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Reviving grapevine massal selection in the context of climate change: A strategy for resilient vineyards in the 21st century

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ABSTRACT

For centuries, grapevine improvement relied primarily on massal selection, a practice in which growers identified and vegetatively propagated individuals with targeted phenotypic traits within vineyard populations of a given variety. Through repeated cycles of observation and multiplication, this empirical process generated populations according to production objectives that formed the foundation of early directed selection for wine production. In the 20th century, clonal and sanitary selection emerged as a decisive advance, delivering uniformity, health status, in particular with regard to viral diseases, and greater consistency in propagation material. Nevertheless, the widespread adoption of a narrow set of certified clones has led to significant genetic erosion, reducing the capacity of vineyards to buffer environmental fluctuations, adapt to climate change and resist existing or emerging diseases and pests. Despite this evidence, a persistent perception remains that massal selections may offer complementary advantages over clonal material. This review synthesises the historical trajectory of grapevine domestication and the emergence of modern varieties, the mechanisms underlying intra-varietal variation, including somatic mutations, epigenetic modifications, and virome composition, and the consequences of clonal standardisation on genetic diversity. Drawing on palaeogenomic, phenotypic and molecular evidence, it suggests that massal populations can serve as dynamic genetic reservoirs, preserving rare alleles, structural variants and adaptive trait combinations that may be lost in clonal systems. Recent studies reveal that even within certified clonal collections, substantial exploitable variation persists, with moderate to high heritability and strong genotype-by-environment interactions enabling resilience under present and projected conditions. The strategic revalorisation of massal selection, supported by high-throughput genotyping, metagenomics and precision tools, emerges as a powerful strategy to enhance viticultural competitiveness. By maintaining diverse populations that distribute risk across genotypes, epigenotypes and viromes, massal approaches may contribute to more stable yields, improved stress tolerance and sustained terroir expression without altering varietal identity. This review argues that the strategic co-existence of clonal and massal selection represents the ultimate expression of precision viticulture, allowing diverse populations to be matched to specific terroirs for enhanced long-term adaptability in a changing climate.

KEYWORDS: *Vitis vinifera*, clone, massal selection, diversity, phenotype, genotype

INTRODUCTION

Modern viticulture faces a critical paradox. The widespread adoption of clonal selection in the mid-20th century successfully standardised production and eliminated major viral pathogens, but it unintentionally created a genetically simplified vineyard landscape. As climate change imposes increasing pressures (heat waves, droughts, emerging diseases and pests), the limited adaptability of monoclonal vineyards has become a vulnerability. In this context, massal selection is being re-evaluated not as an obsolete practice, but as a complementary strategy for resilience. This review synthesises historical, genomic, epigenetic, and viromic evidence to show how diverse massal populations function as dynamic genetic reservoirs, and can provide the buffering capacity required for vineyards to adapt to future challenges.

1. DOMESTICATION AND THE EMERGENCE OF INTRAVARIETAL DIVERSITY

1.1. The *Vitis* complex and the domestication syndrome

The grapevine is one of the oldest and most economically significant horticultural crops, with a history tightly interwoven with the cultural and technological development of human societies in the Near East and the Mediterranean basin. The cultivated form (*V. vinifera* subsp. *vinifera* or *sativa*) has been distinguished from its wild progenitor (*V. vinifera* subsp. *sylvestris*) by clear morphological and reproductive traits (Magris *et al.*, 2021; This *et al.*, 2006). Wild populations are dioecious (obligate cross-pollination between male and female individuals), whereas domestication was driven by the selection of hermaphroditic genotypes. This transition to self-fertility was not only a biological change but also an agronomic prerequisite, as it ensured reliable fruit set and yield stability independent of pollen vectors. It also allowed the discarding of the maintenance costs of unproductive male pollinators (Zou *et al.,* 2021).

The set of morphological changes associated with domestication, commonly referred to as the "domestication syndrome", includes larger berry size, higher sugar content and modifications in seed morphology (Myles *et al.*, 2011). Geometric morphometric analyses have played a central role in documenting this change. Terral *et al.* (2010) and Bouby *et al.* (2024) showed that pip shape provides a robust discriminator between wild and cultivated forms, allowing domestication events to be identified in the archaeological record even in the absence of preserved DNA. These morphometric data indicate that early viticulture showed a selection pressure that modified seed phenotype, and that this change correlates strongly with the geographical expansion of the crop.

1.2. Origins: from "Noah's Ark" to the dual domestication model

For decades, the prevailing narrative (often termed the "Noah's Ark" hypothesis) proposed a single primary domestication centre in the Transcaucasian region (modern-day Georgia, Armenia, and Azerbaijan) approximately 8000 years ago, from which all noble varieties spread westwards (Grassi & De Lorenzis, 2021). This linear model is now challenged by recent palaeogenomic evidence. A large-scale genomic analysis by Dong *et al.* (2023) supports a "dual domestication" model, in which two distinct domestication events occurred concurrently but independently in Western Asia and in the Caucasus/Central Asia region. These lineages appear to have diverged early, with the table-grape lineage separating from wine-grape cultivars approximately 2500 years ago. This genomic separation challenges a simplistic monophyletic origin and suggests that the varieties we recognise today arose from a broader genetic base than previously assumed. Field evidence from traditional viticulture regions further illustrates that domestication processes may still be active. Maraš *et al.* (2020) analysed 419 samples from old Montenegrin vineyards, identifying 144 unique genetic profiles (over 100 cultivated), reflecting multiple historical introductions and a complex parentage network among autochthonous varieties. The detection of putative proto-varieties suggests ongoing generation of diversity or even secondary domestication events *in situ*. In addition, the genetic structure of modern Western European cultivars cannot be explained solely by a Transcaucasian origin. As viticulture expanded westward across the Mediterranean, domesticated vines introduced from the East came into contact with widespread local wild populations. Several studies have demonstrated substantial introgression between these incoming cultivars and local *sylvestris* genotypes (Grassi & De Lorenzis, 2021; Myles *et al.*, 2011). This reticulate evolutionary process implies the existence of secondary domestication centres, particularly in Italy and the Iberian Peninsula, which played a decisive role in shaping the current germplasm (De Lorenzis *et al.*, 2019; Dong *et al.*, 2023). Consequently, European varieties should be viewed as complex mosaics of ancient Eastern heritage and local wild adaptations (Magris *et al.*, 2021), a configuration that likely contributed to their resilience across diverse *terroirs*.

1.3. The Roman viticultural model: A technological turning point

Initial domestication relied on the selection of seedlings (sexual propagation), but the stabilisation of specific phenotypes required a technological shift towards vegetative propagation. A seminal study on archaeological pips from the Chianti region dated the onset of this "Roman viticultural model" to around 200 BCE (Aversano *et al.*, 2017). During the Etruscan period, seeds displayed morphological traits intermediate between wild and domesticated forms, suggesting viticulture based on managed wild vines or on seedling populations. The transition to the Roman era is marked by a sudden morphological stabilisation and

an increase in seed size, associated with the adoption of intensive management practices such as pruning and, crucially, grafting and propagation by cuttings. This shift is central for understanding the emergence of massal selection. Ancient Roman agricultural authors such as Columella started to describe vines not only by their geographical origin (*e.g.*, "wine from Falernum") but also by distinct varietal names (*e.g.*, Aminea, Allobrogica), to which they attributed specific agronomic behaviours (Columella, 1941). This indicates a deliberate effort to identify individuals which matched the production objectives and multiply them vegetatively. Unlike modern clonal selection, which seeks to isolate a single genotype to minimise variation, this ancient propagation was inherently massal. It involved the multiplication of multiple elite individuals sharing a common phenotype, thereby maintaining high levels of intravarietal genetic diversity within the "variety" (Pagnoux *et al.*, 2015). Direct palaeogenomic evidence now confirms this picture. A recent whole-genome study of 49 archaeological grape pips from France spanning ~4000 years demonstrates that vegetative (clonal) propagation was already widespread by the mid-Iron Age (~625–500 BCE) and became a pillar of viticultural practice during the Roman period. Genetically identical clones were recovered from sites separated by hundreds of kilometres, and specific clonal lineages were deliberately circulated across long distances (Noraz *et al.*, 2026).

1.4. The emergence and persistence of modern varieties

The question of how long current varieties have existed is central to understanding the accumulation of intravarietal diversity. Palaeogenomic data indicate that several modern cultivars form lineages extending back to the Middle Ages or even to the Roman period. Ramos-Madrigal *et al.* (2019) identified direct parent–offspring relationships connecting medieval seeds with modern varieties such as Savagnin (Traminer) and Chenin blanc, demonstrating continuity of vegetative propagation over nearly a millennium. In France, morphometric analyses of seeds from the 1st to the 15th centuries CE reveal a dynamic history. Bonhomme *et al.* (2021) documented the presence of southern, "East-Table group" varieties in northern France during the Roman period, which were later replaced or supplemented by cultivars adapted to cooler climates, likely precursors of Champagne varieties. This turnover suggests that massal selection operated not as a static preservation mechanism but as a dynamic response to climatic fluctuations such as the Medieval Climate Anomaly (Bouby *et al.*, 2024; Lamb, 1965). In Spain, the history of Tempranillo offers a clear example of how diversity becomes stratified within a named variety. Genome resequencing has identified three distinct clonal lineages within Tempranillo, geographically structured along the Ebro and Duero River basins (Tello *et al.*, 2025). This pattern confirms that what is perceived today as a single variety is, in fact, a collection of divergent sub-populations, shaped by centuries of local selection and the accumulation of somatic mutations. This line of evidence has been substantially extended by Noraz *et al.* (2026), who documented genetically identical clones persisting across more than a millennium: a Roman-period pip from Limoges (170–240 CE) was genetically identical to a Medieval sample from Valenciennes (1100–1200 CE), nearly 530 km distant; moreover, a pip from Valenciennes dated to 1400–1500 CE was genetically identical to modern Pinot noir, establishing direct clonal continuity over approximately 600 years. These findings provide the most compelling palaeogenomic evidence to date that widely named varieties represent the long-term survival of clonal lineages propagated continuously and masally over centuries.

1.5. Genetic structure and human geography

The present-day distribution of grapevine genetic diversity reflects historical human migrations and selection pressures. Large-scale genotyping with SSR markers has shown that cultivated germplasm clusters into three main genetic pools: Western Europe, the Balkans/Levant and the Iberian Peninsula (Bacilieri *et al.*, 2013). This structure is mirrored by genomic landscape analyses that reconstruct viticulture dissemination routes along the northern and southern shores of the Mediterranean (Liang *et al.*, 2019). Within regional populations, such as those of north-western Italy or the *Criollas* cultivars in South America, diversity is often derived from a limited number of founder parents (Aliquó *et al.*, 2017; De Lorenzis *et al.*, 2013; Torres *et al.*, 2022). This creates an apparent paradox: while the global diversity of *V. vinifera* is vast, the genetic base supporting certain regionally specific *terroir* wines can be remarkably narrow in terms of pedigree. One of the drivers of intra-varietal genetic diversity is mutation. Mutations occur over time; hence, older grapevine varieties are generally more diverse than more recent grapevine varieties (Gonçalves & Martins, 2012).

1.6. Conclusion: The legacy of massal propagation

The historical and genomic evidence presented here converges on a clear conclusion: the varieties inherited by modern viticulture are not static, uniform genetic entities. Rather, they are complex populations that have persisted through centuries of environmental fluctuation and human selection. Vegetative propagation made it possible to preserve elite traits over long periods, but at the same time favoured the accumulation of somatic mutations (intra-varietal diversity) and the vertical transmission of systemic pathogens (viral load). This duality provides the framework for understanding the 20th-century shift towards clonal selection. Whereas the "Roman model" of massal propagation prioritised the maintenance of a productive population, the modern industrial model has increasingly emphasised the sanitary and genetic purity of the individual (Golino *et al.*, 2017a; Grenan *et al.*, 2000; Walter & Martelli, 1998). Recognising this historical baseline is essential for evaluating the relevance of reviving massal selection under current and future climatic conditions.

2. THE STANDARDISATION OF VINEYARDS: CLONAL SELECTION AND GENETIC EROSION

2.1. The sanitary imperative and the shift to clonal selection

Vegetative propagation enabled the fixation of desirable traits but it also favoured the vertical transmission of viruses (Fuchs, 2024). For centuries, growers managed intra-varietal diversity empirically through massal selection while removing diseased vines. The intensification of viticulture after phylloxera and World War II, combined with the concentration of propagation in commercial nurseries, created a strong demand for healthy and uniform planting material (Golino *et al.*, 2017b). This led to the systematic adoption of clonal selection, which aims to select and propagate one or a very small number of genotypes after a rigorous sanitary and agronomic screening (Bovey, 1975; Forneck *et al.*, 2009). Although clonal selection dramatically reduced the impact of major viruses (grapevine fanleaf virus, grapevine leafroll-associated viruses), it came at the cost of reduced intra-varietal diversity.

2.2. Genetic bottlenecks and the loss of intra-varietal diversity

The massive use of a limited number of certified clones created a genetic bottleneck (Myles *et al.*, 2011). In many premium wine regions, thousands of hectares are now planted with only a handful of clones of the same variety. Monoclonal or oligoclonal vineyards respond uniformly to stress, making them more vulnerable to climate anomalies and new biotic threats. In contrast, ancient polyclonal vineyards were inherently more resilient because different genotypes buffered environmental variation (Carvalho *et al.*, 2025). While direct empirical comparisons between monoclonal and massal vineyards for vulnerability to specific stressors remain scarce in the viticultural literature, population genetics theory and evidence from other crop systems (Zhu *et al.*, 2000; Altermatt & Ebert, 2008) predict that genotypic uniformity increases biotic stress vulnerability. Evidence for differential resistance among grapevine clones to downy mildew, linked to stilbene production, provides a specific viticultural example (van Leeuwen *et al.*, 2013). We acknowledge that designing rigorous field experiments comparing clonal and massal populations under defined stress scenarios remains an important research gap. Early clonal programmes often prioritised yield and sanitary status, inadvertently discarding rare alleles with potential adaptive value. Despite this, somatic mutations continue to generate new diversity within clones (Pelsy, 2010), although at a rate too slow to compensate for the diversity lost through widespread clonal replacement (Calderón *et al.*, 2021).

2.3. The role of somaclonal variation

Despite the strong standardisation imposed by clonal propagation, the grapevine genome remains dynamic. Somatic mutations continue to arise in clonal lineages, giving rise to somaclonal variation (Pelsy, 2010). Over long time scales, this mechanism generates new diversity within clones and can partially compensate for the loss of variation caused by selection. However, the spontaneous mutation rate is too low to replenish, in the short and medium term, the diversity that has been rapidly removed through the replacement of massal populations with a narrow set of certified clones (Calderón *et al.*, 2021). Consequently, the reliance on this reduced genetic base represents a critical vulnerability of modern viticulture and underscores the need to re-evaluate conservation strategies such as massal selection.

3. INTRAVARIETAL VARIABILITY I: PHENOTYPIC DIVERSITY AMONG CLONES

3.1. Introduction: The quantifiable reality of clonal heterogeneity

Despite the standardisation achieved by clonal selection, significant intravarietal diversity persists within certified clones. This diversity arises from somatic mutations and epigenetic modifications accumulated over time. Modern characterisation programmes have quantified variation in agronomic, qualitative and physiological traits, showing that, for certain adaptive characters, the phenotypic variance among clones within a variety can equal or even exceed that observed between some varieties.

3.2. Diversity in agronomic traits: yield components and stability

Clonal characterisation has historically focused on production components (Cirami *et al.*, 1993). Yield is a complex quantitative trait determined by the interaction among bunch number, berry number per bunch and berry size (Keller, 2015). Several studies that explicitly dissect these components have shown that clonal selection can isolate distinct biotypes within a variety.

3.2.1. Vigour and production architecture

In Greco Bianco, both morphological and molecular markers were used to identify distinct clonal groups (Villano *et al.*, 2023). Even within this minor variety, an "exploitable variation" in vigour and yield per vine was detected. Certain clones allocated a larger proportion of biomass to vegetative growth, whereas others prioritised reproductive output. This shows that the vigour–yield balance is not fixed at the varietal level, but is a clone-specific trait that can be matched to site potential, training system and management objectives. Similarly, clonal evaluations of Tempranillo in the Rioja region reported wide ranges in production parameters (Portu *et al.*, 2024). These studies highlighted a key agronomic trade-off: the relationship between yield and quality is often non-linear. Some clones maintained high yields without the pronounced decline in polyphenolic parameters typically associated with over-cropping, indicating that the genotypic capacity to ripen fruit under load differs between clones. Altogether, these results

confirm that clonal material does not form a homogeneous block, but rather a set of agronomically distinct options within the same variety.

3.2.2. Fruit set and reproductive efficiency

A specific, highly heritable component of yield is fruit set, defined as the proportion of flowers that develop into berries. In Malbec, clonal trials have quantified natural genetic variation in fruit-set rates (Calderón *et al.*, 2025). These trials identified clones with consistently high coulure (flower drop) and others with high fruit retention. This variation is particularly relevant in the context of climate change, where adverse weather during flowering (heat waves, cold spells, or rain events) is expected to become more frequent. Clones with naturally higher fruit-set potential provide a buffer against "sink-limited" years, contributing to more stable yields across vintages. This supports the view that yield stability depends not only on climate and management practices but also on intrinsic genetic traits that vary at the clonal level.

3.3. Qualitative plasticity: from metabolites to sensory profiles

Beyond gross agronomic metrics, berry composition exhibits remarkable plasticity among clones. This variation is the most direct link with *terroir* expression, since the clone acts as the filter through which the environment is translated into primary and secondary metabolites, and ultimately into wine sensory attributes (Barbeau *et al.*, 1998).

3.3.1. Sugar accumulation and acidity kinetics

In Merlot selections from California's Central San Joaquin Valley, Fidelibus *et al.* (2007) reported clonal differences in the rate of soluble-solids accumulation and acidity degradation. At a common harvest date, distinct clones showed significant variation in soluble solids and pH. This phenological spread can be exploited to stagger harvest operations, distribute winery loads in time or select "low-sugar accumulation" clones as a strategy to mitigate the impact of warming on potential alcohol. Similar observations were reported for Cabernet franc in van Leeuwen *et al.* (2013).

3.3.2. Secondary metabolites: The fingerprint of typicity

In aromatic varieties, variation in secondary metabolites is the defining quality parameter. Clonal differences in terpene profiles have been documented both at the molecular level, through variants in the DXS gene that determine Muscat flavour, including in the Chardonnay musqué clone (Emanuelli *et al.*, 2010; Duchêne *et al.*, 2009), and at the oenological level, with clone-specific aroma profiles persisting from berry to sparkling wine (Prévide Bernardo *et al.*, 2022). These examples also illustrate the difficulty of drawing a sharp boundary between varietal and clonal variation, since the same biosynthetic genes can harbour both inter-varietal polymorphisms and intra-varietal somatic mutations. Beyond aromatics, clonal variation in phenolic composition represents an equally relevant quality parameter. In Tempranillo, clonal evaluations revealed a wide range in colour intensity and anthocyanin content, with some clones showing stable expression across years and sites and others showing strong environmental dependence (Portu *et al.*, 2024). In Malbec, a large-scale analysis of 131 clones grown in a single vineyard demonstrated substantial clonal variation in anthocyanin profiles, largely driven by differences in malvidin derivatives, and linked these differences to differential expression of genes involved in hydroxylation (F3′5′H), methylation (OMT1) and transport (AM2) of anthocyanins (Muñoz *et al.*, 2014). These patterns reveal substantial mechanistic diversity in anthocyanin biosynthesis among clones. Combined with evidence of genotype-by-environment interactions documented in multi-site studies (Pagliarani *et al.*, 2019; Robinson *et al.*, 2025), they support the hypothesis that some clones may perform differently under contrasting environmental conditions, making them particularly relevant for strategies aimed at colour stability and phenolic balance under climate-change scenarios.

3.4. Comparative analysis: clonal ranges *vs* massal expectations

Clonal selection narrows the bell curve of variation. While it efficiently eliminates low-performing genotypes, it also discards rare alleles and extreme phenotypes that may confer resilience. Understanding the remaining clonal ranges is essential for exploiting existing diversity and recognising the limits of monoclonal systems (Table 1).

3.5. Physiological mechanisms and adaptation to changing environments

As climate change imposes new constraints, particularly more frequent droughts, heat waves and a possible decoupling of the timing of desirable berry composition characteristics like phenolic and sugar ripeness (Sadras & Moran, 2012), the focus of clonal selection is shifting from pure productivity towards physiological efficiency and plasticity (Buesa *et al.*, 2022). Intravarietal variability in physiological traits offers a way to enhance adaptation without changing the varietal identity that underpins regional wine typicity (van Leeuwen & Destrac-Irvine, 2017).

3.5.1. The "water-saver" genotypes

Water scarcity is emerging as one of the major challenges for viticulture in many traditional growing regions. Recent physiological studies have started to unravel the mechanisms underlying intravarietal variability in water-use efficiency (WUE) (Tortosa *et al.*, 2016). In Grenache, for example, clones with contrasting WUE strategies were identified, and these differences were linked to intrinsic variations in stomatal conductance (g_s) and mesophyll conductance (g_m) (Buesa *et al.*, 2022). These results show that "water-saver" clones already exist within widely planted varieties and can be targeted to improve drought tolerance without changing cultivar. A comparative analysis of inter- and intra-varietal diversity concluded that, for WUE, the intra-varietal fraction of variance can equal the inter-varietal fraction (Medrano *et al.*, 2015; Tortosa *et al.*, 2016). This finding has profound implications: instead of replacing a variety

Table 1. Range of variation (minimum and maximum values) for yield and quality traits in clonal groups of various grapevine cultivars according to different authors.

	Cv	Clones number	Bunchs/plant		Yield (kg/plant)		Berry weight (g)		Soluble sugars (°Brix)		pH		Total acidity (g/L tart. eq.)	
			Min	Max	Min	Max	Min	Max	Min	Max	Min	Max	Min	Max
Fidelibus *et al.*, 2006	Chardonnay	6	78 *	105 *	19.90 *	23.20 *	1.50 *	1.60 *	22.4 *	23.7 *	3.60 *	3.70 *	5.3 *	5.8 *
Fidelibus *et al,*, 2007	Merlot	6	85 *	103 *	18.11 *	22.21 *	1.54 *	1.73 *	23.4 *	24.5 *	3.87 *	3.94 *	3.7 *	4.0 *
Belfiore *et al.*, 2024	Pinot gris	17	34 *	48 *	5.50 *	7.70 *	1.31 NS	1.53 NS	17.2 NS	20.3 NS			6.5 NS	7.3 NS
Mendes Lemos *et al.*, 2020	Tempranillo	30							20.6 NS	24.1 NS	4.00 *	4.23 *	4.1 NS	5.9 NS
Mendes Lemos *et al.*, 2020	Tempranillo	30							18.3 *	24.2 *	3.87 *	4.23 *	3.3 *	4.9 *
Cirami *et al.*, 1993	Cabernet-Sauvignon	8	96 *	104 *	7.30 *	8.10 *	0.84 NS	0.88 NS	22.7 *	23.2 *	3.44 *	3.49 *	5.0 *	5.4 *
Portu *et al.*, 2024	Tempranillo	33 NT	15 NT	20 NT	3.60 NT	7.30 NT	1.42 NT	2.37 NT	20.9 NT	23.8 NT	3.60 NT	3.80 NT	3.7 NT	5.3 NT
Ewart *et al.*, 1993	Sauvignon blanc	6			3.40 *	7.23 *			22.4 *	25.7 *	2.38 *	3.49 *	7.8 *	8.8 *
Villano *et al.*, 2023	Greco Bianco	17							20.2 *	24.4 *	2.96 *	3.21 *	1.6 *	3.2 *
van Leeuwen *et al.*, 2013	Cabernet franc	10	6.7 *	9.2 *	0.969 *	1.478 *	1.12 *	1.33 *	21.7NS	23.0NS	3.39 *	3.53 *	5.0 *	5.5 *

* indicates significant differences, NS indicates non-significant differences, NT indicates that no statistical significance was provided.

such as Tempranillo with a more drought-tolerant cultivar (thus altering the regional identity), growers could replant with drought-tolerant clones of Tempranillo, preserving typicity while adapting to warmer and drier conditions.

3.5.2. Root architecture and osmotic stress

Adaptation to water deficit is not restricted to above-ground traits. Studies evaluating genetic diversity under osmotic stress have examined root architecture in both rootstocks and scion clones, relating clonal variation in root branching density and depth to the capacity for soil exploration and water uptake (Peiró *et al.*, 2020). Genotypes with more aggressive and deeper root systems are better able to maintain turgor under osmotic stress, thereby sustaining physiological activity during prolonged dry periods. These "hidden" below-ground traits represent an important component of intra-varietal diversity and should be considered when defining drought-adapted clonal material.

3.5.3. Phenological shifts

Adjusting phenology is another key strategy to mitigate the effects of climate change (Wolkovich *et al*., 2017). Delayed phenology is an interesting lever for adaptation to climate change, because it shifts grape ripening later in the season when temperatures are lower (van Leeuwen *et al.*, 2024). A study on natural genetic variation in phenology quantified the range of budburst, flowering, and veraison dates among clones within the same variety (Van Houten *et al.*, 2020). Similar patterns emerged in the evaluation of 13 new putative clones of Graciano, where Portu *et al.* (2025) recorded broader ranges in the timing of four phenological stages (budburst, flowering, veraison, and harvest) compared with two registered clones of the cultivar, highlighting intra-varietal potential for delayed cycles. This intra-varietal plasticity extends to complex traits, as demonstrated by Robinson *et al.* (2025), who analysed 14 years of data across eight clonal populations (including Pinot noir and Riesling), revealing substantial phenotypic variation in agronomic (*e.g.*, yield), quality (*e.g.*, sugar), and disease-related traits, with moderate to high broad-sense heritability. Three phenological stages emerge as key areas where heterogeneity could have a high impact on productivity. Clones with a delayed budburst date could evade late frost in the spring. Moreover, vineyards with a spread in the flowering time could be more tolerant to events like Zonda wind (Norte, 2015) which during short periods of time produce a dramatic increase of the temperature and decrease of atmospheric humidity, both conditions known to severely affect the fruit set by desiccation of stigma (Greer & Weston, 2010) or, more generally, all sorts of adverse conditions during flowering. The identification of "late-ripening" clones in otherwise early-ripening cultivars provides a tool to delay harvest into cooler autumn periods, thereby preserving acidity and aromatic freshness. A delay of 7–10 days in veraison relative to the clonal population mean effectively shifts the ripening window away from the peak of heat stress, which is particularly relevant for regions such as Mendoza or South Australia. Robinson *et al.* (2025) further highlight strong genetic correlations, underscoring the need for multi-trait selection to balance trade-offs in clonal breeding. This underscores the role of GxE interactions when searching for clonal diversity benefits, as observed in Portu *et al.* (2025), where environmental variability influenced trait expression across clones.

3.6. Differential tolerance to biotic stress

Compared with agronomic and oenological traits, clonal differences in susceptibility to pathogens have been less extensively explored, yet they represent a critical frontier for reducing chemical inputs and improving sustainability. In a comparison of 10 non-commercial Cabernet franc clones, van Leeuwen *et al.* (2013) showed substantial differences in *in vitro* susceptibility to downy mildew (*Plasmopara viticola*). These differences are related to differential stilbene concentrations in leaves. A trial with 17 Pinot gris clones grown under high *Botrytis cinerea* pressure revealed important differences in susceptibility among clones (Belfiore *et al.*, 2024). This variability was associated mainly with morphological traits (cluster compactness, berry size, and cuticle thickness) rather than with major resistance genes, indicating that morphological resistance can be exploited through clonal choice. Selecting clones with looser clusters and thicker skins provides a passive but effective avenue for disease management. Similarly, in Pinot noir, clonal evaluations have demonstrated genetic differences that translate into contrasting cluster architectures (Richter *et al.*, 2020). These differences modulate not only disease development, but also berry microclimate and ripening dynamics. Taken together, current evidence shows that the characterisation of intravarietal diversity has evolved from simple visual observations to a sophisticated mapping of phenotypic ranges across physiological, agronomic, wine-quality-related and sanitary traits. While clonal selection has undoubtedly reduced the overall genetic width of grapevine populations compared with massal selection, the diversity that remains within certified material is still substantial, quantifiable, and agronomically actionable (Table 1).

4. INTRAVARIETAL VARIABILITY II: GENETIC DIVERSITY DETERMINED BY MOLECULAR TOOLS

4.1. The genetic black box

Previously, we examined the extensive phenotypic plasticity observed within grapevine varieties. For decades, this visible diversity posed a paradox for ampelographers and geneticists: clones that were clearly distinct in the vineyard (by cluster architecture, berry colour, or ripening kinetics) often appeared identical when analysed with early molecular tools (Cretazzo *et al.*, 2010; Doulati Baneh *et al.*, 2009). The classical definition of a grapevine variety as a vegetative lineage implies genetic stability, yet centuries of clonal propagation suggest a dynamic genome continually shaped by somatic mutation. Here, we will trace the evolution of molecular tools used to resolve that paradox. It follows the progression from the first generation of molecular markers,

which lacked the resolution to discriminate clones, to the advent of high-throughput genomics, which has progressively revealed the "hidden" diversity of the grapevine genomes. This technological leap has not only confirmed the genetic basis of clonal variation, but also provided quantitative tools to measure it, reconstruct clonal lineages and design conservation strategies for massal populations.

4.2. The era of molecular markers: limitations of SSRs and AFLPs

The first attempts to characterise intravarietal diversity relied on the same tools that had been highly successful for varietal identification and pedigree analysis: microsatellites (SSRs) and Amplified Fragment Length Polymorphisms (AFLPs). While these markers were revolutionary for distinguishing Cabernet-Sauvignon from Merlot (Bowers & Meredith, 1997), they proved largely insufficient for separating clones within a single variety.

4.2.1. The resolution ceiling

SSRs target highly polymorphic repetitive regions and became the standard for variety identification because of their high reproducibility and discriminating power among cultivars. However, their mutation rate, though high in evolutionary terms, is often too slow or too stochastic to capture the somatic mutations that accumulate between clonal generations. In cv. Keshmeshi, for example, a combination of SSRs and AFLPs was used to assess diversity among selected clones (Doulati Baneh *et al.*, 2009). Although some clonal variation was detected, the authors concluded that the resolution was limited and that the true variability of the population was likely underestimated. In other words, the markers could not show the fine-scale mutations responsible for many of the observed phenotypic differences.

4.2.2. The phenotype–genotype gap

This limitation was particularly evident in a study of a spontaneous mutant and selected clones of cv. Italia (Fanizza *et al.*, 2003). Despite clear phenotypic divergence (the mutant showed conspicuous morphological differences), AFLP analysis revealed very few polymorphisms. This discrepancy highlighted a fundamental issue: the genetic changes driving somatic variation (often single-nucleotide variants or specific structural rearrangements) may occur outside the restriction sites or primer-binding regions sampled by AFLPs. Similarly, an assessment of the Muscat group, including Muscat of Alexandria clones, used SSRs and AFLPs to evaluate diversity (Regner *et al.*, 2015). While the analyses confirmed varietal identity and separated some accessions, the ability to discriminate closely related clones from selection programs was low. Collectively, these early studies established two key points: clones are genetically distinct entities, but the "signal" of their divergence is often too faint to be detected by low-resolution marker systems.

4.3. The structural revolution: Transposable Elements (TEs) as engines of variation

The first major breakthrough in understanding the mechanism of clonal diversity did not come from adding more markers, but from elucidating the dynamic architecture of the grapevine genome. Genome sequencing revealed a landscape extremely rich in TEs, mobile genetic sequences capable of moving and inserting at new locations (Canaguier *et al.*, 2017; The French–Italian Public Consortium for Grapevine Genome Characterization, 2007; Velasco *et al.*, 2007).

4.3.1. Mobile elements and somatic polymorphism

Carrier *et al*. (2012) provided a paradigm-shifting demonstration that TEs are a major cause of somatic polymorphism in *V. vinifera*. Their work showed that inserting retrotransposons such as Gret1 into regulatory regions can drastically alter phenotypes. A classic example is the modulation of berry colour: TE insertions in the VvMybA1 gene cluster can switch anthocyanin synthesis off (producing white grapes) or on (reverting to red or grey variants). This mechanism redefined clonal variation as not merely the slow accumulation of point mutations, but a landscape of potentially dramatic structural changes driven by mobile elements, often activated by stress. Consistently, the white variety of Tempranillo has been shown to carry a large number of genomic rearrangements compatible with such processes (Carbonell-Bejerano *et al.*, 2017).

4.3.2. Structural variations and chromosomal rearrangements

Beyond individual TE insertions, the grapevine genome is subject to larger-scale structural rearrangements. Pelsy (2010) described chromosome replacements and deletions as frequent drivers of clonal polymorphism, particularly for berry colour. Large deletions or the replacement of one chromosome arm by its homolog (loss of heterozygosity) in regions harbouring colour genes generate the Pinot blanc, gris, and noir variants from a common origin. Population genetics and comparative genomics further reveal their role in clonal divergence, with haplotype-phased assemblies showing hemizygosity in approximately one in seven genes, strong purifying selection against inversions and translocations, and dramatic gene gain and loss in domesticated lineages, including transitions toward asexual reproduction genes and ~8 % accession-specific families, highlighting somatic variation as a driver of intravarietal diversity (Zhou *et al.*, 2019; Long *et al.*, 2024). These "macroscopic" genomic events help to explain why some clones are phenotypically unstable and why AFLPs (which sample the genome randomly) often fail to detect the causal structural changes. A further dimension of clonal structural diversity is periclinal chimerism, in which somatic mutations affect a single meristematic cell layer and generate stable mosaics in which distinct genotypes coexist across tissues of the same plant. This mechanism has been documented in grapevine at the berry colour locus and beyond: chromosome-level replacements confined to one cell layer explain several pale-berry bud sports of Cabernet-Sauvignon and Pinot

(Pelsy *et al.*, 2015; Walker *et al.*, 2006), and phased long-read assembly of Merlot has identified 51 to 53 periclinal chimeras per haplotype, several within coding regions (Sichel *et al.*, 2023). For massal selection, chimerism represents an invisible layer of diversity that escapes whole-plant genotyping and can generate phenotypically distinct individuals through cell-layer sorting during vegetative propagation.

4.4. The genomic era: Whole Genome Sequencing (WGS) and clonal lineages

The advent of Next-Generation Sequencing (NGS) and the progressive reduction in sequencing costs enabled a shift from targeted markers to WGS. This marked the transition from simple "fingerprinting" to true phylogenomics, making it possible to reconstruct clonal lineages at high resolution.

4.4.1. Reconstructing clonal history: The case of Chardonnay

In a landmark study, Roach *et al.* (2018) used population-level sequencing of multiple Chardonnay clones to infer their evolutionary history. By identifying thousands of high-confidence single-nucleotide variants (SNVs), they constructed a phylogenetic tree of the variety that resolved distinct clonal lineages. The analyses also revealed evidence of ancestral inbreeding, providing insight into the historical origins of Chardonnay and its founder genotypes. Importantly, the clonal lineages inferred from genomic data were consistent with historical records of dissemination and with documented phenotypic differentiation among clones. This work demonstrated that clones do not form a flat, unstructured set of entities, but rather a stratified population with deep evolutionary branches.

4.4.2. Geographic structuring: The case of Malbec

A similar WGS-based strategy applied to Malbec revealed clonal lineages that are geographically structured (Calderón *et al.*, 2021). Whole-genome resequencing combined with custom genotyping allowed the identification of specific markers that distinguish pre-phylloxera European material from South American massal selections. The results showed that the introduction bottleneck into the New World, followed by several generations of local massal selection, generated distinct genomic signatures. This provides a molecular basis for the concept of "Argentine Malbec" as not only phenotypically, but also genomically differentiated from its French progenitors. This evidence supports the concept that South American viticulture (particularly in Argentina and Chile) represents a unique global case study. Unlike European regions where post-phylloxera replanting was often driven by early clonal standardisation, these countries maintain tens of thousands of hectares of commercial vineyards established through massal propagation. Consequently, these regions act as large-scale *in situ* reservoirs of pre-clonal genetic diversity, preserving a complexity that has been eroded elsewhere. This vast genetic capital, validated by the genomic divergence found in Malbec (Calderón *et al.*, 2021), offers an unparalleled resource for adaptation and selection.

4.4.3. Accumulation of somatic variation in narrow-founder cultivars: The case of Carménère

Carménère exemplifies the accumulation of somatic variation in a narrow-founder cultivar maintained primarily through massal propagation. Introduced from France in the mid-19th century and preserved in Chile in the absence of phylloxera, the variety experienced a severe genetic bottleneck followed by over 150 years of vegetative multiplication. Whole-genome resequencing of 12 Chilean clones (36 biological replicates) using a new chromosome-scale Carménère reference genome identified more than 9000 clone-private SNVs and small indels per clone (Garcia *et al.*, 2026). Although most variants mapped to repetitive regions, a substantial subset affected coding sequences, with genes involved in plant–pathogen interactions, transport and secondary metabolism being most frequently impacted. These results demonstrate that historic massal populations can preserve significant intravarietal diversity even after strong founder effects.

4.5. High-throughput genotyping: from discovery to discrimination

While WGS offers maximal resolution, it remains too costly and data-intensive for routine screening of thousands of vines. The current frontier, therefore, lies in translating WGS discoveries into cost-effective, high-throughput genotyping platforms, such as amplicon sequencing, Genotyping-by-Sequencing (GBS) and SNP arrays. These tools aim to capture the most informative polymorphisms (SNVs and InDels) identified by WGS, and deploy them at scale for clone identification and conservation.

4.5.1. Targeted panels and amplicon sequencing

To bridge the gap between cost and resolution, Urra *et al.* (2023) developed a proof-of-concept panel based on high-throughput amplicon sequencing targeting 46 InDel markers, demonstrating that much higher clonal resolution than SSRs is achievable at manageable cost. The design principles and discrimination statistics of this approach are discussed in detail in Section 7.3.1.

4.5.2. Genotyping-by-Sequencing (GBS)

GBS has emerged as a powerful tool for characterising large clonal collections and guiding conservation strategies. Applied to Primitivo, it generated approximately 38,000 SNPs across 35 clones, enabling discrimination of genetically unique individuals and identification of groups associated with oenological traits (Procino *et al.*, 2025). The methodological details and broader applications of GBS-based population typing are covered in further detail in Section 7.2.1. The molecular characterisation of grapevine clones has evolved from a state of near "blindness" to high-definition genomic resolution. We now know that the grapevine genome is fluid, shaped by mobile elements and structural rearrangements that generate continuous somatic polymorphism. The transition from SSRs and AFLPs to WGS and high-throughput genotyping has confirmed that intravarietal diversity is not a conceptual artefact but

a measurable genomic reality. These tools now make it possible to distinguish clonal lineages, trace the historical trajectories of varieties, and, crucially, design data-driven strategies for the conservation of massal populations.

5. INTRAVARIETAL VARIABILITY III: BEYOND THE DNA SEQUENCE – EPIGENETICS AND THE VIRAL COMPONENT

5.1. The missing heritability of the clone

A substantial fraction of observed phenotypic plasticity cannot be explained by DNA sequence variation alone. Two additional layers modulate clonal performance: epigenetic variability and the virome.

5.2. Epigenetics: The molecular memory of *terroir*

Epigenetics refers to heritable changes in gene expression that occur without alterations to the underlying DNA sequence. In grapevine, a perennial species propagated vegetatively, epigenetic mechanisms (primarily cytosine DNA methylation, 5mC) play a central role in phenotypic plasticity and adaptation (Fortes & Gallusci, 2017). Unlike annual crops, where epigenetic marks are frequently reset during meiosis, vegetative propagation allows the grapevine to transmit environmentally induced epigenetic states to the next generation of cuttings, potentially fixing adaptive traits. Recent perspectives highlight that these mechanisms, including stress-induced epigenetic memories, could serve as an innovative lever for grapevine improvement under climate change by exploiting the somatic inheritance possible in clonally propagated perennials (Berger *et al.*, 2023; Berger *et al.,* 2025).

5.2.1. Mechanisms of epigenetic variation

The main mechanism explored in grapevine is variation in cytosine methylation across the genome, particularly in promoter regions and regulatory elements. Increased methylation in a promoter typically represses transcription, effectively silencing the associated trait; conversely, demethylation can restore gene expression. This mechanism was first demonstrated for skin colour, where hyper-methylation of the VvMybA1 promoter results in green berries (Azuma *et al.*, 2009). Evidence for sequence-independent epigenetic divergence among clones comes from studies tracking methylation changes under environmental pressure in vegetatively propagated material (Varela *et al.*, 2020; Varela *et al.*, 2024; Baránek *et al.*, 2015). This mechanism is not limited to individual sports or clones; it appears to have played a broader role throughout domestication. Rodriguez-Izquierdo *et al.* (2024) compared methylation patterns between 18 wild and cultivated grapevine accessions using reduced-representation bisulfite sequencing. They found significantly higher global methylation levels in cultivated varieties, identifying 9.955 differentially methylated cytosines (DMCs), of which 78 % were hypermethylated in cultivars. Core methylated genes (consistently methylated in both wild and cultivated) were enriched in stress response and terpenoid/isoprenoid metabolic pathways, while differentially methylated genes were associated with peroxisome protein targeting, ethylene regulation, histone modifications, and defence responses. These findings suggest that DNA methylation contributed significantly to the fixation of adaptive traits during domestication, potentially acting as a molecular substrate for the emergence of intra-varietal diversity observed today. Epigenetic responses to specific stresses further illustrate this dynamic. De Giovanni *et al.* (2015) surveyed methylation in NCED genes (key in ABA biosynthesis and drought response), identifying symmetric and asymmetric CpG islands that modulate expression under normal *vs* drought conditions. This suggests NCED as candidates for 'epigenetic memory', where stress-induced methylation patterns could persist, influencing phenotypic plasticity and adaptation in clones. The dynamics of these changes highlight both reversibility and persistence: Baránek *et al.* (2015) showed that *in vitro* stress induces methylation alterations, with 40 % reverting within a year (transient acclimation) but 60 % persisting as mitotically heritable epimutations. Sequencing variable regions linked 19.5 % to known genes (*e.g.*, Gret1 retrotransposon, auxin-responsive factor) and 51.2 % to hypothetical stress-sensitive proteins, suggesting epigenetic drift contributes to clonal divergence under environmental pressure.

5.2.2. Epigenetics as a driver of *terroir* expression

The concept of *terroir* has traditionally been framed in terms of soil properties, climate, and management practices (Seguin, 1969; van Leeuwen & Seguin, 2006; Muñoz *et al.*, 2026; Muñoz *et al.*, 2021). Recent work adds a molecular dimension to this framework, proposing that the environment "programmes" the genome through stable, site-specific methylation patterns (Dal Santo *et al.*, 2016).

- Global methylation patterns: Studies of global DNA methylation have shown that methylation landscapes differ significantly between vineyards and regions, generating distinct epigenetic fingerprints (Xie *et al.*, 2017). These patterns are robust enough to cluster vines according to their geographical origin, suggesting that local environments induce stable changes in gene-expression potential that contribute to *terroir*-specific phenotypes.
- Clone-dependent responses in Malbec: Work on Malbec in Mendoza has provided some of the most detailed evidence of this interaction (Varela *et al.*, 2020). It was shown that vineyard environments influence both phenotypic traits and methylation profiles in a clone-dependent way: some clones exhibit high epigenetic plasticity and respond strongly to environmental change, whereas others show relatively rigid methylation patterns.
- Plasticity *versus* stability over time: A three-year study following transplanted Malbec material revealed that certain methylation marks adjust rapidly after relocation (acclimation), while others remain stable and retain a "memory" of the original environment

(Varela *et al.*, 2024). This raises important questions for clonal certification: a given clone produced in a low-altitude nursery and the same genetic clone propagated for decades at high altitude may differ substantially at the epigenomic level, even if their DNA sequence is identical (Varela *et al.*, 2024, Varela *et al.*, 2020).

– Clone-specific responses to repeated drought stress: In two cultivars (Debina and Dichali), repeated drought cycles induced differential morpho-physiological, genetic and epigenetic responses, with 'Dichali' showing higher tolerance (Maniatis *et al.*, 2024). Grafted plants on 'Richter 110' rootstock exhibited greater resilience than self-rooted ones, suggesting beneficial scion–rootstock interactions. Gene expression revealed up-regulation of most stress-related genes in 'Dichali', including a key module involving miR159 up-regulation and strong down-regulation of the transcriptional co-repressor VvTOPLESS-4-like. MSAP analysis further identified genotype-specific DNA methylation patterns under stress. Although conducted in pots under controlled conditions, these results illustrate how autochthonous germplasm can harbour clone-dependent epigenetic and genetic plasticity that enhances adaptation to recurring abiotic stress in Mediterranean environments.

These observations support a model in which epigenetic mechanisms act as a molecular substrate for *terroir*, modulating clonal phenotypes in response to environmental history. This view is reinforced by evidence that grapevine can form stable, mitotically heritable epigenetic memories of (a)biotic stresses, providing a mechanism for long-term acclimation in clonally propagated perennials (Berger *et al.*, 2025).

5.3. The viral component: The "extended genotype"

While epigenetic variability represents an internal layer of regulation, viruses constitute an external but intrinsic component of clonal identity. The grapevine virome is among the most extensively documented in any crop species, likely reflecting centuries of global germplasm exchange, grafting across rootstock-scion combinations and long-term vegetative propagation, among other contributing factors (Fuchs, 2024; Tzanetakis *et al.*, 2025). In the context of clonal diversity, viruses should therefore be considered not only as pathogens to be eliminated, but as elements of a holobiont that modulate plant phenotype and may contribute to intravarietal variability.

5.3.1. The "healthy" *versus* "diseased" dichotomy

Historically, clonal selection was closely tied to sanitary selection: the elimination of viruses to restore vigour and yield (Golino *et al.,* 2017b; Walter & Martelli, 1998). A pioneering comparison between healthy and leafroll-affected planting stocks showed that high viral loads cause severe agronomic penalties, including reduced vigour, lower yields, and delayed sugar accumulation, thereby justifying the implementation of clean-stock programmes (Lider *et al.*, 1975). However, this binary view (infected *versus* clean) oversimplifies the biological reality. In practice, vines are rarely virus-free; instead, they harbour complex viromes comprising multiple latent or mildly pathogenic viruses, such as members of the Betaflexiviridae (*e.g.*, grapevine rupestris stem pitting-associated virus), that may not cause obvious symptoms but subtly alter physiological processes (Meng & Rowhani, 2017). Moreover, grapevines can also host mycoviruses through their associated fungal communities, further complicating the holobiont structure (Debat *et al.*, 2025).

5.3.2. Viral modulation of clonal phenotypes

The interaction between a given clone and its viral community is dynamic and can generate long-term phenotypic trajectories. A 17-year longitudinal study on Pinot noir compared vines infected with different sources of grapevine leafroll-associated viruses and documented distinct, strain-specific effects on ripening and yield (Reynard *et al.*, 2022). Rather than being simply "less productive", infected vines followed alternative phenotypic trajectories, with altered phenology, delayed maturation and modified sugar–acid balances that persisted over nearly two decades. More broadly, several studies have shown that viral infections can mimic genetic or epigenetic effects on traits such as vigour, yield, sugar accumulation, and colour development. A mild leafroll infection, for example, may reduce sugar accumulation and delay harvest, a combination of traits that could be misinterpreted in a blind trial as a "late-ripening clone" rather than as a clone–virus interaction (Dayer *et al.*, 2017).

5.3.3. A confounding factor in clonal comparison

These observations lead to a critical hypothesis regarding historical clonal characterisation. Many "clones" described in the 20th century were selected solely on phenotypic grounds (*e.g.*, looser clusters, reduced vigour, delayed ripening) and with the sanitary selection tools available at the time of selection (ELISA or indexing), without systematic screening for latent or mild viral infections. The availability of transcriptomic tools has provided a new perspective in the sanitary status assessment of grapevines, enabling the identification of previously unknown viruses. In such cases, the recorded "clonal differences" may in fact reflect, at least in part, differences in virome composition rather than fixed genetic or epigenetic divergence. To test this hypothesis, we performed a meta-analysis of public transcriptomic datasets associated with phenotypic clonal evaluations. Specifically, we re-examined RNA-Seq data from 'Tempranillo' clones previously characterised for bunch compactness (Grimplet *et al.*, 2019; BioProject PRJNA448744). Using a de novo assembly approach to reconstruct non-grapevine transcripts, we identified the presence of seven viral species not originally detailed in the physiological study, including Grapevine virus A (GVA) and GLRaV-2 in specific clones. Notably, the viral composition varied among clones that were being compared for morphological traits. This finding underscores a critical caveat: many clones in genomic repositories or historical trials may actually represent distinct holobionts, where phenotypic differences are driven or amplified by differential viral loads. If a "clone" is defined

by a specific phenotype, but that phenotype is conferred by a viral endophyte, the removal of the virus during heat therapy would effectively "erase" the clone. This implies that a significant portion of what is categorised as "intravarietal diversity" may actually represent viral diversity superimposed on a uniform genetic background.

Recognising viruses and epigenetic variability as integral components of the extended genotype reframes the definition of a clone. A clone can no longer be considered a purely genetic entity; instead, its phenotype emerges from the combined effects of its DNA sequence, its environmentally programmed epigenome and its interacting virome. This tripartite complexity may help explain why massal selection, which conserves the full diversity of genomes, epigenomes and viromes within a population, is frequently associated with greater vineyard resilience, adaptability and wine complexity compared to strictly monoclonal plantings. However, this potential advantage remains largely observational and requires further experimental validation.

6. THE RELEVANCE OF MASSAL SELECTIONS IN THE CONTEXT OF "CLONAL VITICULTURE"

6.1. Redefining massal selection

Clonal selection played a key role in overcoming the sanitary crises of the 20th century by providing healthy and uniform planting material. Nevertheless, the resulting reduction in intra-varietal diversity has created new vulnerabilities. Given the pressures of climate change and rising biotic stresses, there is growing interest in revisiting massal selection as a complementary approach to clonal selection, one that maintains broader diversity across genomes, epigenomes, and viromes.

Massal selection is traditionally defined as a method of vine propagation in which the grower selects budwood from multiple individuals with desirable traits within a vineyard to establish new plantings. Unlike clonal selection, which seeks to isolate and propagate a single genotype, massal selection deliberately propagates a population of genotypes. As highlighted by Grassi and De Lorenzis (2021), this process, applied over millennia of domestication, generated the local adaptations and intravarietal diversity that we value today. In practice, some similarity can be established with a breeding programme: a continuous, empirical filter aligning grapevine populations with their specific environments.

6.2. Why clonal selection became the standard in european viticulture?

Clonal selection prevailed primarily for sanitary reasons. Massal populations often carried latent viruses that became problematic when material was moved to new environments or grafted onto different rootstocks. Certified clonal material offered a reliable "virus-free" guarantee that massal selection could not match (Rühl *et al.*, 2011). As a result, in Germany and France massal populations were largely replaced by a small set of certified clones, leading to the situation where over 95 % of planting material became clonal.

6.3. Massal selection as a genetic reservoir

The consequences of this replacement are now measurable at the genomic scale. Magris *et al.* (2021) analysed the genomes of 204 *V. vinifera* accessions and revealed a striking dichotomy in diversity across European regions. Areas that maintained a tradition of massal selection, such as parts of Portugal and Spain, retained significantly higher levels of intravarietal diversity compared with regions that adopted early and extensive clonal replacement, such as France and Germany. This diversity is not merely of academic interest; it constitutes the evolutionary fuel of the species. Massal populations act as genetic reservoirs, storing rare alleles and unique trait combinations (including somatic mutations and epigenetic variants, as discussed above) that are impoverished by clonal selection. Recent reviews and long-term field studies confirm that even within established clonal populations, substantial exploitable variation persists (Callipo *et al.,* 2025, Robinson *et al.,* 2025) and that this diversity is largely lost when vineyards rely on only one or a few certified clones. Similar patterns emerge in Southern Italian varieties, where SNP analysis of 138 clones revealed geographic structuring and loci associated with environmental adaptation, while structural variant population genetics shows that clonal lineages accumulate SVs contributing to phenotypic diversity and resilience (Villano *et al.*, 2023, Zhou *et al.*, 2019). As Gonçalves *et al.* (2019) argue, the intravarietal diversity historically generated and maintained by massal selection is a key resource for future adaptation. By preserving mainly the "productive" centre of the bell curve (the widely planted clones), modern systems have effectively lost the distribution tails, where traits conferring resilience to extreme or as-yet-unknown conditions are often located. Concrete examples, such as the broader phenological ranges observed in newly prospected clones of minority varieties like Graciano (Portu *et al.*, 2025), illustrate how these tail-end variants (preserved in ancient massal vineyards) may hold critical adaptive potential.

6.4. Mechanisms of resilience: The "buffer" effect

A monoclonal vineyard responds uniformly to stress; if a clone is susceptible to late frost or to a particular mildew strain, the entire crop is placed at risk. In contrast, a massal population functions as a portfolio of diverse assets, distributing risk across genotypes, epigenotypes and viromes. This buffering is underpinned by centuries of accumulated somatic mutations and epigenetic modifications, as reviewed by Callipo *et al.* (2025), who highlight how clonal propagation has generated intra-varietal diversity in traits such as yield, phenology, and stress tolerance without altering varietal identity. Long-term field evidence strongly supports this buffering mechanism. Robinson *et al.* (2025) analysed 14 years of phenotypic records from eight clonal populations of the major varieties in Germany, covering six agronomic, quality and disease-related traits. Using linear mixed models, they demonstrated substantial intra-varietal phenotypic variation across all traits, with moderate to

high broad-sense heritability estimates (typically 0.4–0.8), indicating that a meaningful proportion of the observed differences is genetically determined and heritable among clones. Critically, year-to-year and year-by-field variance components dominated the total phenotypic variance in several traits. This implies that different clones within the same variety exhibit differential responses to the same environmental stresses (frost, heatwaves, pathogen pressure), thereby distributing risk and reducing the likelihood of uniform crop failure. Furthermore, the authors identified both strong positive and strong negative genetic correlations among traits, revealing real trade-offs that must be carefully managed through informed multi-trait selection within existing clonal diversity. These results illustrate that even within established clonal populations, there is already considerable exploitable genetic variation capable of providing a natural buffer against biotic and abiotic stresses, a buffer that is largely forfeited when vineyards are restricted to one or a very small number of certified clones. However, the apparent abundance of clonal variation is not without debate. While Callipo *et al.* (2025) advocate harnessing somatic mutations and epigenetic variability for accelerated selection within clones, other authors argue that prolonged vegetative propagation limits long-term polymorphism (Magris *et al.*, 2021; Myles *et al.*, 2011) and that historical introgression enriched Mediterranean germplasm in ways that clonal systems alone cannot replicate over time (Grassi & De Lorenzis, 2021). This tension raises a central question: does existing clonal diversity, rigorously exploited through massal selection, provide a resilient and sustainable buffer in the medium and long term, or does it represent only a partial solution that may deplete? The answer will determine whether the most effective strategy lies in maximising selection within what already exists or reconsidering other intra-varietal diversity management avenues (always within traditional varieties' framework).

6.5. The polyclonal compromise and the portuguese model

Recognising both the sanitary risks of pure massal selection and the genetic erosion associated with strict monoclonal selection, several authors have proposed intermediate models. Gonçalves *et al.* (2019) describe the Portuguese approach, which combines clonal rigour with massal diversity through polyclonal selection. In this system, instead of releasing a single clone, a group of 7 to 20 genotypes that respond to local production objectives is selected and propagated together. This "polyclonal blend" maintains a minimum level of genetic diversity while still operating under clonal selection and sanitary control. Gonçalves and Martins (2023) support this strategy as a pragmatic way to conserve variability in ancient varieties while meeting the requirements of modern certification schemes.

6.6. Massal selection as a "super-instance" of adaptation

Although polyclonal selection represents a significant improvement for adaptation over strictly monoclonal systems, true massal selection can be viewed as a "super-instance" of adaptation because it explicitly preserves the unknown. A polyclonal mixture is, by design, a curated population based on known criteria such as yield or sugar accumulation. A massal population, in contrast, retains individuals whose value may not yet be apparent (vines that could carry tolerance to a pest that has not yet arrived, or resilience to a temperature threshold that has not yet been reached). Roby *et al.* (2014) argue that the preservation of grapevine genetic resources requires a cohabitation policy: institutional clonal selection for mainstream markets, private clonal selection for niche specificity and massal selection for a high-end, resilience-oriented tier and preservation of intra-varietal diversity. The persistent limitations of massal selection remain its sanitary status and the difficulty of "typing" or certifying the population as a whole. However, with the advent of high-throughput genotyping and metagenomics, the point at which massal populations can be genotyped and sanitary-profiled without reducing them to a single, uniform clone is approaching.

7. NEW GENOTYPING TOOLS AND THEIR APPLICATION FOR POPULATION TYPING

7.1. From individual fingerprinting to population genomics

The main technical barrier to certifying massal selections has been traceability. High-throughput genotyping now makes it possible to characterise entire populations rather than single clones.

7.2. The democratisation of high-density genotyping

The transition from expensive WGS to cost-effective screening has been driven by methods that reduce genome complexity, concentrating sequencing effort on informative regions rather than on the entire genome.

7.2.1. Genotyping-by-Sequencing (GBS) and dd-RAD

A foundational contribution introduced GBS, in which restriction enzymes digest genomic DNA and only the ends of the resulting fragments are sequenced (Elshire *et al.*, 2011). This approach bypasses large fractions of repetitive DNA, including many TEs, and preferentially samples gene-rich regions. In terms of scale and cost, GBS enables the simultaneous discovery and genotyping of thousands of single-nucleotide polymorphisms (SNPs) across hundreds of individuals in a single sequencing run. In viticulture, Procino *et al.* (2025) demonstrated the power of this method in a study of Primitivo clones. Using GBS, they generated approximately 38,000 SNPs across 35 clones and used this high-density dataset to cluster clones into genetic groups that correlated with oenological traits. Likewise, the application of GBS and ddRAD in a collection of 138 clones from six Southern Italian varieties identified polymorphic groups and functional divergence in stress pathways, supporting the utility of these methods for characterising intra-varietal diversity in massal populations (Villano *et al.*, 2023).

This work shows that GBS is not merely a research tool, but a practical method for scanning germplasm collections to identify redundancy and uniqueness, and to rationalise conservation and breeding efforts.

7.2.2. KASP: The rapid validator

Whereas GBS is a discovery-oriented technology, Kompetitive Allele-Specific PCR (KASP) is a high-throughput screening tool. Xi *et al.* (2023) demonstrated its efficacy in grapevine by developing KASP assays for a locus controlling stenospermocarpy (seedlessness), showing that this platform can robustly genotype key alleles at low cost. KASP relies on fluorescence-based detection to identify which allele is present at a given SNP or small InDel. In Rubus, Clare *et al.* (2023) showed that a minimal panel of 24–48 SNPs converted into KASP assays could distinguish virtually all commercial propagated lineages. While the genetic distances between Rubus lineages are broader than those typically separating grapevine clones within a variety, the methodological principle suggests that once variety- or clone-specific somatic mutations (SNVs) are identified through WGS, they can be converted into inexpensive KASP markers. Nurseries can then screen thousands of mother plants at low cost per sample, ensuring true-to-type propagation of prestigious clones or specific massal lines at an industrial scale. In this context, KASP becomes the operational tool that transforms genomic discoveries into routine diagnostics.

7.3. High-resolution discrimination: The power of InDels and amplicons

Recent evidence suggests that, although SNPs are extremely abundant, InDels can provide higher resolution for recent somatic divergence, particularly when they arise from TEs mobilisation as described previously.

7.3.1. Clonal amplicon sequencing

Urra *et al.* (2023) presented a key advance with high-throughput amplicon sequencing. They designed a targeted panel of 46 InDel markers and, by amplifying and sequencing only these specific regions, achieved a discrimination rate of approximately 78 % among closely related clones. This strategy is particularly relevant for massal selection, because it enables the design of variety-specific panels (*e.g.*, "Malbec panel", "Cabernet-Sauvignon panel") composed of 50–100 hyper-variable loci. Using such a panel, a laboratory could process leaf samples from 1000 individual vines in a massal vineyard and assign each vine a molecular barcode, effectively mapping the genetic structure of the field. This level of resolution allows viticulturists to:

- quantify how many distinct genotypes are present;
- estimate their relative frequencies;
- identify rare or unique genotypes of high interest for conservation or selection.

In practical terms, Amplicon-seq panels provide a scalable, intermediate solution between low-resolution SSRs and full WGS, well-suited for characterising massal populations.

7.4. Typifying the "massal population": A statistical approach

The combination of these tools makes it possible to move from purely phenotypic descriptions ("this vineyard produces complex wines") to genomic population typing.

7.4.1. Determining genotypic frequencies

Consider a historic Malbec vineyard planted in 1920. Using GBS or a dense KASP/InDel panel, one could sample a statistically robust subset of the population (for instance, 10 % of the vines) and obtain the following information:

- Dominant genotype: Identification of the core genetic profile that defines the variety in that plot.
- Variant frequencies: Estimation of the proportion of plants carrying specific somatic variants, for example, alleles affecting anthocyanin pathways or traits associated with root architecture and vigour.
- Off-types: Detection of intruding varieties or clearly distinct clones that do not belong to the desired profile, which may have entered through accidental mixing or later re-plantings.

From these data, a viticulturist can derive a complexity index for the population and define reproducible profiles. Instead of offering a generic "Massal Selection Malbec", a nursery could commercialise "Massal Selection Malbec – Profile A", characterised by a specific ratio of genotypes (*e.g.*, 60 % Type A, 20 % Type B, 20 % Type C) known to produce a given organoleptic style (for example, enhanced floral notes associated with Type B). This approach transforms the amorphous concept of massal selection into a standardised yet inherently diverse product.

7.4.2. Case example: clonal discrimination

Work by groups such as Lijavetzky and collaborators has pioneered the use of high-density arrays and resequencing to discriminate clones within populations such as Malbec (Calderón *et al.*, 2021). By identifying unique SNVs segregating among clonal lineages, it becomes possible to reconstruct the ancestry of massal populations. With this information, one can determine whether a given massal vineyard represents:

- a monoclonal expansion, where diversity is low and likely derived from a single historical introduction; or
- a polyclonal assembly, where diversity is high, indicating multiple introductions or substantial somatic diversification over time.

This distinction is crucial for conservation planning: polyclonal populations with rich clonal structure represent high-value resources, whereas monoclonal expansions, though perhaps interesting historically, contribute relatively little to the overall genetic pool.

7.5. The "sanitary genomic" layer: metagenomics and the virome

Perhaps the most impactful application of these new tools is the integration of sanitary status into the genotyping workflow. Traditionally, virus testing relied on targeted assays (ELISA, RT-PCR) for a limited set of pathogens such as GLRaV-3 or GFLV; a negative result for these targets led to the vine being labelled "healthy", ignoring the possible presence of untested viruses (Bruisson *et al.*, 2017; Saldarelli *et al.*, 2017).

7.5.1. High-Throughput Sequencing (HTS) for virome analysis

Next-Generation Sequencing supports metagenomic approaches in which the total RNA (or DNA) of a vine is sequenced (Al-Rwahnih *et al.*, 2025; Saldarelli *et al.*, 2017). In RNA-seq experiments, reads derive not only from the plant transcriptome, but also from associated fungi, bacteria, and viruses (Debat *et al.*, 2025). This makes it possible to reconstruct the complete virome of a massal population and to classify:

- Pathogenic agents: Acute viruses and viroids are associated with decline or severe quality losses.
- Latent/cryptic viruses: Ubiquitous and often asymptomatic agents such as Grapevine rupestris stem pitting-associated virus (GRSPaV) or Grapevine virus L (GVL), whose effects may be subtle or context-dependent (Cuello *et al.*, 2026; Debat *et al.*, 2019).

By combining host genotyping and virome analysis, one can generate a sanitary–genomic profile of each vine and of the population as a whole (Coetzee *et al.*, 2010; Cuello *et al.*, 2026; Vemulapati *et al.*, 2025).

7.5.2. Surgical sanitation *vs* mass eradication

In the traditional clonal model, the presence of almost any virus justified the elimination of the plant. In a massal-genomic framework, a more nuanced strategy – surgical sanitation – becomes feasible. For example, in a massal population of 1000 vines, HTS might reveal that 50 vines harbour aggressive leafroll strains, while the remaining 950 carry only mild or latent viruses. Rather than discarding the entire population, one can remove only the 50 high-risk individuals, preserving the holobiont diversity (plant plus mostly benign virome) described previously. In this scenario, HTS data serve as a sanitary passport, certifying that the population is free of harmful agents without imposing virological sterility, which might itself alter subtle vine–virus–environment interactions relevant to *terroir*.

7.6. The era of Precision Massal Selection

The convergence of KASP, dd-RAD/GBS and Amplicon-seq, together with viromics tools, has brought to viticulture a level of analytical power previously restricted to model species. The sector is no longer constrained to choose between "Uniformity" (clones) and "Uncertainty" (massal). Instead, these tools enable: high-resolution fingerprinting of massal populations; quantitative assessment of how distinct genotypes contribute to global vineyard phenotypes; and surgical cleaning of populations, removing only vines carrying detrimental viruses while preserving adaptive holobiont diversity. This technological framework underpins a new approach: Precision Massal Selection. It validates the historical wisdom of the population-based model using 21st-century genomic and metagenomic data, and provides a practical pathway to vineyards that are simultaneously diverse, traceable and sanitary-compliant. Furthermore, integrating multi-omics approaches enables us to move beyond the individual clone to understand the vineyard as a complex adaptive system considering genotypes, epimodifications, and viromes together (Yadav *et al.*, 2024). It should be noted that sequence-based platforms cannot capture chimera-mediated diversity or epigenetic variation lacking a DNA footprint. Multi-year phenotypic field observation, therefore, remains an indispensable complement to, and not a substitute for, the molecular tools described here.

8. CONCLUSIONS: TOWARDS A PARADIGM SHIFT IN GRAPEVINE SELECTION

For most of its cultivated history, the grapevine was managed as a population. Growers selected from among dozens or hundreds of individuals within a given variety, propagated budwood from the vines that were close to the local production objectives and allowed the resulting genetic mosaic to buffer whatever the season brought. This logic was never formalised as a multiplication strategy, but it worked, and the molecular evidence accumulated over the past two decades leaves little doubt as to why. The varieties inherited by modern viticulture are not static genetic entities. They are complex, layered populations shaped by centuries of somatic mutation, epigenetic drift and virus–host co-evolution, and it is precisely that complexity that sustained them across climatic fluctuations far more protracted than anything currently modelled for the next century.

The clonal system interrupted this logic, for reasons that were at the time entirely justified. The sanitary crises of the mid-20th century required a response that massal selection, by its nature and the tools available at the time, could not provide. However, the replacement of heterogeneous populations by a handful of certified clones was not a neutral sanitary intervention. It was, in genomic terms, a severe and largely irreversible bottleneck. The diversity lost was not random: it was the distributional tails of intra-varietal variation that were systematically eliminated, and it is in those tails (the irregular, the low-yielding, the agronomically inconvenient) that the allelic combinations conferring resilience to extreme or poorly anticipated stresses tend to concentrate.

Recovering that diversity does not require starting from scratch. Although more frequent in certain regions, old massal vineyards still exist across the world. In South America, South Africa, Portugal, Georgia, the terraced hillsides of Spain and Southern Italy, and even in prestigious French

estates in Bordeaux (such as Château Cheval Blanc in Saint-Émilion and Château Haut-Brion in Pessac-Léognan), these vineyards represent some of the largest existing reservoirs of pre-phylloxeric intra-varietal variation still under cultivation.

These are not relics awaiting conservation; they are functional genetic resources, validated today by palaeogenomic, phenotypic and molecular evidence, that retain precisely the complexity that has been eroded elsewhere. The question is no longer whether this diversity exists but how to manage it deliberately and at scale.

Here, we want to insist on an aspect that the available literature has not always made explicit. The value of massal populations does not reside in their capacity to yield superior individuals that can then be extracted and clonally propagated. That approach simply reproduces the bottleneck in a different way. What massal populations offer is something qualitatively different: a population of genotypes that, taken together, distributes risk across genetic backgrounds in ways that no individual clone, however well-characterised, can replicate. Managing that population, curating it sanitarily without dismantling it, is the core of what we are proposing.

The tools to do this now exist, and their convergence is arguably the most important practical development discussed in this review. High-throughput genotyping platforms can characterise the genetic composition of a massal population at a cost compatible with commercial viticulture. Metagenomic virome analysis can map the sanitary status of hundreds of individuals simultaneously, distinguishing aggressive pathogens from the latent or mildly pathogenic viral community that may in fact be integral to long-established vine–environment interactions. Combining these two layers of information makes it possible to ask, for the first time, whether the removal of a given infected individual is sanitarily necessary and genomically safe, that is, whether its removal meaningfully impairs the allelic richness or structural integrity of the population it belongs to. Where a rare or genotypically unique vine carries a damaging infection, the answer need not be elimination; thermotherapy or shoot-tip recovery preserves the genotype while resolving the sanitary risk. This kind of population-aware sanitary curation is technically feasible today, though it remains institutionally unrecognised. We also recognise that in many practical contexts, sustained field monitoring combined with targeted elimination of the most damaging viruses may be the only viable option, and one that captures dimensions of diversity that no current sequencing platform can fully resolve.

Beyond institutional barriers, commercial interests also hinder the paradigm shift we propose. Although the technical tools needed to certify massal selections as characterised populations already exist, the necessary regulatory framework is still missing. Furthermore, the current economic model, in which the entities selecting the clones – research institutions or private companies – often receive royalties from clonal material, may reinforce the preference for clonal selection over polyclonal approaches

The technical foundation for certifying a massal selection not as an individual genotype but as a characterised population, with a defined genomic composition, a quantified sanitary profile and a documented range of adaptive variation, is already in place. What is lacking is the regulatory framework to make it operational. The Portuguese polyclonal model offers a precedent worth extending; the emergence of population genomics as a mainstream viticultural tool suggests the moment is ripe for a more ambitious formulation.

None of this is straightforward, and it would be naive to present it as such. Old massal vineyards are being removed at rates that outpace conservation efforts in many regions. The economic incentives that drive viticultural decisions still favour the predictability of the certified clone over the managed uncertainty of a diverse population. And the scientific community has yet to generate, in most varieties, the longitudinal field data needed to quantify precisely how much phenotypic buffering a massal population of a given genetic complexity provides under specific climatic scenarios. These are real gaps, not rhetorical ones, and they define the research agenda that should follow from this review.

The grapevine is a perennial, clonally propagated crop with a cultivated history measured in millennia, and its capacity to persist across that history was built on population-level diversity, not individual uniformity. Restoring the population as the fundamental unit of viticultural selection, using the genomic, epigenomic and metagenomic tools now available, does not represent a regression to pre-scientific practice. It represents, rather, the most scientifically informed application of what viticulture has always, at its best, understood: that the vine is not a machine to be standardised, but a living system to be accompanied.

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