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Grapevine cultivation at Cetamura del Chianti: multiproxy evidence for centuries of continuity from the Etruscans to the Romans

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ABSTRACT

Roman writers provide detailed accounts of viticulture practices in ancient Mediterranean civilisations. While records describe varieties, methods of vine management, and consumption traditions, major questions remain about how varieties were spread and whether viticulture traditions were impacted during Roman expansion. At the site of Cetamura del Chianti (Siena, Tuscany), waterlogged grape seeds from two wells dated between ca. 300 BCE and ca. 1200 CE provided an opportunity to integrate multiple methodologies to investigate Etruscan and Roman viticulture. Genetic testing of 80 grape seeds revealed that the deepest parts of the wells were associated with higher endogenous DNA content, and complementary near-infrared spectroscopy found patterns with well-preserved pips. Both genome-wide DNA data and geometric morphometric analysis indicated that most seeds originated from domesticated vines associated with winemaking, however, the latter suggested that some seeds with little DNA may derive from wild vines. Following enrichment of genetic markers, relatedness analyses demonstrated links to the past and present: one Cetamura seed was closely related to a Roman seed from Mont Ferrier in France while another pip had affinity to the modern Hungarian variety 'Baratcsuha szurke'. Within the wells, genetic data and radiocarbon dating revealed continuity from Etruscan to Roman periods, with over a quarter of the seeds belonging to one clonal variety maintained for centuries. Furthermore, genetic markers associated with anthocyanin content indicated the dominant clonal variety likely produced white berries; however, red wine was presumably not unknown at Cetamura, as two other pips were consistent with a dark berry phenotype.

1. Introduction

The cultivation and domestication of the grapevine (*Vitis vinifera* subsp. *vinifera*) have significantly influenced human history, shaping cultural, economic, and social development (McGovern, 2019). The earliest evidence of grapevine domestication is found in southwestern Asia during the Neolithic period, around 6000–4000 BCE, originating from its wild ancestor (*Vitis vinifera* subsp. *sylvestris*) (Bouby et al., 2013; Deckers et al., 2024; Dong et al., 2023; Harutyunyan and Malfeito-Ferreira, 2022; Limier et al., 2018). Since then, thousands of grape cultivars have emerged through vegetative propagation and crossbreeding for consumption as table grapes, raisins, and wine (Myles et al., 2011). However, the continuity of grapevine cultivation practices through different time periods and the extent of past grapevine diversity remain unresolved. Vegetative propagation is crucial for sustained grapevine production, and it allows for generating genetically identical clones of valuable cultivars, ensuring consistent grape yields and the preservation of desirable traits (Goncalves and Martins, 2012; Kızıldeniz et al., 2022). Exploring the historical and scientific aspects of grapevine propagation enhances our understanding of ancient agricultural

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practices. It provides insight into modern viticulture, explaining why specific cultivars have become extinct while others have shown greater adaptability or have been consistently favoured for winemaking.

In the Mediterranean Basin and neighbouring regions, researchers have examined archaeological grape pips to understand the history of domestication and management of cultivars across time. For example, archaeobotanists have capitalised on variations in seed shape to differentiate between wild and domesticated seed (Ucchesu et al., 2015), as well as different varieties (Bonhomme et al., 2021; Bouby et al., 2024). Complementary analyses of ancient DNA (aDNA) in non-charred pips has allowed insights on the genetic legacy of vine management in the western (Noraz et al., 2026; Ramos-Madrigal et al., 2019) and eastern (Cohen et al., 2023) reaches of the Mediterranean Sea. Expanded investigations can allow for refined understanding of regional uses of grapevine and the impact of key cultural phases. The history of winemaking associated with the Romans is particularly important to investigate, as the Roman Republic and Roman Empire were heavily invested in the wine trade, ultimately establishing many winemaking traditions which survive today. Grapevine cultivation and wine production are well-documented in classical texts by Roman writers. The earliest known agricultural text in Latin, *De Agricultura*, attributed to Marcus Porcius Cato the Elder (ca. 234–149 BCE), offers practical guidance on cultivating vines and olives, as well as recipes for winemaking (Dalby, 1998). He suggests that grapes produce the best wine when they receive sufficient sunlight, therefore recommending that vines be grown in trees called "married vines" (Dalby, 1998, 2011; Phillips, 2001). Lucius Junius Moderatus Columella, in his *De* Re *Rustica* (ca. 1st century CE), gives a comprehensive guide to vineyard management, detailing practices such as pruning, grafting and soil preparation (Columella, 1941; Homet et al., 2024; Stubert et al., 2020). In *Naturalis Historia*, Gaius Plinius Secundus (Pliny the Elder, ca. 23–79 CE) described 91 grape varieties and styles of wine in detail, such as 50 kinds of generous wines, 38 foreign wines, and 18 sweet wines (Dougherty, 2012). Among these, he mentions the "Raetica" grape, which was a white variety cultivated during his time, especially around the Central Alps (Cattonaro et al., 2014). Some ampelographers have drawn tentative connections between cultivars named by Latin writers and modern grapevine varieties (see Stavrakaki et al., 2020), but conclusive links have not been established. In addition, while historic texts provide rich detail about Roman viticulture, they provide little information on the winemaking traditions practised by earlier groups or on what happened to local grapevine cultivars over the course of Roman colonisation.

Archaeological evidence across Etruscan sites indicates a highly developed viticulture tradition, with pruning hooks and written testaments showing that wine was a significant part of Etruscan culture (de Grummond, 2018; Dodd, 2022; Marvelli et al., 2013; Nesto and Di Savino, 2016; Pecci et al., 2020; Riva, 2018). Thanks to an exceptional record of well-preserved archaeological grape pips, the site of Cetamura del Chianti provides a valuable case study to refine our understanding of grapevine cultivation in Etruscan and later periods. Located within Tuscany's Chianti region, an area known for its historical significance in winemaking and its celebrated dry, red wine produced from 'Sangiovese' berries (Dodd, 2022; Mocarelli and Vaquero Piñeiro, 2019), Cetamura del Chianti stands at a crossroads between major Etruscan settlements like Chiusi, Arezzo, Volterra and Fiesole (Fig. 1a). The site has been a major focus of archaeological excavations by de Grummond (2020) and colleagues, leading to new insights on the cultural development of the Etruscans, their interactions with neighbouring civilisations, and the disintegration of Etruscan settlements in the series of wars between southern Etruria and the Romans from the 4th to the 1st centuries BCE. The Roman conquest of Etruria led to the integration of Etruscan viticultural knowledge into Roman practices (Dodd, 2022). However, the extent to which local traditions persisted and adapted, influenced or became absorbed into Roman practices, remains uncertain.

Excavations at Cetamura have yielded abundant material culture, including pottery, coins, glass, and metal objects, alongside well-preserved organic remains from well deposits such as pollen, wood, seeds, and animal bones (de Grummond, 2017, 2020; Mariotti Lippi et al., 2020). Within the broad assemblage of finds, de Grummond

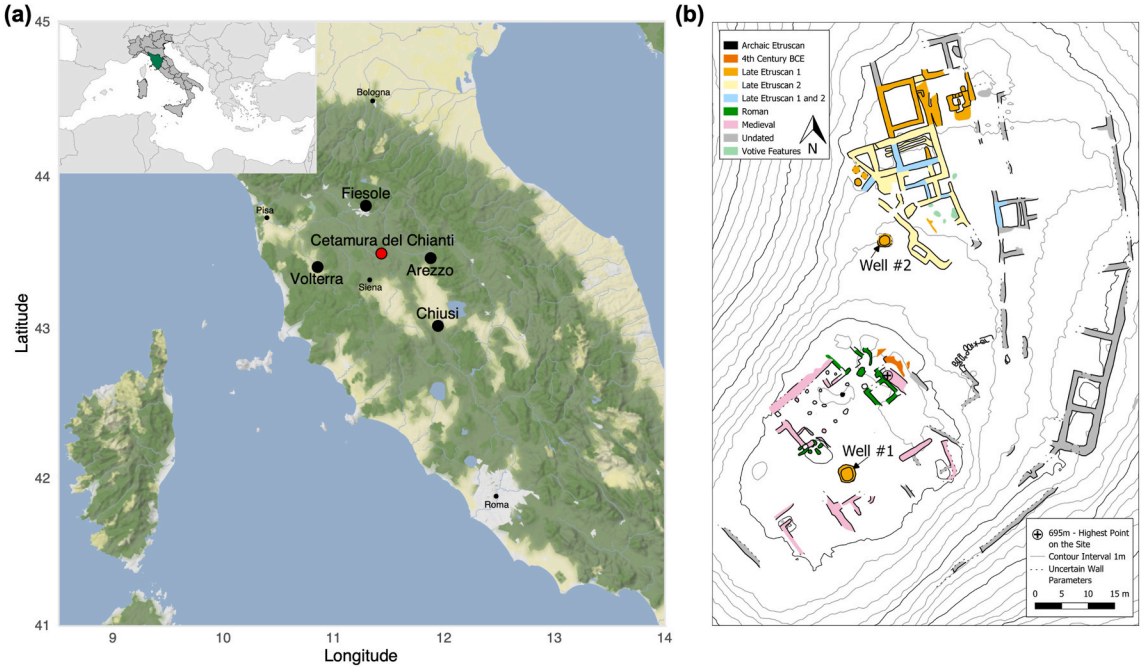

Fig. 1. Maps and site plan of Cetamura del Chianti. (a) The site is located in the Tuscany region of Italy, highlighted in green in the inset map. The prominent Etruscan settlements of Fiesole, Volterra, Arezzo and Chiusi are situated within 100 km of the site. The maps were created in R version 4.1.2 (R Core Team, 2021) using data from Natural Earth (Massicotte and South, 2026) and Stadia Maps (https://stadiamaps.com). **(b)** The site plan defines two primary excavation zones, each containing a well wherein the archaeological grape pips were recovered. The contour lines indicate the elevation, with the highest point marked at 695 m. Site plan prepared by Kurtis A. Butler. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

(2020) has argued that various artefacts indicate wine consumption at the site. Key evidence includes two decorated bronze situlae, widely identified as wine buckets, from Etruscan deposits dating to the 4th or 3rd centuries BCE. In addition to the situlae, the bronze handle of a wine strainer was excavated. While the sieve portion of the Cetamura strainer was not recovered, similar strainers are depicted on Etruscan frescos as being part of banqueting rituals, such as at the Tomb of the Leopards at the Monterozzi necropolis (Poulsen, 1922, p. 32).

Plant remains, including seeds, fruits, and wood, recovered from the two wells at Cetamura (Fig. 1b) have helped researchers shed light on daily life, the environment, and agricultural practices from the Etruscan period around 400 BCE to the Late Roman Empire ca. 300–400 CE (de Grummond, 2018). Pollen grains analysed from sediment collected at various depths of Well #1 showed the presence of numerous plant species, with *Vitis* constituting its highest percentage in the deeper layers (Mariotti Lippi et al., 2020). The waterlogged condition of 310 grape pips enabled detailed geometric morphometric (GMM) analysis (Bouby et al., 2017; Mariotti Lippi et al., 2020), with results indicating that the Cetamura grapevines were predominantly of domesticated origin. While most pips were found to have domesticated phenotypes, based on the full GMM dataset, Mariotti Lippi et al. (2020) observed that ~8% of Well #1 specimens were similar to wild pips, suggesting possible collection of wild berries. In addition, Mariotti Lippi and colleagues determined that seed shapes were relatively consistent across the strata, which the researchers interpret as centuries of viticulture stability at the settlement. Using a different archaeobotanical approach on Cetamura pips, Aversano et al. (2017) reach a different conclusion, and argue the accessions cannot be classified as wild or cultivated. This biometric investigation yielded an intermediate Stummer shape index score (Stummer, 1911), suggesting the seeds had an intermediate form. Aversano et al. also hypothesise a shift toward larger seeds starting at 200 BCE, which they argue may have been caused by changes in vine management strategies (but see de Grummond, 2018).

The partially inconsistent GMM and biometric results highlight some of the limitations of visual assessments of archaeobotanical remains (Portillo et al., 2020). For example, GMM reference databases may not be fully representative or seed morphology may be impacted by confounding factors (e.g., pathogens, pruning, and irrigation practices). To overcome these challenges, genetic testing of archaeological pips can provide a complementary line of evidence, and limited work has shown aDNA is preserved in Cetamura's wells. Aversano et al. (2017) first reported DNA analysis of 15 seeds from Well #1 using microsatellite amplification of Simple Sequence Repeat (SSR) markers, finding genetic similarities across chronologies even though morphological differences were observed. While intriguing, SSR analyses can have limited resolution because these genetic markers tend to be too long to amplify in degraded samples (Arandjelovic and Thalmann, 2012). In the place of SSR approaches, most aDNA researchers now rely on high-throughput DNA sequencing to characterise single nucleotide polymorphisms (SNPs), and as shown by Wales et al.'s (2017) exploratory work, some pips from Cetamura's wells are exceptionally well preserved and ideal for state-of-the-art palaeogenomic methods.

To capitalise on Cetamura's well preserved DNA and favourable depositional and stratigraphic context, a multifaceted investigation was developed to integrate different lines of evidence. A battery of scientific methods were employed, including GMM analysis, aDNA testing, near-infrared (NIR) spectroscopy, scanning electron microscopy (SEM) and radiocarbon dating, with the primary aim of better understanding the history of viticulture from the Etruscan to Roman periods.

2. Materials and methods

2.1. Archaeological samples

Waterlogged grape seeds were excavated from two wells at the Cetamura del Chianti archaeological site. Well #1 (ca. 300 BCE–1200 CE) was excavated between 2011 and 2014, while Well #2 (ca. 0–400 CE) was discovered in 2014, with excavations concluding in 2016. To prevent degradation, seeds were collected in situ, placed in individual tubes containing water from the depositional environment, and stored at 4 °C. As it was unclear if certain methodologies might lead to DNA contamination or degradation (Bolognesi et al., 2025), a varied strategy was employed, and therefore, multiple methods were applied to a subset of the specimens.

The sequence and number of methods applied to individual pips was developed to ensure that some specimens would have minimal risk of DNA contamination. First, GMM was applied to 71 pips, leaving 9 untouched in case GMM processing introduced contamination. All 80 seeds in the assemblage were tested with DNA shotgun sequencing, with 25 specimens completely used for the destructive DNA testing and 55 processed as half-seeds, providing a corresponding half for other methods. 52 pips were enriched for genetic loci of interest, 50 were examined with near-infrared (NIR) spectroscopy and high-powered microscopy, 10 were examined under scanning electron microscopy (SEM), and 5 were selected for accelerator mass spectrometry (AMS) radiocarbon dating. Overall, 66 pips had at least three methods applied (Supplementary Table S1), enabling inferences and comparisons across techniques.

2.2. Geometric morphometric (GMM) analysis

Archaeological grape seeds (n = 71) were photographed for morphometric analysis in a dedicated clean room at the Institute of Evolutionary Science of Montpellier (ISEM), France, to avoid contamination from modern DNA. All surfaces and tools were cleaned with 3% bleach between each sample, and images were taken using a microscope (Dino-Lite Pro HR AD-7013) that had not previously been used for modern grape samples. GMM findings for Well #1 were originally reported by Bouby et al. (2017), but presented in full here, along with all data for Well #2.

Seed shape was analysed using Elliptical Fourier Transform (EFT) analysis of seed outlines (Bonhomme et al., 2021; Bouby et al., 2024; Terral et al., 2010), with the addition of seed length in the analysis (Supplementary Methods 1). It has been corrected for taphonomic deformation with an average reverse vector of experimentally determined shape changes (Bouby et al., 2023, 2024). Linear discriminant analysis (LDA) was used to determine the wild or domesticated status of seeds, classifying them into regional use and variety groups following Bouby et al. (2024) as East-Table, Balkans-Wine, Iberian-Wine, and West-Wine. Pip lengths were used in a linear model to infer the ancient grape berry volume (Bouby et al., 2024).

2.3. Near-infrared (NIR) spectroscopy

Near-infrared (NIR) spectroscopy has become a transformative tool in archaeology. It offers a non-destructive method for analysing the chemical and structural characteristics of archaeological samples (Choi et al., 2020; Sciuto et al., 2022). NIR is therefore used here as a descriptive and exploratory approach to identify spectral patterns associated with DNA preservation, and its predictive potential may be further developed through additional testing, including analyses of grapes from different contexts or other plant remains. Fifty halved seeds were dried at 25 °C for two days to reduce moisture content before spectral analysis at the McDonald Institute for Archaeological Research, University of Cambridge, UK (Supplementary Methods 2). The data were collected over two days, analysing both interior and exterior seed surfaces across a 350–2500 nm wavelength range. To improve data quality, wavelengths outside the 400–2400 nm range were excluded before conducting a Principal Component Analysis (PCA) to identify patterns associated with grapevine DNA content. The first two principal components were visualised with 95% confidence ellipses showing data distribution and variability. The DNA content was categorised into

groups based on the percentage of grapevine DNA.

2.4. Ancient DNA analysis

Archaeological grape seeds (n = 80) were processed in dedicated aDNA facilities at the University of York, UK and the University of Copenhagen, Denmark, following established aDNA laboratory practices and contamination control procedures (Knapp et al., 2012, 2015). Dino-Lite 2.0 microscopy (AM4815ZTL-Edge) equipped with an Extended Depth of Field (EDOF) captured images of a selection of the grape pips before aDNA analysis in case the seeds were damaged during transportation. This manual investigation analysed the seeds' colour, shape, and texture and compared these phenotypic characteristics with endogenous DNA data obtained through shotgun sequencing. After imaging, to remove contaminant DNA adhering to the exterior of specimens, seeds were washed in 5% sodium hypochlorite (NaOCl) for 30 s and rinsed with molecular-grade water. Some samples were cut in half for DNA extraction, and the other half was retained for AMS dating or other future analyses (Supplementary Table S1). Radiocarbon dating was conducted at specialised laboratories (Supplementary Methods 4). Whole or half seeds were then individually pulverised, and DNA was isolated using methods that proved optimal for recovering very short and damaged nucleic acids from archaeological plant remains (Supplementary Methods 3.1) (Wales et al., 2014; Wales and Kistler, 2019). The DNA extracts were converted into double-stranded Illumina libraries (Carøe et al., 2018; Wales et al., 2015) or single-stranded libraries (Kapp et al., 2021). The extracts were split into two for single-stranded library preparation, with one portion undergoing uracil-DNA glycosylase (UDG) treatment before targeted enrichment (Supplementary Methods 3.2) (Briggs et al., 2010).

The libraries were shotgun sequenced on an Illumina HiSeq 2500 or NovaSeq X to determine the amount of endogenous DNA (Supplementary Methods 3.3). All samples with more than 1% grapevine DNA (n = 43) were subsequently enriched using custom-designed RNA probes, including some seeds with low endogenous DNA (n = 12) for control purposes (Ramos-Madrigal et al., 2019). These capture probes target informative genes involved in grape domestication and approximately 10,207 SNPs in the GrapeReSeq reference panel (Laucou et al., 2018; Le Paslier et al., 2019). Libraries (n = 55) were captured at 55 °C hybridisation temperature with two rounds of enrichment following the myBaits High Sensitivity Protocol v.5 (Daicel Arbor Biosciences) (Supplementary Methods 3.4). Sequencing reads from the pre-captured libraries were only utilised to screen for the preservation of grapevine DNA in the samples, while reads from the target enrichment libraries were used for population-level analyses, including Principal Component Analysis, relatedness analysis, and berry colour analysis.

2.5. Sequencing data processing

Palaeogenomic data were analysed following the bioinformatic methods and parameters established by Ramos-Madrigal et al. (2019) and Cohen et al. (2023) for ancient grapevine specimens. In brief, Illumina high-throughput short-read data were processed using the Paleomix v.1.3.7 pipeline (Supplementary Methods 3.5) (Schubert et al., 2014). The adapters and low-quality reads were clipped with AdapterRemoval 2.3.3 (Schubert et al., 2016). Reads longer than 25 base pairs were subsequently aligned to the grape nuclear reference genome 12X.v2 (Canaguier et al., 2017) using BWA v0.7.17, with seeding disabled to enhance the mapping sensitivity for aDNA reads (Schubert et al., 2012). Reads with mapping quality below 30 were removed with samtools and PCR duplicates were filtered out using Picard MarkDuplicates. Using mapDamage2.0, the mapped reads were evaluated for length distribution and aDNA damage patterns (Jónsson et al., 2013). Archaeological samples showed increased C-to-T and G-to-A substitutions, along with short reads, consistent with aDNA characteristics (Dabney et al., 2013). MapDamage was also performed to rescale the quality of ancient sequence bases, enhancing mapping accuracy and reducing genotype calling due to aDNA damage. To explore the genetic diversity within the dataset, samples with a minimum average SNP coverage depth of 0.1× (n = 43) were included in Principal Component Analysis (PCA) using smartpca (Patterson et al., 2006), with SNPs called using samtools mpileup and processed through pileupCaller to generate haploid genotypes (Supplementary Methods 3.6). Only samples with a minimum average coverage of 8× (n = 32) were included in the relatedness analysis by KING (Manichaikul et al., 2010), and genotype calling was restricted to the SNP sites with a minimum depth of coverage of 10× by using GATK HaplotypeCaller. The degree of relatedness was based on the kinship coefficients and the proportion of sites with zero alleles identical by state (IBS0), categorising pairs into groups such as identical clones, closer than parent-offspring (through inbreeding), parent-offspring, highly related individuals (such as full siblings), or unrelated samples (Supplementary Methods 3.7).

2.6. Berry colour analysis

Genome-wide association analysis (GWAS) was used to investigate berry skin colour in 32 archaeological pips, following the methodologies proposed by Laucou et al. (2018) and Cohen et al. (2023). Their analysis identified that the signal for berry skin colour was on chromosome 2 between 9 and 19 Mbp. A reference dataset containing SNP genotypes of wild and cultivated grapevine samples was used (Laucou et al., 2018; Le Paslier et al., 2019). The dataset was filtered to generate phenotype data including four categories with known berry skin colour (white = 373, rose = 20, red = 24 and black = 311). The association between SNPs and phenotype data was tested using the –assoc function from PLINK v1.9. This produced an output file containing association results for each SNP, including p-values and effect sizes (BETA). SNPs were extracted based on their p-value <5E-08 (Supplementary Table S5). The genotype data for ancient grapevines was filtered to include 51 SNPs on chromosome 2. The selected SNPs were then used to calculate the polygenic score for archaeological samples using the –score option from PLINK v1.9. The scoring process calculates a weighted genetic score for each sample considering the effect size of the SNP, the ploidy of the sample (2 for grapes), the total number of alleles included in the analysis and the number of effective allele count in the sample (https://github.com/choishingwan/PRS-Tutorial.git).

To further evaluate the relationship between polygenic score and observed berry colour in a statistical framework, Bayesian regression model was conducted using brms package in R (Bürkner, 2017, 2021). The modern grapevine dataset was restricted to retain only samples categorised as “White”, “Rose”, “Red” and “Black” in the GrapeReSeq database (i.e., 16 varieties recorded as “Black-Red”, “Grey”, or “White-Rose” were excluded from the regression, as were 10 accessions listed as an “Unknown” berry colour). Berry colour was treated as a categorical response variable, with “White” berry colour set as the reference level. The polygenic score was standardised using mean = 11.74 and standard deviation = 15.54 calculated from the training dataset. The model was fitted using a categorical likelihood with a logit link function. The model was estimated using Markov Chain Monte Carlo (MCMC) sampling with 4 chains, each consisting of 2000 iterations, including 1000 warm-up iterations (Bürkner, 2021). For each sample, the model was used to estimate the probability of belonging to each berry colour category: white, rose, red and black. These probabilities were calculated by averaging predictions across all iterations of the model (Supplementary Table S6).

2.7. Modern DNA reference panel

The GrapeReSeq panel was used as a reference database to evaluate the genetic relationships between archaeological grape seeds and modern-day varieties. This panel was designed specifically for

genotyping *Vitis* species to preserve genetic diversity (https://urgi.versailles.inra.fr/Species/Vitis/GrapeReSeq_Illumina_20K) (Laucou et al., 2018). It contains 783 modern grape cultivars (*V. vinifera subsp. vinifera)* and 112 wild grape varieties (*V. vinifera subsp. sylvestris*). These cultivars were genotyped on 10,207 SNP sites, which are informative regarding the ancestry of domesticated grape varieties. Genotype data for the domesticated varieties (https://doi.org/10.15454/1.4861359557068474E12) and wild varieties (https://doi.org/10.15454/9RUCEP) were sourced from the INRA-Dataverse repository (Laucou et al., 2018; Le Paslier et al., 2019; Ramos-Madrigal et al., 2019). Passport data, including information on the VIVC ID, the colour of berry skin, and the variety of origin for both cultivated and wild grapes, is accessible in the VIVC database (http://www.vivc.de/). In this study, the reference dataset was used for SmartPCA, relatedness, and berry colour analysis.

3. Results and discussion

3.1. Ancient DNA preservation

Shotgun sequencing was performed on 80 archaeological grape seeds excavated from Well #1 and Well #2 in Cetamura del Chianti (Fig. 2). Of

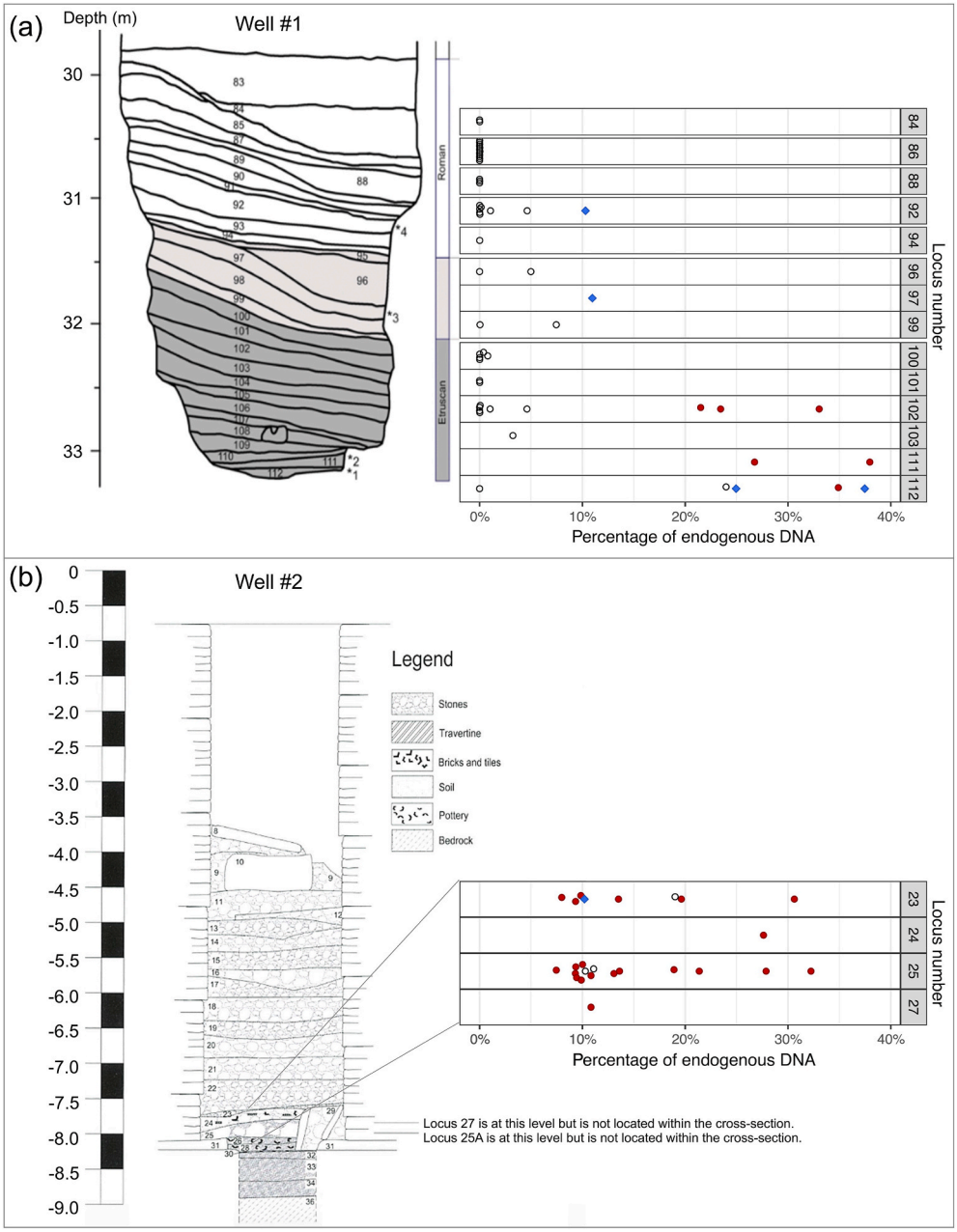

Fig. 2. Endogenous content of grape seeds across stratigraphic sections of the wells at Cetamura del Chianti. Clonal pips are represented by red circles, non-clonal pips represented by blue diamonds and other samples represented by white circles (i.e., those with insufficient aDNA data for relatedness analysis). Samples have been placed within a locus panel using the beeswarm package (Eklund and Trimble, 2021) to improve visualisation of each data point (i.e. vertical placement within a locus panel does not reflect the physical position in the stratigraphic layer). **(a)** Well #1: Sediment layers at depths of 30 to 33 m with loci designated as follows: Loci 83–94 correspond to the Roman period, Loci 95–99 date to the Transitional Etruscan-Roman period and Loci 100–112 are Etruscan (image modified from Mariotti Lippi et al., 2020) **(b)** Well #2: Sediment layers at approximately 9 m depth, with pips identified in Loci 23–27, all corresponding to the Roman Empire (image modified from de Grummond, 2017). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

the 80 seeds, 43 had more than 1% endogenous DNA (grape DNA) and were subjected to target enrichment of 10,207 single nucleotide polymorphism (SNP) loci (Supplementary Table S2). A further nine seeds with <1% were also enriched for control purposes. Of the libraries which underwent sequence enrichment, the depth of coverage on the targeted SNPs was 0–269× (mean = 34×). The DNA damage patterns and read length distribution were consistent with those expected for aDNA, with an average read length of 62 bp (Supplementary Table S2; Supplementary Fig. S1a/b and S2a/b).

3.2. Correlation between endogenous content and other metrics

The highly variable amounts of endogenous content in the Cetamura pips provided an opportunity to explore patterns in preservation within the site and whether the proportion of grapevine DNA correlated with other metrics (see detailed discussions in Supplementary Section 1.5). Such correlations could provide a baseline for preferentially selecting samples for genomic studies at Cetamura and other sites to conserve resources and avoid the destruction of archaeobotanical samples which are unlikely to contain sufficient DNA for genome-wide analyses. The first and simplest approach, visual inspection of seed photographs, did not yield consistent patterns between endogenous content and seed colour or integrity (Fig. 3, Supplementary Fig. S3). Similarly, no patterns were found for grape DNA content and the mass of the seed (Fig. S4). In contrast to the visual appearance or mass, DNA preservation varied by stratigraphic layer (Fig. 2), with higher levels of endogenous content at the bottom of both wells, emphasising the role that sediment depth and the associated environmental conditions play in preserving aDNA, with deeper layers potentially providing a more stable environment that protects DNA from degradation over time. Similarly, analysis of NIR data showed clustering of samples by endogenous DNA content (Fig. 4), suggesting that non-destructive testing of light absorption at different wavelengths may be able to identify pips with >5% endogenous DNA content. It is important to note that NIR is almost certainly not directly measuring DNA, but rather gives an indication of organic preservation. Expanded testing of NIR in other contexts will help determine its reliability, but these observations suggest that careful selection of archaeobotanical remains from specific deposits or refined NIR-testing may provide a means to focus resources on the most promising material for genomic research.

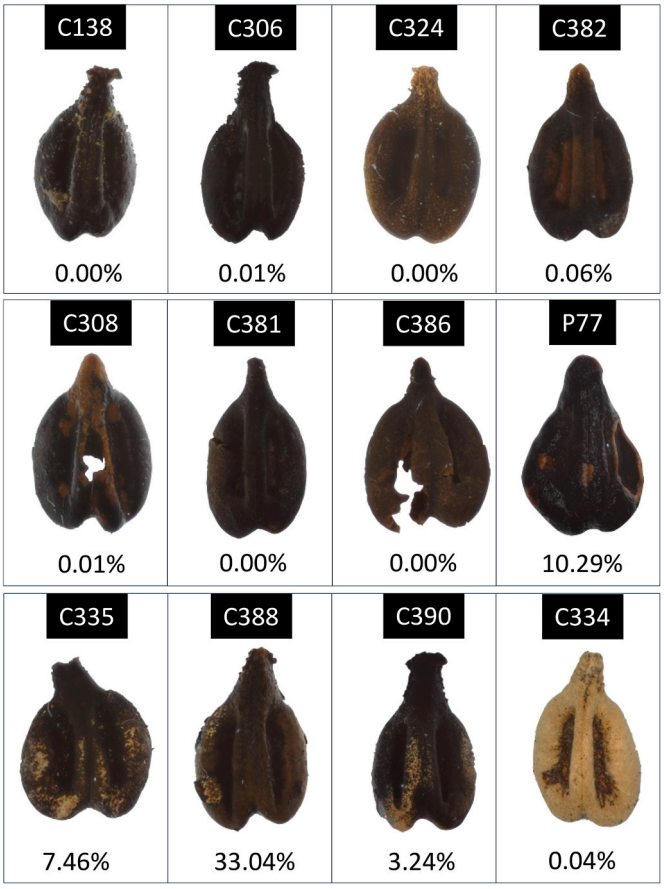

Fig. 3. Representative images of Cetamura pips and corresponding endogenous content. Each row corresponds to seeds categorised as intact, broken or damaged. The background has been removed from the images, and the seeds have been scaled to the same size for visual consistency, which does not reflect the differences in their actual size. A manual comparison of the seed images showed no consistent patterns between the proportion of endogenous DNA and whether a seed is intact, broken, or damaged. See Supplementary Fig. S3a and S3b for all photographed seeds from Well #1 and Well #2.

3.3. Identification of an enduring variety at Cetamura

Following targeted enrichment, 32 archaeological grape seeds from Cetamura yielded sufficiently high depth of coverage on SNP sites for inclusion in the relatedness analysis. Analysis of called genotypes with KING (Manichaikul et al., 2010) revealed that 27 seeds correspond to a single one clonal group (Fig. 5, see Supplementary Table S3). The domination of the assemblage by one clonal lineage may be unexpected, but the data are robust as specimens were identified using the various permutations of lab methodologies (i.e., processing of both half and full seeds, extraction in separate aDNA laboratories, multiple library protocols, with and without UDG treatment and sequencing at multiple facilities) and the genotype calls are based on well-characterised SNP loci (mean = 58.1×, range = 8.9–269×).

To establish a timeline for the presence and continuity of this predominant grape variety at Cetamura, direct AMS dating was conducted on four seeds identified as part of the clonal lineage (Fig. 5, Supplementary Table S1, Supplementary Table S4, Supplementary Fig. S5). Small archaeobotanical remains have the potential to move through bioturbation and other site formation processes, and therefore, AMS dating can help confirm the age of individual specimens. Sample C398 (2599 ± 30 BP) falls within the Villanovan/Orientalising period between 818 and 674 BCE. Sample C387, with a reading of 2295 ± 29 BP, dates to between 406 and 211 BCE, placing it in the Middle/Late Etruscan. Sample P3 (1943 ± 29 BP) is dated to 26 BCE–203 CE, and sample P17 (1877 ± 29 BP) corresponds to 83–235 CE, aligning with the Roman period. The results show the longevity of this clonal group from the Villanovan/Orientalising period (818–674 BCE) through to the Roman period (83–235 CE).

It is important to note that the earliest clonal sample, pip C398 (818-674 BCE), has an unexpectedly early age given the established chronology at Cetamura. The seed was recovered from the bottom of Well #1 where artefacts and one other radiocarbon date suggests an age of 300 BCE, with no other evidence of habitation at Cetamura as early as the 9th century BCE. Thus, while C398 may mark the earliest possible instance of grape cultivation at the site, the radiocarbon measurement may be erroneous. Excluding the potentially anomalous C398 date, Bayesian analysis of three remaining pips yields a minimum time span of 362 years (calculated in OxCal v4.4.4 using a 95.4% confidence level). When including the 23 additional clonal pips from earlier and later strata, the chronology provides compelling evidence for centuries of maintenance of the Cetamura clonal lineage.

3.4. Genetic relationships between Cetamura grapevines and modern varieties

The modern reference panel provides information on wild and domesticated grapevines, and projecting ancient samples (n = 43) onto that diversity allows for inferences on wild/domesticated status. Seed

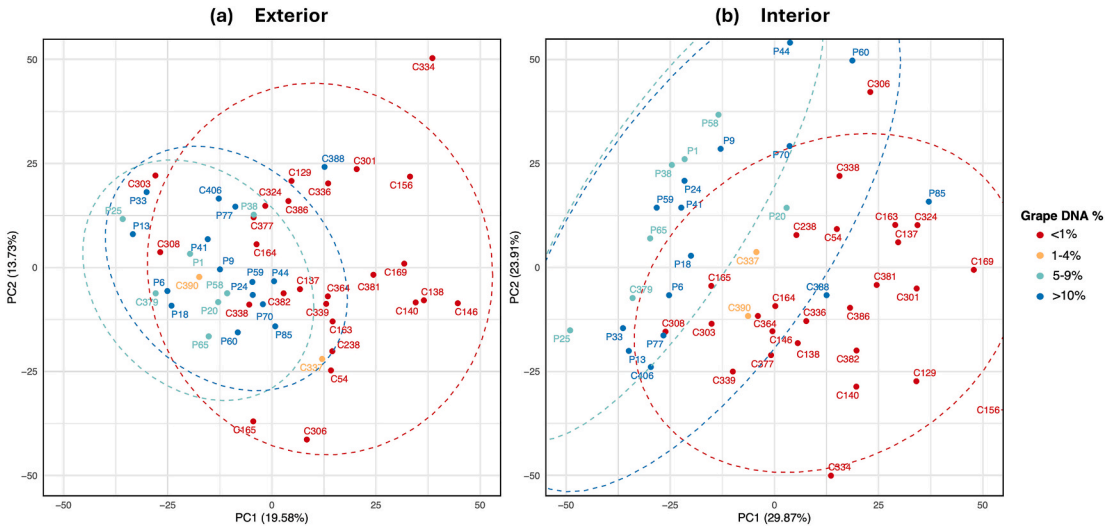

Fig. 4. Principal Component Analysis (PCA) of Near-Infrared Reflectance (NIR) spectroscopy data from 50 archaeological grape seeds from Cetamura. Spectra were collected from each seed's exterior (a) and interior (b) surfaces. Seeds are colour-coded based on the percentage of grapevine DNA. The ellipses represent 95% confidence intervals for groups with sufficient data points. No ellipse is shown for seeds with 1–4% DNA due to the limited number of samples. Note that pips with >5% endogenous DNA largely segregate from pips with <1% endogenous DNA, especially for the interior surface. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

C402 falls near the wild populations but moves to Western and Central European wine grapes in the PCA analysis when only domesticated grapes are considered, suggesting a possible gene flow from local wild populations into some domesticated varieties. Another noteworthy outlier in the PCA is seed C335, which shows closer affinity to wine grapes from the Balkans. Although the data is dominated by the Cetamura clonal group (and four additional pips–C297, C390, P6, and P41–that cluster with the clonal group but did not have sufficient SNP coverage for the kinship analysis), our study also shows substantial genetic diversity among varieties present at the site. This diversity is particularly evident in samples C406, C389, C337, and C379 from the Late Etruscan period (Fig. 6). The presence of diverse varieties alongside the clonal group indicates that Late Etruscan viticulture was not only characterised by the consistent propagation of a dominant variety but also by the cultivation of multiple distinct types of grapes, most of them being associated with Western and Central European wine grapes, as well as other domesticated varieties. This diversity also reflects a dynamic approach to viticulture, with different varieties potentially being selected for specific uses such as wine production or adaptation to local environmental conditions.

New varieties were evidenced at the site during the Transitional Etruscan-Roman period (ca. 100-50 BCE). The PCA analysis of samples C335, C328, C325, and C299 indicates that these varieties have a distinct genetic profile compared to those of the earlier Etruscan varieties. For example, C335 plots near to modern Balkan varieties, suggesting movement of vines from eastern regions of the Roman world. The presence of these new varieties alongside the existing Etruscan grapes suggests the integration of local practices with new varieties introduced from afar. This introduction diversified the genetic pool at the site and likely contributed to the development of varied wine profiles, which may have aligned with changing tastes. The process of diversification and integration played an important role in shaping the biodiversity of grapevines that grow across Europe today, highlighting the lasting impact of Etruscan and Roman agricultural practices on viticulture. It is necessary to note that while there is evidence for new introductions, it is also possible that some newly identified varieties existed during the Etruscan period but were not detected due to missing varieties in our dataset.

3.5. Geometric morphometric (GMM) analysis and comparison to inferences from DNA

Of the 71 pips characterised by GMM, 59 (83.1%) were classified as domesticated and 12 (16.9%) were classified as wild, indicating the presence of both cultivated and wild-like morphologies at Cetamura (Supplementary Table S1). Due to the experimental design, most seeds tested with GMM were also tested for DNA, facilitating a comparison of GMM and genetic results for 39 pips. Within this set of 39 pips, GMM identified 4 wild pips, yet DNA testing indicated that all pips belonged to domesticated vines. This incongruence could be due to known limitations of GMM, such as the retention of some wild morphological traits in domesticated lineages, potentially reflecting an early stage of domestication or the persistence of wild-type characteristics within cultivated populations (Bonhomme et al., 2021; Haile et al., 2023; Bouby et al., 2024).

Despite the apparent incongruence between the GMM and DNA results, it is also worth highlighting that GMM provided assessments for 32 pips where DNA data was insufficient to infer domestication status. For these, GMM found a significant number of apparently wild pips (25% of this subset). While one could again argue that some pips originate from domesticated vines with wild-like features, it is equally plausible that wild berries were collected by humans or deposited by other animals, and due to smaller seeds or different processing of the berries, less DNA survived to the present. One could also consider if wild grapevine remains may have entered the well via a different path than the domesticated pips, with the precise taphonomic history impacting DNA preservation. For example, wild seeds digested by birds could have much lower endogenous DNA content than domesticated seeds discarded after pressing for wine. Environmental conditions such as temperature, humidity, and soil acidity accelerate DNA degradation over time, and the inherent characteristics of the seeds play an important role (Naef et al., 2023). For instance, seeds with thinner seed coats, which are often found in wild species, may provide less protection against environmental factors, making their DNA more susceptible to degradation (Souza and Marcos-Filho, 2001).

Further classification within GMM and aDNA analyses provides additional insights into the diversity of domesticated grapes. Using an LDA approach with a reference panel of four well-defined regional groups, GMM classified the 35 putatively domesticated pips to three

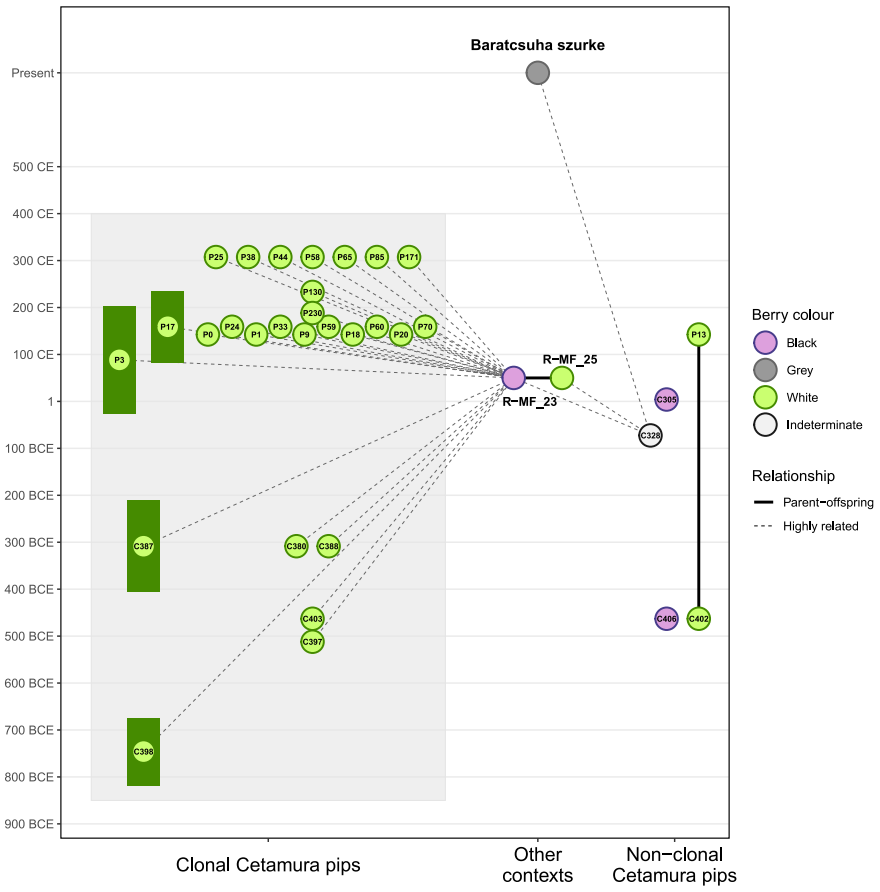

Fig. 5. Genetic relationship and predicted berry colours of archaeological grape pips. Thirty-two Cetamura seeds are plotted by their chronological age, based upon direct or associated radiocarbon dates. Four clonal Cetamura pips with direct AMS dates are presented with a vertical bar representing the age range of the calibrated date (95.4% confidence interval). Twenty-six other Cetamura pips are displayed as the midpoint of the radiocarbon range from grape pips in the associated stratigraphic layer. Two Cetamura pips (P130 and P230) originate from layers without a radiocarbon date and are placed in a representative location based on the dates of neighbouring stratigraphic layers. Two archaeological seeds from the Roman site of Mont Ferrier date to the first century CE. The modern variety 'Baratcsuha szurke' is shown at the top of the chronology with a time gap (time interval is not drawn to scale). Parent-offspring and "highly-related" (e.g. sibling or similar) relationships are shown with connecting lines. Note that clonal connections are not displayed in the figure, however, all 351 pairwise combinations of the 27 Cetamura clonal pips were independently detected as having an identical genotype (Table S3). Colours indicate inferred berry colour for archaeological pips and the known grey berry colour of 'Baratcsuha szurke'. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

groups: 26 pips as Western and Central European varieties used in winemaking, 6 pips as Balkan varieties used for wine, and 3 pips as table grapes (Supplementary Table S1). Utilising a PCA approach and allowing for an "other domesticated" category for admixed and geographically ambiguous varieties, the aDNA analysis found that only two of the Cetamura pips (C379 and C337) fall well within the PCA space defined by Western and Central European wine grapes (Fig. 6b); all other Cetamura pips align with the "other domesticated" category in the PCA space.

3.6. Genetic relatedness analyses between ancient samples and modern varieties

Relatedness analyses were conducted to investigate genetic relationships within the Cetamura grape varieties (818 BCE–381 CE), between archaeological grapevine samples from Cetamura and French grapevines (510 BCE–1200 CE) (Ramos-Madrigal et al., 2019), and between Cetamura and modern grape varieties in the GrapeReSeq panel. Kinship coefficients and the proportion of IBS0 sites were computed using KING (Manichaikul et al., 2010).

Within the Cetamura pips, our results showed a parent-offspring relationship between sample C402 (540–386 BCE) and P13 (26 BCE–311 CE), providing another example of related lineages separated by centuries. At present it is not possible to determine if this connection represents a local lineage that was allowed to sexually reproduce or if either variety may have been widespread in Etruscan or Roman sites. The seeds C406 and C305 were identified as unique genotypes, with no genetic relationship detected between them and the other ancient or modern varieties analysed in this study.

For the archaeological French samples, genetic connections were identified between Cetamura pips and two samples excavated from a 1st century CE context at a Roman farm at Mont Ferrier, Tourbes (Supplementary Fig. S6). The Cetamura clonal group and pip C328 (Transitional Etruscan-Roman) were found to be highly related (full sibling or similar relationship) to R-MF_23. Cetamura pip C328 was additionally found to be highly related to R-MF_25. These findings provide direct genetic evidence of the magnitude of Roman trade networks, ultimately leading to closely related vines being grown in different parts of the Empire. The propagation of genetically similar vines over such distances suggests deliberate viticulture involving selecting, transporting, and cultivating specific lineages. This exchange may have aimed to reproduce desirable grape traits or standardise wine production across regions. However, it remains unclear whether these reflect frequent trade or occasional transfers. Further research is needed to understand the scale and motivations behind these interactions.

Only one genetic connection was found between an archaeological

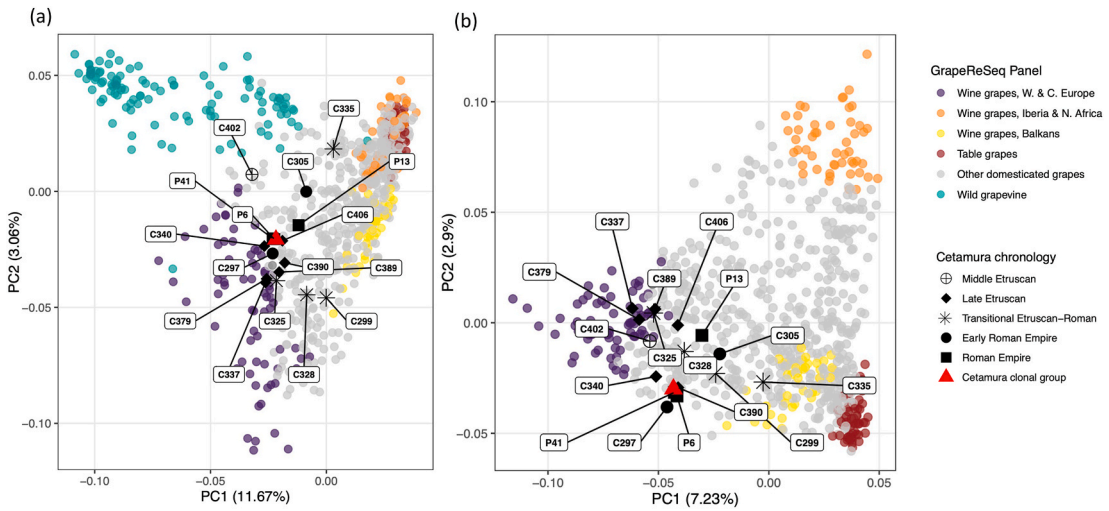

Fig. 6. Principal Component Analysis (PCA) of genetic relationships among archaeological grape seeds and modern *Vitis vinifera* accessions. The colours represent the main ancestry clusters identified in (Laucou et al., 2018), and archaeological samples are represented by different symbols based on Cetamura chronology. The "Other domesticated" group includes multi-use cultivars, cultivars of unknown use, and varieties with admixed ancestry, following the classification of Laucou et al. (2018). **(a)** The PCA plot displays wild *V. vinifera* subsp. *sylvestris*, domesticated varieties and archaeological samples, in which the clonal group was averaged and highlighted by a red triangle for clarity. **(b)** The PCA is redone using a restricted set of reference samples (only domesticated grapes) and archaeological samples. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

pip from Cetamura and a modern variety in the GrapeReSeq panel: sample C328 (162 BCE– 17 CE) and Hungarian variety 'Baratcsuha szurke' (GrapeReSeq ID: B00ER7R). The analysis showed a kinship coefficient of 0.184 and an IBS0 value of 0.025 across 6376 SNP sites, categorising the relationship as "highly related", which is compatible with a sibling or similar relationship. Tracing modern lineages of grapes is often challenging, in part due to language-specific variety names; however, there are indications that this modern variety has ancient roots. Within the VIVC database, 'Baratcsuha szurke' (VIVC 17431) is identified as a somatic mutation of Austrian variety 'Koelner Blau' (or 'Blauer Kölner', VIVC 6344), which in turn is identified having 121 synonyms. Within the 'Koelner Blau' clonal group, perhaps the most well known synonymous name is 'Žametovka', a Slovenian variety which is reported to have the oldest living vine, surviving over 400 years in the city of Maribor (Vršič et al., 2015). In short, these genetic data support a direct link between Cetamura and centuries-old vines from the wider region—largely corresponding to the Roman province of Pannonia—thereby supporting the hypothesis that Romans and later groups would perpetuate vines with few cycles of sexual reproduction.

3.7. Berry colour analysis

Berry colour is one of the most iconic and diverse traits in domesticated grapevine. While wild grapevines produce berries with dark skins (This et al., 2006), it is an open question when humans first identified and propagated vines with white berries. The earliest purported evidence for white berries in the archaeological record come from Middle and Late Bronze Age deposits at Sa Osa, Sardinia (associated calibrated ages ranging 1377–1088 BCE), where Ucchesu et al. (2015) used morphometric analysis to identify hundreds of archaeological pips with features found in modern pips from white berries. Even though berry colour is not considered to have been an initial target of selection during domestication (Fournier-Level et al., 2010), the wide geographic spread of vines with white berries indicate these lineages may have been cultivated for millennia. Thus, the presence of white berries at Sa Osa during the Bronze Age is compatible with current understandings of the development of the domesticated grapevine. Nonetheless, this exciting inference solely relies on seed morphometric features, and as highlighted in this dataset in section 3.5, seed shape analyses can be incongruent with other results, potentially due to reference database biases.

Genetic testing of well preserved archaeological pips provides a way to examine the underlying pathways that lead to diverse berry colours are caused by mutations in *VvMybA* genes (*VVMybA1–VVMYbA3*) (Fournier-Level et al., 2010; Laucou et al., 2018; Walker et al., 2007). Mutations in these regulatory genes encoding enzymes in the anthocyanin synthesis pathway determine whether anthocyanin accumulates sufficiently to produce dark berries or remains absent, as in white grapes (Gao et al., 2023; Walker et al., 2007; Yang et al., 2022). The best characterised mutation in this set of genes is the Gret1 retrotransposon in the promoter region of *VvMybA1* (Ferreira et al., 2018; Strioto et al., 2022). However, directly observing this insertion is difficult in ancient grapevine DNA datasets because aDNA is highly fragmented and retrotransposons with similar sequences are present in different parts of the genome (Kobayashi et al., 2004; Nakajima et al., 2023). While one might be able to identify DNA segments that span the Gret1 insertion site, this is still challenging in aDNA datasets, so an alternative approach has been developed which uses SNPs in *VvMybA1* that are correlated with berry colour. Building upon Cohen et al.'s (2023) approach to investigate berry colours from Byzantine pips, polygenic scores were calculated based on 51 SNPs associated with white (n = 370), rose (n = 20), red (n = 24) and black (n = 311) berry-coloured grapes from the reference dataset (Laucou et al., 2018; Le Paslier et al., 2019; Pain et al., 2022). Our analysis of archaeological grape seeds from Cetamura del Chianti suggests the presence of both black and white berry colours at the site (Fig. 5; Supplementary Fig. S7). Using a Bayesian regression modelling with the modern reference panel, the Cetamura clonal lineage was determined to have a 92.2% likelihood of yielding white berries (as represented by P60, a clonal pip with genotype data for all 51 SNPs, Supplementary Table S6). Two additional archaeological samples, C402 (Middle Etruscan) and P13 (Roman Empire), also display low polygenic scores, with 79.1% and 78.4% likelihood of white berries, respectively. C328 (Transitional Etruscan-Roman) presents an intermediate score, consistent with an equal probability of producing white or dark berries. In contrast, C406 (Late Etruscan) and C305 (Early Roman Empire) are most likely derived from dark-berried varieties, with likelihoods of 80.7% and 69.9%. While it is important to recognise the inherent uncertainty in polygenetic scores, especially for this trait in grapevine (i.e., 20.0% of modern varieties with white, red, rose or black berries are incorrectly predicted), these findings indicate that a range of berry

colours were present at Cetamura for centuries.

Although it is known that wine was a cherished commodity for the Etruscans (Dodd, 2022; Riva, 2018), these genetic inferences from archaeological seeds provides what is arguably the most concrete evidence for white berries, and therefore very likely white wine, in this time period. The inference of white wine is consistent with archaeological evidence from pre-Roman and Roman Italy, which indicates that grape processing commonly involved treading floors and vats, where grapes were crushed and the juice has been drained or be pressed under their own weight (Dodd, 2022). Even in cases where full separation of skins was not practised, the resulting wine would have been lighter or yellowish-orange colour compared to red wine (Van Limbergen and Komar, 2024). In addition to the insights at Cetamura, these positive results also encourage investigations of other archaeological pips to further refine our understanding of the timing of white berry cultivation. Of particular relevance is the assemblage from Sa Osa, where two waterlogged pips were previously found to have small amounts of endogenous DNA (Wales et al., 2016).

While the discovery of ancient white-berried grapevines may seem incongruous for a region renowned for its red wine, it is important to note that the winemaking traditions of Chianti are diverse and include the cultivation of white varieties. For example, in the 19th century, Barone Bettino Ricasoli's Chianti recipe traditionally blended 'Sangiovese' grapes with an indigenous white grapevine, 'Malvasia Bianca Lunga', to help soften the wine and make it suitable for daily consumption (George, 2011; Robinson et al., 2013). The blending of white berries in Chianti Classico wine was forbidden by 2006 regulations (George, 2011; Robinson et al., 2013), but white varieties continue to be cultivated in the region. Interestingly, neither 'Sangiovese' nor 'Malvasia Bianca Lunga' were found to have close genetic links with Cetamura del Chianti's archaeological pips. The lack of a connection between modern Chianti varieties and ancient lineages could reflect a shift in winemaking practices, driven by changing cultivation strategies and consumer preferences. Future studies with larger reference panels and expanded SNP datasets should provide opportunities to track nuanced developments of past grapevine cultivation as well as refine our understandings of complex phenotypes in archaeological contexts, including intermediate berry colours and flavours (Dong et al., 2023; Liu et al., 2024).

4. Conclusion

By integrating GMM, aDNA, NIR spectroscopy, and AMS dating, our study provides a detailed perspective of ancient viticulture at Cetamura del Chianti. With the most extensive genetic testing of grape pips from a single archaeological site, we find elements of continuity between Etruscan and Roman periods, with centuries of maintenance of a dominant grapevine variety that likely produced white berries. Following the Roman conquest of the settlement, new grapevine varieties appear at the site, hinting at the introduction of choice varieties from the expanding Roman Empire. Genetic connections between the long-lived Cetamura variety and a 1st century CE pip from Gaul provide further evidence of the wide-reaching agricultural network developed by the Romans. The ancient systems of grapevine management also laid the foundation for modern practices, demonstrated by a highly related genetic link between a transitional Etruscan-Roman Cetamura pip and a variety still grown in Central and Eastern Europe.

Methodologically, this work highlights the research value of multi-proxy investigations of archaeological grape pips. Complementary GMM and aDNA testing provided distinct avenues to recognise wild and domesticated lineages at Cetamura. The level of DNA preservation varied within the site, with higher levels of endogenous DNA in the lower reaches of the wells, suggesting stable, consistently waterlogged, anoxic conditions enabled DNA survival. The variation in endogenous content showed correlations with NIR spectra, suggesting this non-destructive tool may be able to identify archaeological seeds with better DNA preservation. Following similar multifaceted approaches on other archaeobotanical assemblages, we anticipate that significant steps can be made to understand ancient agricultural systems and their connections to the present.

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CRediT authorship contribution statement

Oya Inanli: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Visualization, Writing – original draft, Writing – review & editing. **Laurent Bouby:** Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Writing – review & editing. **Vincent Bonhomme:** Data curation, Formal analysis, Writing – review & editing. **Nancy de Grummond:** Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Resources, Writing – review & editing. **Lara González Carretero:** Investigation, Methodology, Writing – review & editing. **Roberto Bacilieri:** Investigation, Writing – review & editing. **Hannes Schroeder:** Funding acquisition, Supervision, Writing – review & editing. **Jazmín Ramos-Madrigal:** Conceptualization, Investigation, Methodology, Software, Writing – review & editing. **Nathan Wales:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Supervision, Visualization, Writing – original draft, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jas.2026.106605.

Data availability

Raw sequencing data (fastq) from the samples in this study are

publicly available on the European Nucleotide Archive under accession PRJEB89110.

References

Arandjelovic, M., Thalmann, O., 2012. Microsatellites in historic and ancient DNA. https://doi.org/10.1002/9780470015902.a0023631.

Aversano, R., Basile, B., Buonincontri, M.P., Carucci, F., Carputo, D., Frusciante, L., Di Pasquale, G., 2017. Dating the beginning of the Roman viticultural model in the Western mediterranean: the case study of Chianti (central Italy). PLoS One 12, e0186298. https://doi.org/10.1371/journal.pone.0186298.

Bolognesi, G., Latorre, A., Marini, M., Codato, A., Fontani, F., Saggioro, F., Luiselli, D., Basso, P., Cilli, E., Bellin, D., 2025. Optimizing ancient DNA recovery from archaeological plant seeds. Sci. Rep. 15, 36595. https://doi.org/10.1038/s41598-025-21743-7.

Bonhomme, V., Ivorra, S., Lacombe, T., Evin, A., Figueiral, I., Maghradze, D., Marchal, C., Pagnoux, C., Pastor, T., Pomarèdes, H., Bacilieri, R., Terral, J.-F., Bouby, L., 2021. Pip shape echoes grapevine domestication history. Sci. Rep. 11, 21381. https://doi.org/10.1038/s41598-021-00877-4.

Bouby, L., Bonhomme, V., Ivorra, S., Bacilieri, R., Ben Makhad, S., Bonnaire, E., Cabanis, M., Derreumaux, M., Dietsch-Sellami, M.F., Durand, F., Evin, A., Figueiral, I., Flottes, L., Hallavant, C., Jedrusiak, F., Lacombe, T., Marinval, P., Martin, L., Matterne, V., Pagnoux, C., Pastor, T., Pinaud, R., Pradat, B., Preiss, S., Ros, J., Rovira, N., Ruas, M.P., Schaal, C., Tillier, M., Toulemonde, F., Wiethold, J., Terral, J.F., 2024. Seed morphometrics unravels the evolutionary history of grapevine in France. Sci. Rep. 14, 22207. https://doi.org/10.1038/s41598-024-72692-6.

Bouby, L., Bonhomme, V., Ivorra, S., Pastor, T., 2023. Experimental waterlogging of grape seeds, impact on seed shape and geometrical reversing for morphometric inference. J. Archaeol. Sci. Rep 51, 104204. https://doi.org/10.1016/j.jasrep.2023.104204.

Bouby, L., Figueiral, I., Bouchette, A., Rovira, N., Ivorra, S., Lacombe, T., Pastor, T., Picq, S., Marinval, P., Terral, J.-F., 2013. Bioarchaeological insights into the process of domestication of grapevine (*Vitis vinifera* L.) during Roman times in Southern France. PLoS One 8, e63195. https://doi.org/10.1371/journal.pone.0063195.

Bouby, L., Ivorra, S., Terral, J.-F., 2017. Morphometric analysis of *Vitis* seeds from well #1 at Cetamura del Chianti: first results. In: de Grummond, N.T. (Ed.), Wells of Wonders. New Discoveries at Cetamura Del Chianti. Edifir Edizioni, Florence, pp. 289–293.

Briggs, A.W., Stenzel, U., Meyer, M., Krause, J., Kircher, M., Pääbo, S., 2010. Removal of deaminated cytosines and detection of in vivo methylation in ancient DNA. Nucleic Acids Res. 38, e87. https://doi.org/10.1093/nar/gkp1163.

Bürkner, P.-C., 2017. Brms: an R package for Bayesian multilevel models using Stan. J. Stat. Softw. 80. https://doi.org/10.18637/jss.v080.i01.

Bürkner, P.-C., 2021. Bayesian item response modeling in R with brms and stan. J. Stat. Softw. 100. https://doi.org/10.18637/jss.v100.i05.

Canaguier, A., Grimplet, J., Di Gaspero, G., Scalabrin, S., Duchêne, E., Choisne, N., Mohellibi, N., Guichard, C., Rombauts, S., Le Clainche, I., Bérard, A., Chauveau, A., Bounon, R., Rustenholz, C., Morgante, M., Le Paslier, M.-C., Brunel, D., Adam-Blondon, A.-F., 2017. A new version of the grapevine reference genome assembly (12X.v2) and of its annotation (VCost.v3). Genom. Data 14, 56–62. https://doi.org/10.1016/j.gdata.2017.09.002.

Carøe, C., Gopalakrishnan, S., Vinner, L., Mak, S.S.T., Sinding, M.H.S., Samaniego, J.A., Wales, N., Sicheritz-Pontén, T., Gilbert, M.T.P., 2018. Single-tube library preparation for degraded DNA. Methods Ecol. Evol. 9, 410–419. https://doi.org/10.1111/2041-210x.12871.

Cattonaro, F., Testolin, R., Scalabrin, S., Morgante, M., Gaspero, G.D., 2014. Genetic diversity in the grapevine germplasm. In: Genomics of Plant Genetic Resources, pp. 683–704. https://doi.org/10.1007/978-94-007-7572-5_27.

Choi, Y.J., Lampel, J., Fiedler, S., Jordan, D., Wagner, T., 2020. A new method for the identification of archaeological soils by their spectral signatures in the vis-NIR region. J. Archaeol. Sci. Rep 33, 102553. https://doi.org/10.1016/j.jasrep.2020.102553.

Cohen, P., Bacilieri, R., Ramos-Madrigal, J., Privman, E., Boaretto, E., Weber, A., Fuks, D., Weiss, E., Erickson-Gini, T., Bucking, S., Tepper, Y., Cvikel, D., Schmidt, J., Gilbert, M.T.P., Wales, N., Bar-Oz, G., Meiri, M., 2023. Ancient DNA from a lost Negev highlands desert grape reveals a late antiquity wine lineage. Proc. Natl. Acad. Sci. U. S. A. 120, e2213563120. https://doi.org/10.1073/pnas.2213563120.

Columella, 1941. On Agriculture, Volume I: Books 1-4, Loeb Classical Library. Harvard University Press, LOEB, Cambridge, MA.

Dabney, J., Meyer, M., Pääbo, S., 2013. Ancient DNA damage. Cold Spring Harb. Perspect. Biol. 5. https://doi.org/10.1101/cshperspect.a012567 a012567–a012567.

Dalby, A., 1998. Cato: on Farming—De Agricultura: a Modern Translation with Commentary. Prospect Books, London, UK.

Dalby, A., 2011. Geoponika—Farm Work: a Modern Translation of the Roman and Byzantine Farming Handbook (Introduction and Contents). Prospect Books, London.

de Grummond, N.T., 2017. Wells of Wonders: New Discoveries at Cetamura Del Chianti. Edifir, Florence.

de Grummond, N.T., 2018. Grape pips from Etruscan and Roman Cetamura del Chianti: on stratigraphy, literary sources and pruning hooks. Etruscan Stud. 21, 27–57. https://doi.org/10.1515/etst-2018-0013.

de Grummond, N.T., 2020. Cetamura Del Chianti, Cities and Communities of the Etruscans. University of Texas Press, Austin, TX.

Deckers, K., Riehl, S., Meadows, J., Tumolo, V., Hinojosa-Baliño, I., Lawrence, D., 2024. A history of olive and grape cultivation in Southwest Asia using charcoal and seed remains. PLoS One 19, e0303578. https://doi.org/10.1371/journal.pone.0303578.

Dodd, E., 2022. The archaeology of wine production in Roman and pre-Roman Italy. Am. J. Archaeol. 126, 443–480. https://doi.org/10.1086/719697.

Dong, Y., Duan, S., Xia, Q., Liang, Z., Dong, X., Margaryan, K., Musayev, M., Goryslavets, S., Zdunić, G., Bert, P.-F., Lacombe, T., Maul, E., Nick, P., Bitskinashvili, K., Bisztray, G.D., Drori, E., De Lorenzis, G., Cunha, J., Popescu, C.F., Arroyo-Garcia, R., Arnold, C., Ergül, A., Zhu, Y., Ma, C., Wang, S., Liu, S., Tang, L., Wang, C., Li, D., Pan, Y., Li, J., Yang, L., Li, X., Xiang, G., Yang, Z., Chen, B., Dai, Z., Wang, Y., Arakelyan, A., Kuliyev, V., Spotar, G., Girollet, N., Delrot, S., Ollat, N., This, P., Marchal, C., Sarah, G., Laucou, V., Bacilieri, R., Röckel, F., Guan, P., Jung, A., Riemann, M., Ujmajuridze, L., Zakalashvili, T., Maghradze, D., Höhn, M., Jahnke, G., Kiss, E., Deák, T., Rahimi, O., Hübner, S., Grassi, F., Mercati, F., Sunseri, F., Eiras-Dias, J., Dumitru, A.M., Carrasco, D., Rodriguez-Izquierdo, A., Muñoz, G., Uysal, T., Özer, C., Kazan, K., Xu, M., Wang, Y., Zhu, S., Lu, J., Zhao, M., Wang, L., Jiu, S., Zhang, Y., Sun, L., Yang, H., Weiss, E., Wang, S., Zhu, Y., Li, S., Sheng, J., Chen, W., 2023. Dual domestications and origin of traits in grapevine evolution. Science 379, 892–901. https://doi.org/10.1126/science.add8655.

Dougherty, P.H., 2012. Introduction to the Geographical Study of Viticulture and Wine Production. The Geography of Wine, pp. 3–36. https://doi.org/10.1007/978-94-007-0464-0_1.

Eklund, A., Trimble, J., 2021. The bee swarm plot, an alternative to stripchart. https://doi.org/10.32614/CRAN.package.beeswarm.

Ferreira, V., Pinto-Carnide, O., Arroyo-García, R., Castro, I., 2018. Berry color variation in grapevine as a source of diversity. Plant Physiol. Biochem. 132, 696–707. https://doi.org/10.1016/j.plaphy.2018.08.021.

Fournier-Level, A., Lacombe, T., Le Cunff, L., Boursiquot, J.-M., This, P., 2010. Evolution of the VvMybA gene family, the major determinant of berry colour in cultivated grapevine (*Vitis vinifera* L.). Heredity 104, 351–362. https://doi.org/10.1038/hdy.2009.148.

Gao, L., Wang, W., Li, H., Li, H., Yang, Y., Zheng, H., Tao, J., 2023. Anthocyanin accumulation in grape berry flesh is associated with an alternative splicing variant of VvMYBA1. Plant Physiol. Biochem. 195, 1–13. https://doi.org/10.1016/j.plaphy.2022.12.025.

George, R., 2011. Treading Grapes: Walking Through the Vineyards of Tuscany. Transworld Digital, London, England.

Goncalves, E., Martins, A., 2012. Genetic variability evaluation and selection in ancient grapevine varieties. In: Plant Breeding. InTech. https://doi.org/10.5772/27903.

Haile, Bewuketu, Tesfaye, Bizuayehu, Olango, Temesgen Magule, 2023. Fruit and seed morphological divergence between wild and cultivated enset (Ensete ventricosum [Welw.] Cheesman). S. Afr. J. Bot. 163, 87–94. https://doi.org/10.1016/j.sajb.2023.10.021. https://linkinghub.elsevier.com/retrieve/pii/S0254629923006221.

Harutyunyan, M., Malfeito-Ferreira, M., 2022. The rise of wine among ancient civilizations across the Mediterranean basin. Heritage 5, 788–812. https://doi.org/10.3390/heritage5020043.

Homet, P., Gallardo-Reina, M.Á., Aguiar, J.F., Liberal, I.M., Casimiro-Soriguer, R., Ochoa-Hueso, R., 2024. Viticulture and the European Union's common agricultural policy (CAP): historical overview, current situation and future perspective. J of Sust Agri & Env 3, e12099. https://doi.org/10.1002/sae2.12099.

Jónsson, H., Ginolhac, A., Schubert, M., Johnson, P.L.F., Orlando, L., 2013. mapDamage2.0: fast approximate Bayesian estimates of ancient DNA damage parameters. Bioinformatics 29, 1682–1684. https://doi.org/10.1093/bioinformatics/btt193.

Kapp, J.D., Green, R.E., Shapiro, B., 2021. A fast and efficient single-stranded genomic library preparation method optimized for ancient DNA. J. Hered. 112, 241–249. https://doi.org/10.1093/jhered/esab012.

Knapp, M., Clarke, A.C., Horsburgh, K.A., Matisoo-Smith, E.A., 2012. Setting the stage - building and working in an ancient DNA laboratory. Ann. Anat. 194, 3–6. https://doi.org/10.1016/j.aanat.2011.03.008.

Knapp, M., Lalueza-Fox, C., Hofreiter, M., 2015. Re-inventing ancient human DNA. Investig. Genet. 6, 4. https://doi.org/10.1186/s13323-015-0020-4.

Kobayashi, S., Goto-Yamamoto, N., Hirochika, H., 2004. Retrotransposon-induced mutations in grape skin color. Science 304, 982. https://doi.org/10.1126/science.1095011.

Kızıldeniz, T., Movila, M., Bettoni, M.M., Abdullateef, S., Candar, S., 2022. Grapevine propagation method with two temperature controlling process. Tekirdag Vitic Res Inst 2, 45–53. https://doi.org/10.52001/vis.2022.10.45.53.

Laucou, V., Launay, A., Bacilieri, R., Lacombe, T., Adam-Blondon, A.-F., Bérard, A., Chauveau, A., de Andrés, M.T., Hausmann, L., Ibáñez, J., Le Paslier, M.-C., Maghradze, D., Martinez-Zapater, J.M., Maul, E., Ponnaiah, M., Töpfer, R., Péros, J.-P., Boursiquot, J.-M., 2018. Extended diversity analysis of cultivated grapevine *Vitis vinifera* with 10K genome-wide SNPs. PLoS One 13. https://doi.org/10.1371/journal.pone.0192540.

Le Paslier, M.-C., Choisne, N., Bacilieri, R., Boursiquot, J.-M., Bras, M., Brunel, D., Chauveau, A., Hausmann, L., Lacombe, T., Laucou, V., Launay, A., Marchal, C., Martinez-Zapater, J.-M., Berard, A., Quesneville, H., Töpfer, R., Torres-Perez, R., Adam-Blondon, A.-F., 2019. A dataset of 9.896 single nuclear polymorphisms for 112 wild grapes, obtained with the GrapeReSeq 18K Vitis chip. https://doi.org/10.15454/9RUCEP.

Limier, B., Ivorra, S., Bouby, L., Figueiral, I., Chabal, L., Cabanis, M., Ater, M., Lacombe, T., Ros, J., Brémond, L., Terral, J.-F., 2018. Documenting the history of the grapevine and viticulture: a quantitative eco-anatomical perspective applied to modern and archaeological charcoal. J. Archaeol. Sci. 100, 45–61. https://doi.org/10.1016/j.jas.2018.10.001.

Liu, Z., Wang, N., Su, Y., Long, Q., Peng, Y., Shangguan, L., Zhang, F., Cao, S., Wang, X., Ge, M., Xue, H., Ma, Z., Liu, W., Xu, X., Li, C., Cao, X., Ahmad, B., Su, X., Liu, Y., Huang, G., Du, M., Liu, Z., Gan, Y., Sun, L., Fan, X., Zhang, C., Zhong, H., Leng, X., Ren, Y., Dong, T., Pei, D., Wu, X., Jin, Z., Wang, Y., Liu, C., Chen, J., Gaut, B., Huang, S., Fang, J., Xiao, H., Zhou, Y., 2024. Grapevine pangenome facilitates trait genetics and genomic breeding. Nat. Genet. 56, 2804–2814. https://doi.org/10.1038/s41588-024-01967-5.

Manichaikul, A., Mychaleckyj, J.C., Rich, S.S., Daly, K., Sale, M., Chen, W.-M., 2010. Robust relationship inference in genome-wide association studies. Bioinformatics 26, 2867–2873. https://doi.org/10.1093/bioinformatics/btq559.

Mariotti Lippi, M., Mori Secci, M., Giachi, G., Bouby, L., Terral, J., Castiglioni, E., Cottini, M., Rottoli, M., de Grummond, N., 2020. Plant remains in an Etruscan-Roman well at Cetamura del Chianti, Italy. Archaeol. Anthropol. Sci. 12, 1–18. https://doi.org/10.1007/s12520-019-00992-4.

Marvelli, S., Siena, S., Rizzoli, E., Marchesini, M., 2013. The origin of grapevine cultivation in Italy: the archaeobotanical evidence. Ann. bot. 3, 155–163. https://doi.org/10.4462/ANNBOTRM-10326.

Massicotte, P, South, A, 2026. rnaturalearth: World Map Data from Natural Earth. R package, version 1.2.0.9000. https://docs.ropensci.org/rnaturalearth/.

McGovern, P.E., 2019. Ancient Wine: the Search for the Origins of Viniculture, Princeton Science Library. Princeton University Press.

Mocarelli, L., Vaquero Piñeiro, M., 2019. Viniculture in the Italy of the Mezzadria (Tuscany, Umbria and Marche). In: Palgrave Studies in Economic History, pp. 227–251. https://doi.org/10.1007/978-3-030-27772-7_9.

Myles, S., Boyko, A.R., Owens, C.L., Brown, P.J., Grassi, F., Aradhya, M.K., Prins, B., Reynolds, A., Chia, J.-M., Ware, D., Bustamante, C.D., Buckler, E.S., 2011. Genetic structure and domestication history of the grape. Proc. Natl. Acad. Sci. U. S. A. 108, 3530–3535. https://doi.org/10.1073/pnas.1009363108.

Naef, T., Besnard, A.-L., Lehnen, L., Petit, E.J., van Schaik, J., Puechmaille, S.J., 2023. How to quantify factors degrading DNA in the environment and predict degradation for effective sampling design. Environ. DNA 5, 403–416. https://doi.org/10.1002/edn3.414.

Nakajima, I., Kawahigashi, H., Nishitani, C., Azuma, A., Haji, T., Toki, S., Endo, M., 2023. Targeted deletion of grape retrotransposon associated with fruit skin color via CRISPR/Cas9 in Vitis labrascana "Shine Muscat.". PLoS One 18, e0286698. https://doi.org/10.1371/journal.pone.0286698.

Nesto, B., Di Savino, F., 2016. Chianti Classico: the Search for Tuscany's Noblest Wine. University of California Press.

Noraz, R., Chauvey, L., Wagner, S., Estrada, O., Wales, N., Bonnaire, E., Cabanis, M., Derreumaux, M., Figueiral, I., Hallavant, C., Marinval, P., Matterne, V., Ros, J., Rovira, N., Tillier, M., Bovagne, M., Chausserie-Laprée, J., Nicolas, C., Daveau, I., Delassus, D., Gailledrat, E., Ginouvez, O., Houix, B., Jung, C., Kuchler, P., Leroux, L., Macario, R., Marlière, E., Pasqualini, M., Piques, G., Pomaredes, H., Robert, J., Roms, C., Roth-Zehner, M., Scrinzi, M., Taras-Thomas, M., Torres Costa, J., Besnard, G., Terral, J.-F., Bacilieri, R., Bouby, L., Orlando, L., 2026. Ancient DNA reveals 4000 years of grapevine diversity, viticulture and clonal propagation in France. Nat. Commun. 17, 2494. https://doi.org/10.1038/s41467-026-70166-z.

Pain, O., Gillett, A.C., Austin, J.C., Folkersen, L., Lewis, C.M., 2022. A tool for translating polygenic scores onto the absolute scale using summary statistics. Eur. J. Hum. Genet. 30, 339–348. https://doi.org/10.1038/s41431-021-01028-z.

Patterson, N., Price, A.L., Reich, D., 2006. Population structure and eigenanalysis. PLoS Genet. 2, e190. https://doi.org/10.1371/journal.pgen.0020190.

Pecci, A., Borgna, E., Mileto, S., Dalla Longa, E., Bosi, G., Florenzano, A., Mercuri, A.M., Corazza, S., Marchesini, M., Vidale, M., 2020. Wine consumption in Bronze Age Italy: combining organic residue analysis, botanical data and ceramic variability. J. Archaeol. Sci. 123, 105256. https://doi.org/10.1016/j.jas.2020.105256.

Phillips, R., 2001. A Short History of Wine. Penguin Books, Harlow,England.

Portillo, M., Ball, T.B., Wallace, M., Murphy, C., Pérez-Díaz, S., Ruiz-Alonso, M., Aceituno, F.J., López-Sáez, J.A., 2020. Advances in morphometrics in archaeobotany. Environ. Archaeol. 25, 246–256. https://doi.org/10.1080/14614103.2019.1569351.

Poulsen, F., 1922. Etruscan Tomb Paintings: Their Subjects and Significance. Clarendon Press, Oxford, England.

R Core Team, 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Ramos-Madrigal, J., Runge, A.K.W., Bouby, L., Lacombe, T., Samaniego Castruita, J.A., Adam-Blondon, A.-F., Figueiral, I., Hallavant, C., Martínez-Zapater, J.M., Schaal, C., Töpfer, R., Petersen, B., Sicheritz-Pontén, T., This, P., Bacilieri, R., Gilbert, M.T.P., Wales, N., 2019. Palaeogenomic insights into the origins of French grapevine diversity. Nat. Plants 5, 595–603. https://doi.org/10.1038/s41477-019-0437-5.

Riva, C., 2018. Wine production and exchange and the value of wine consumption in sixth-century BC Etruria. J. Mediterr. Archaeol. 30, 237–261. https://doi.org/10.1558/jmea.35407.

Robinson, J., Harding, J., Vouillamoz, J., 2013. Wine Grapes: a Complete Guide to 1,368 Vine Varieties, Including Their Origins and Flavours. Penguin UK.

Schubert, M., Ermini, L., Der Sarkissian, C., Jónsson, H., Ginolhac, A., Schaefer, R., Martin, M.D., Fernández, R., Kircher, M., McCue, M., Willerslev, E., Orlando, L., 2014. Characterization of ancient and modern genomes by SNP detection and phylogenomic and metagenomic analysis using PALEOMIX. Nat. Protoc. 9, 1056–1082. https://doi.org/10.1038/nprot.2014.063.

Schubert, M., Ginolhac, A., Lindgreen, S., Thompson, J.F., Al-Rasheid, K.A.S., Willerslev, E., Krogh, A., Orlando, L., 2012. Improving ancient DNA read mapping against modern reference genomes. BMC Genom. 13, 178. https://doi.org/10.1186/1471-2164-13-178.

Schubert, M., Lindgreen, S., Orlando, L., 2016. AdapterRemoval v2: rapid adapter trimming, identification, and read merging. BMC Res. Notes 9, 88. https://doi.org/10.1186/s13104-016-1900-2.

Sciuto, C., Cantini, F., Chapoulie, R., Cou, C., De la Codre, H., Gattiglia, G., Granier, X., Mounier, A., Palleschi, V., Sorrentino, G., Raneri, S., 2022. What lies beyond sight? Applications of ultraportable hyperspectral imaging (VIS-NIR) for archaeological fieldwork. J. Field Archaeol. 47, 522–535. https://doi.org/10.1080/00934690.2022.2135066.

Souza, F.H.D.D.E., Marcos-Filho, J., 2001. The seed coat as a modulator of seed-environment relationships in Fabaceae. Rev. Bras. Bot. 24, 365–375. https://doi.org/10.1590/s0100-84042001000400002.

Stavrakaki, M., Bouza, D., Biniari, K., 2020. Differentiation of Greek grapevine cultivars (Vitis vinifera L.) based on the combination of ampelographic description and microsatellite markers. Genet. Resour. Crop Evol. 67, 21–40. https://doi.org/10.1007/s10722-019-00860-z.

Strioto, D.K., Mangolin, C.A., de Oliveira Collet, S.A., das Neves, A.F., Cantagalli, L.B., Machado, M. de F.P.S., 2022. *Gret1* retrotransposon and *VvmybA1* gene sequences in somatic mutants of new table grape varieties "Brasil" and –Black Star' (*Vitis vinifera* L.). Ciênc. téc. vitiviníc. 37, 71–78. https://doi.org/10.1051/ctv/ctv2022370171.

Stubert, L., Martín i Oliveras, A., Märker, M., Schernthanner, H., Vogel, S., 2020. Viticulture in the Laetanian region (Spain) during the Roman period: predictive modelling and geomatic analysis. Geosciences 10, 206. https://doi.org/10.3390/geosciences10060206.

Stummer, A., 1911. Zur Urgeschichte der Rebe und des Weinbaues. Mitt. Anthropol. Ges. Wien 61, 283–296.

Terral, J.-F., Tabard, E., Bouby, L., Ivorra, S., Pastor, T., Figueiral, I., Picq, S., Chevance, J.-B., Jung, C., Fabre, L., Tardy, C., Compan, M., Bacilieri, R., Lacombe, T., This, P., 2010. Evolution and history of grapevine (Vitis vinifera) under domestication: new morphometric perspectives to understand seed domestication syndrome and reveal origins of ancient European cultivars. Ann. Bot. 105, 443–455. https://doi.org/10.1093/aob/mcp298.

This, P., Lacombe, T., Thomas, M.R., 2006. Historical origins and genetic diversity of wine grapes. Trends Genet. 22, 511–519. https://doi.org/10.1016/j.tig.2006.07.008.

Ucchesu, M., Orrù, M., Grillo, O., Venora, G., Usai, A., Serreli, P.F., Bacchetta, G., 2015. Earliest evidence of a primitive cultivar of Vitis vinifera L. during the Bronze Age in Sardinia (Italy). Veg. Hist. Archaeobot. 24, 587–600. https://doi.org/10.1007/s00334-014-0512-9.

Van Limbergen, D., Komar, P., 2024. Making wine in earthenware vessels: a comparative approach to Roman vinification. Antiquity 98, 85–101. https://doi.org/10.15184/aqy.2023.193.

Vršič, S., Ivančič, A., Šušek, A., Zagradišnik, B., Valdhuber, J., Šiško, M., 2015. The World's oldest living grapevine specimen and its genetic relationships. Vitis 50. https://doi.org/10.5073/VITIS.2011.50.167-171, 167–167.

Wales, N., Andersen, K., Cappellini, E., Avila-Arcos, M.C., Gilbert, M.T.P., 2014. Optimization of DNA recovery and amplification from non-carbonized archaeobotanical remains. PLoS One 9, e86827. https://doi.org/10.1371/journal.pone.0086827.

Wales, N., Carøe, C., Sandoval-Velasco, M., Gamba, C., Barnett, R., Samaniego, J.A., Madrigal, J.R., Orlando, L., Gilbert, M.T.P., 2015. New insights on single-stranded versus double-stranded DNA library preparation for ancient DNA. Biotechniques 59, 368–371. https://doi.org/10.2144/000114364.

Wales, N., Ramos Madrigal, J., Cappellini, E., Carmona Baez, A., Samaniego Castruita, J. A., Romero-Navarro, J.A., Carøe, C., Ávila-Arcos, M.C., Peñaloza, F., Moreno-Mayar, J.V., Gasparyan, B., Zardaryan, D., Bagoyan, T., Smith, A., Pinhasi, R., Bosi, G., Fiorentino, G., Grasso, A.M., Celant, A., Bar-Oz, G., Tepper, Y., Hall, A., Scalabrin, S., Miculan, M., Morgante, M., Di Gaspero, G., Gilbert, M.T.P., 2016. The limits and potential of paleogenomic techniques for reconstructing grapevine domestication. J. Archaeol. Sci. 72, 57–70. https://doi.org/10.1016/j.jas.2016.05.014.

Wales, N., Ramos-Madrigal, J., Gilbert, M.T.P., 2017. Ancient DNA analysis of Vitis seeds from Cetamura del Chianti: current results. In: Wells of Wonders: New Discoveries at Cetamura Del Chianti. Edifir, Florence, pp. 294–302.

Wales, N., Kistler, L., 2019. Extraction of ancient DNA from plant remains. In: Shapiro, B., Barlow, A., Heintzman, P.D., Hofreiter, M., Paijmans, J.L.A., Soares, A.E. R. (Eds.), Ancient DNA: Methods and Protocols. Springer, New York, pp. 45–55. https://doi.org/10.1007/978-1-4939-9176-1_6.

Walker, A.R., Lee, E., Bogs, J., McDavid, D.A.J., Thomas, M.R., Robinson, S.P., 2007. White grapes arose through the mutation of two similar and adjacent regulatory genes: white grape genes. Plant J. 49, 772–785. https://doi.org/10.1111/j.1365-313X.2006.02997.x.

Yang, Y., Ke, J., Han, X., Wuddineh, W.A., Song, G.-Q., Zhong, G.-Y., 2022. Removal of a 10-kb Gret1 transposon from VvMybA1 of Vitis vinifera cv. Chardonnay. Hortic. Res. 9. https://doi.org/10.1093/hr/uhac201 uhac201.