of its successful longstanding cultivation in the region, we found up to eight varieties deriving from ‘Ohanes’ within the vines analyzed in this work (“*Uva Rosa de Venta Torre*,” “*Quina*,” “*Colgar Roja*,” “*Ciruela Roja*,” “*Imperial Roja*,” “*de Datillillo Largo*,” “*Santa Paula del Marchalejo*,” and “*Uva de Diego Ros*”). As stated above, ‘Ohanes’ is a female-flowered variety, so it was (and still is) artificially pollinated by local farmers to ensure enough fruit production. This practice, named with the Spanish term “engarpe,” was traditionally performed by brushing ‘Ohanes’ inflorescences at full flowering with inflorescences taken from available local hermaphrodite varieties or male wild grapevines (of the subspecies *sylvestris* or of non-*vinifera* *Vitis* species) to promote a successful fertilization to increase fruit and seed set rates. According to Alonso et al. (2006), local farmers commonly used inflorescences from ‘Rágol’ to pollinate ‘Ohanes’ flowers. Rágol is another village of the Almería region, close to Ohanes. Interestingly, we identified six local varieties as offspring of ‘Ohanes’ × ‘Rágol’ (Figure 4). Although these six varieties may have arisen from the spontaneous pollination of ‘Ohanes’ flowers by airborne pollen from ‘Rágol’ (Vargas et al., 2009), they can also derive from this traditional manually assisted pollination process, which could led to viable seeds that derived in plantlets further selected as novel varieties for grape production. This practice might be the origin of the local varieties

“*Uva Rosa de Venta Torre*” and “*Quina*” too, two compatible offsprings of ‘Ohanes’ × ‘Afus Ali’, and ‘Ohanes’ × ‘Negra Rayada’, respectively. Accordingly, we identified different old vines as ‘Afus Ali’ and ‘Negra Rayada’ in the region, indicating their presence and potential use as pollen donor in those crosses. In fact, ‘Afus Ali’ is a variety of long tradition in Southern Spain, where it is known as ‘Roseti’ (García de Luján & Lara, 1998).

In a similar way, we identified three other female-flowered varieties (‘Hebén’, ‘Huevo de Gato’, and ‘Náparo’) as the progenitors of six unidentified local varieties (“*de la Gitana*” and “*de Lanjarón*”, “*Uva Chinche de Tijola*” and “*Albilla Real*”, and “*Uva Rosa de Tahal*” and “*Corazón de Gallo*”, respectively) (Figure 4). This information agrees with the reported relevant role of female varieties on the generation of new varieties in other viticulture regions (Maraš et al., 2020; Raimondi et al., 2020), probably because of their good agronomic performance related to the lack of negative inbreeding depression effects caused by selfing (Cattonaro et al., 2014). Our results also increase the already known dominant role of the variety ‘Hebén’ in the generation of Iberian grapevine varieties (Zinelabidine et al., 2015), with two new identified offsprings (“*de la Gitana*” and “*de Lanjarón*”). As previously indicated (Zinelabidine et al., 2015), the high prolificacy of this variety favored the spread of the chlorotype A in the Iberian Peninsula, likely contributing to its dominant presence (Arroyo-García et al., 2006).

Some varieties from other Mediterranean regions made a minor contribution to the development of local viticulture (Table 1). We identified some old vines as ‘Muscat of Alexandria’ and ‘Sultanina’, two ancient grape varieties extensively spread all over the world given their highly appreciated unique fruit characteristics: muscat flavor and seedlessness, respectively (Crespan & Milani, 2001; Royo et al., 2018). In addition, we identified two old vines as ‘Cornichon Blanc’ and one vine as ‘Beitamouni’ (Table 1). ‘Cornichon Blanc’ is a table grape variety with horn-shaped berries, which is grown in many countries under different names, like ‘de Cuerno’, ‘Mamella de Vaca’, and ‘Pizzutello’ (Crespan et al., 2021; Jiménez et al., 2019; Mena et al., 2014). ‘Beitamouni’ is another table grape variety with horn-shaped berries of putative Lebanese origin. Different reports indicate its presence along the Mediterranean basin, including old vineyards from Israel (known as ‘Asba El Arus’ and ‘Safadi’), Greece (‘Nychato’), and Tunisia (‘Rich Baba Sam’) (Drori et al., 2017; Ghaffari et al., 2013; Lefort & Roubelakis-Angelakis, 2001). Here, we found that ‘Beitamouni’ was maintained under the local name “Cuerno de Buey” (meaning ox horn), term that evokes the shape of its berries, a singularity also represented in other synonyms of this variety (Lefort & Roubelakis-Angelakis, 2001). Therefore, the name “Cuerno de Buey” can be considered a new synonym for ‘Beitamouni’. These examples indicate that local farmers might have selected some exogenous varieties for table grape cultivation if they provided additional benefits through singular fruit features (muscat aroma, seedlessness, and attractive berry shapes). In this line, we found that they also searched for variation in berry color, not only by preserving varieties of different colors but also berry color-somatic variants of the same variety. The sets of SSR and SNP markers used in this work do not differentiate somatic

variants of the same variety, but after crossing genetic data with phenotypic data, we identified 23 old vines as the white-berried variety ‘Beba’ and eight as its already reported red-berried variant ‘Beba Roja’ (García-Muñoz et al., 2011). Similarly, we identified 24 pink/red-berried vines as ‘Ahmeur Bou Ahmeur’ and two as its white-berried somatic variant ‘Teta de Vaca Blanca’ (Jiménez-Cantizano et al., 2018). In this line, we identified an additional case of a local pair of berry color grapevine variants (“*Durilla*” and “*Albilla Negra*,” with white and black berries, respectively). The potential identification of this novel pair color variant is of interest to analyze additional genetic mechanisms involved in berry color determination (Ferreira et al., 2018).

Lastly, we identified some old plants as wine grape varieties (like ‘Garnacha’, ‘Graciano’, and ‘Monastrell’). Although some of these plants were found growing for the production of grapes for fresh consumption, most of them were located in abandoned sites previously devoted to wine grape production, including some nearby abandoned wineries. So, these plants could be marginal survivors reflecting previous winemaking activities of the region, before the intense vineyard replacement experienced in the region in the last 40–50 years (Zambrana-Pineda, 2006).

4.2 | Local farmers saved traditional grape varieties from extinction

After the genetic study of 220 old vines, we found 35 genetic profiles that could not be assigned to a true-to-type variety. Up to 22 genetic profiles were found only once in Almería, so they can be vines directly grown from seeds (on purpose when the use of cuttings for propagation was not feasible or from naturally germinated seeds) or true varieties (which at some point were propagated vegetatively) in a high risk of disappearance. However, 13 of them were found more than once. This finding indicates that these 13 varieties had some interesting features (like fruit quality, adaptation to local stressors, and/or yield stability) that prompted their selection, multiplication, and preservation by local growers until today. In fact, some of these unknown varieties were found at a frequency comparable to other varieties that were (and still are) relevant in the region (Table 1), suggesting their local importance for table grape production. As an additional proof of their value, we found that four of these unidentified local varieties matched the genetic profile of samples previously analyzed by our research group, including two samples held at the IMIDRA (Madrid, Spain) and the INTA (Mendoza, Argentina) national grapevine collections (stored as “Rosaki × Almería” and “Blanca Temprana de Almería,” respectively), and two other samples obtained from two very distant Spanish regions (Aragón and La Rioja, both in Northern Spain). It supports the interest of these local varieties, which prompted that, at some point of their history, someone valued them enough to multiply and preserve them in very different places.

Historical reports and descriptions are an important source of information to evaluate the relevance and evolution of local grapevine varieties in a certain area. Within the available works, the essay of

Clemente y Rubio (1807) is considered a masterpiece for Spanish viticulture, as it describes some agronomical and morphological attributes of more than 200 grapevine varieties grown in Andalucía before the arrival of phylloxera and other disease agents. Although the comparison of historical and modern descriptions does not provide the definitive piece of information to identify a variety, they have been useful to link some modern varieties to old references (Cretazzo et al., 2022; Maul et al., 2016; Popescu et al., 2017; Sancho-Galán et al., 2019). Here, we compared the historical descriptions and botanical illustrations of some varieties with those obtained from modern vines with similar names or with names that are considered synonyms of those used in the old references. This strategy was useful to confirm the longstanding cultivation of two varieties known to be present in the region for centuries: 'Jaén Blanco' (syn. 'Cayetana Blanca') and 'Ohanes' (Alonso et al., 2006; Zinelabidine et al., 2012) (Figure 5). Similarly, we could link some unidentified local vines to some varieties already described by Clemente y Rubio (1807). This is the case of "Flor de Baladre," a minority local variety indicated to be grown in the region of Vélez (Almería) at the beginning of the 19th century (Clemente y Rubio, 1807). The phenotypic features of this ancient cultivar resembled those of an unidentified vine with the same name (Figure 3; Dataset S5) and three others with the same genetic profile (Dataset S1). Interestingly, these four vines were located in different municipalities nearby the Vélez region, which suggests a potential longstanding exploitation of this variety in the same area for, at least, two centuries. Recently, a plant collected in Alicante (southeastern Spain) as "Flor de Baladre" was genetically identified as the pink/red-berried variety 'Ahmeur Bou Ahmeur' (García et al., 2020). Very likely, the term "Flor de Baladre" (meaning "oleander flower") was commonly used by locals to name different varieties of pinkish berries, which is the characteristic color of the flowers of the oleander, a widely spread Mediterranean plant in the region. In this light, we suggest to use "Flor de Baladre" as the prime name of the new variety identified in this work. Besides, we sampled one vine as "Santa Paula," while Clemente y Rubio (1807) differentiated up to three ancient varieties under this name ("Santa Paula" (syn. "Verdal"), "Santa Paula de Granada," and "Santa Paula de Xerez"). Given their morphological resemblance, our homonym vine might correspond to the variety named "Santa Paula" (syn. "Verdal") (Figure 3 and Dataset S5). Interestingly, the genetic profile obtained for this vine did not match that of the registered variety 'Santa Paula' (VIVC: 23941), known as 'Cornichel Branco' in Portugal (Alifragkis et al., 2015) and as 'Ribí Mehur' in Bulgaria (Dzhambazova et al., 2009). To differentiate the new variety identified in this work from 'Santa Paula'/'Cornichel Branco'/'Ribí Mehur', we propose to use the name "*Santa Paula del Marchalejo*."

In other cases, these historical descriptions were useful to discard a connection between some of the varieties found here and those described two centuries ago, as observed for "Ojo de Buey," "Corazón de Gallo," and "de Lanjarón" (Dataset S5). Because of some peculiar phenotypic characteristics of the varieties (berry color and berry shape), or of the regions where they are grown, the convergence of names to denominate different genotypes (homonymy) is very common in grapevine (This et al., 2006). Fortunately, some of them have

been solved by the use of DNA-based markers (Crespan & Milani, 2001; García-Muñoz et al., 2011; Maraš et al., 2020; Mena et al., 2014). Our results suggest some potential cases of homonyms between the varieties described by Clemente y Rubio (1807) and some of the vines studied here, even when they had strong phenotypic differences. It suggests that either the same name was already used at the beginning of the 19th century to refer to different varieties, as already highlighted by Clemente y Rubio himself (Clemente y Rubio, 1807), or that locals maintained these names, even when they were unintentionally re-assigned to a different variety.

Although our findings suggest that some of the unidentified vines analyzed in this work could correspond to some of the ancient varieties cited by Clemente y Rubio (1807), we do not have definitive evidence to support this connection. In fact, some of the links indicated here are partially supported on the description of few agronomic or morphological features. Today, this conclusive information is provided by genetic analyses, which could be carried out only by using traceable historical plant material to perform a comparative genetic study. Interestingly, Clemente y Rubio (1807) collected leaves and shoots from 186 of the ancient varieties described more than two centuries ago, to build an herbarium that is still stored in the facilities of the Royal Botanical Garden (RBG) of Madrid (Madrid, Spain) (Gago et al., 2019). Unfortunately, there are not available samples for some of the most promising matching references found in this work, including "Flor de Baladre" or "Santa Paula" (syn. "Verdal"). For practical reasons, we have only compared the descriptions given by Clemente y Rubio (1807) with that of a vine collected in this work if they shared a similar name, even when it is widely known that varieties names commonly change as soon as they move from one region to another (This et al., 2006). Obviously, any vine studied here might correspond to any entry in the work of Clemente y Rubio (1807), which reinforces the interest of analyzing the 186 specimens stored in the RBG herbarium following a similar genetic profiling strategy to the one performed in this work. If successful, this approach will allow us to have the definitive piece of evidence to prove that the effort conducted by local farmers during centuries was not only useful to maintain a traditional grape production system but also might have been useful to prevent the loss of some historic varieties which nowadays are thought to be lost.

This work remarks that the historical on-site preservation of grapevine genetic diversity was crucial not only to maintain a highly relevant traditional heritage but also to preserve a high number of grapevine genotypes that now can be used to increase the sustainability and stability of table grape production systems. To avoid the future loss of this diversity, the new genetic resources identified in this work have been stored in two dedicated grapevine collections (in Terque, Almería, and Logroño, La Rioja) for their ex situ preservation and future characterization and multiplication. In addition, a local exhibition is organized every year to ultimately show the benefits of preserving this biodiversity to local authorities and grape growers to stimulate coordinated conservation activities (Figure 6). These activities include a tribute to selected local grape growers to acknowledge their efforts in preserving local centenary vines, as well as the free



FIGURE 6 Dissemination activities to promote the cultivation of ancient grapevine varieties from Almería. Posters announcing the local exhibition of historical (a) table grapevine varieties and their (c) free distribution as grafted shoots. (b) Local growers showing some of the table grape varieties analyzed in this work. (d) Distribution of grafted vines to grape growers. Images are reproduced from <https://www.gem.es/biodiversidad.html>.

distribution of grafted vines of these varieties to any interested farmer, that has expanded the in situ maintenance of these resources. These dissemination activities have been very efficient and useful to find some additional old plants in the region, and they have prompted the cultivation of these singular genetic resources by numerous local families, which considerably increased their odds of survival.

AUTHOR CONTRIBUTIONS

Javier Tello was involved in the conceptualization of the research, methodology, data analysis, the preparation of the original draft of the manuscript, and the review and editing of the manuscript. Álvaro Galán and Inmaculada Rodríguez-Torres were involved in methodology and data analysis. José Miguel Martínez Zapater was involved in the conceptualization of the research and in the review of the manuscript. Antonio Rubio Casanova was involved in the conceptualization of the research, location, collection, and submission of samples. Javier Ibáñez was involved in the conceptualization and supervision of the research, methodology, data analysis, and the review of the manuscript. All authors approved the final version of the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to report.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in the supporting information of this article.

ETHICS STATEMENT

All local grape growers interviewed in this study were above 18 years old, and gave informed verbal consent before participating. They were briefed about the aims, procedures, and relevance of the project. Participants were assured that the plant material and data collected would be used strictly for research and preservation purposes. Grupo Ecologista Mediterráneo (GEM) coordinated the collection of plant material and field data, following the Institution's guidelines and approved by its Executive Board. It conformed to the standards of the Code of Ethics of the International Society of Ethnobiology (ISE).

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