



Review

Biodiversity of Oenological Lactic Acid Bacteria: Species- and Strain-Dependent Plus/Minus Effects on Wine Quality and Safety

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Abstract: Winemaking depends on several elaborate biochemical processes that see as protagonist either yeasts or lactic acid bacteria (LAB) of oenological interest. In particular, LAB have a fundamental role in determining the quality chemical and aromatic properties of wine. They are essential not only for malic acid conversion, but also for producing several desired by-products due to their important enzymatic activities that can release volatile aromatic compounds during malolactic fermentation (e.g., esters, carbonyl compounds, thiols, monoterpenes). In addition, LAB in oenology can act as bioprotectors and reduce the content of undesired compounds. On the other hand, LAB can affect wine consumers' health, as they can produce harmful compounds such as biogenic amines and ethyl carbamate under certain conditions during fermentation. Several of these positive and negative properties are species- and strain-dependent characteristics. This review focuses on these aspects, summarising the current state of knowledge on LAB's oenological diversity, and highlighting their influence on the final product's quality and safety. All our reported information is of high interest in searching new candidate strains to design starter cultures, microbial resources for traditional/typical products, and green solutions in winemaking. Due to the continuous interest in LAB as oenological bioresources, we also underline the importance of inoculation timing. The considerable variability among LAB species/strains associated with spontaneous consortia and the continuous advances in the characterisation of new species/strains of interest for applications in the wine sector suggest that the exploitation of biodiversity belonging to this heterogeneous group of bacteria is still rising.

Keywords: malolactic fermentation; lactic acid bacteria; malolactic bacteria; *Oenococcus oeni*; *Lactiplantibacillus plantarum*; wine; aroma; biogenic amines; lactobacilli; biocontrol



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1. LAB in Oenology: Introductory Aspects and Biodiversity

During the winemaking process, lactic acid bacteria (LAB) promote the decarboxylation of L-malic acid to L-lactic acid, which is denoted as malolactic fermentation (MLF) [1]. This biological process occurs at the end of the alcoholic fermentation (AF), the principal phase in winemaking, which is conducted by yeasts (mainly belonging to the *Saccharomyces* genus, but together, in some cases, with selected non-*Saccharomyces* strains) [2–4]. MLF is required for aged red wines and some young red, white, and base sparkling wines, since it supplies microbiological stabilisation by reducing the nutrients in wine and lowers the acidity of the final product [5,6]. Specific management of microbial resources inoculated to promote desired biochemisms (e.g., co-inoculation), can favour a simultaneous progression of AF and MLF [7,8].

MLF enhances wine flavour and aroma complexity by freeing relevant amounts of carbonyl compounds, such as diacetyl (2,3-butanedione), which contributes to a wine's buttery flavour [9]. Moreover, LAB species have demonstrated an ability to promote several biochemical modifications of wine able to enhance its aroma, such as the release of volatile thiols from precursor compounds, methionine metabolism, glycosidases, and esterase activities [10–12]. However, during winemaking, the MLF dynamics are often unpredictable, and it is problematic to monitor or manage. Spontaneous MLF may affect wine quality, since the production of bacteria-derived off-flavour molecules (such as volatile phenols and acetic acid) and compounds dangerous to consumer health, i.e., biogenic amines (BAs) and ethyl carbamate. Thus, it is necessary to exert the microbiological control of this biochemical process throughout the winemaking process to guarantee the final product's quality and safety [13]. A composite microbial consortium is implicated in the winemaking process, comprising yeast, bacteria, fungi, and viruses [14–16]. Concerning LAB, they are indeed present on both grape skins and cellar environment equipment [17], but the operators can directly inoculate them by the addition of selected starter cultures [18].

LAB, microaerophiles, and Gram-positive bacteria specifically produce lactic acid as a primary metabolite of glucose catabolism [19]. Consistent with their glucose catabolic activity, they can be distributed into two groups: bacteria that ferment glucose with lactic acid as the main by-product (homofermentative), and the others that produce ethanol, carbon dioxide, and lactic and acetic acid after glucose fermentation (heterofermentative). The most common LAB isolated from musts and wine are oenococci, lactobacilli and pediococci (Table 1).

Table 1. Species of selected lactic acid bacteria found in association with raw materials in representative phases of winemaking (grape harvest, must alcoholic fermentation, wine malolactic fermentation), according to selected studies [20–25].

Grape and Harvest	Must and AF	Wine and MLF
	<i>Oenococcus oeni</i> (80–100%)	
	<i>Lactiplantibacillus plantarum</i>	
	<i>Lentilactobacillus hilgardii</i>	
	<i>Lentilactobacillus buchneri</i>	
<i>Oenococcus oeni</i> (0–10%)	<i>Lentilactobacillus diolivorans</i>	
<i>Limosilactobacillus alvi</i>	<i>Lacticaseibacillus casei</i>	
<i>Levilactobacillus brevis</i>	<i>Lactilactobacillus curvatus</i>	
<i>Limosilactobacillus frumenti</i>	<i>Limosilactobacillus alvi</i>	
<i>Liquorilactobacillus mali</i>	<i>Levilactobacillus brevis</i>	
<i>Apilactobacillus kunkeei</i>	<i>Limosilactobacillus frumenti</i>	<i>Oenococcus oeni</i>
<i>Fructilactobacillus lindneri</i>	<i>Secundilactobacillus collinoides</i>	<i>Lactiplantibacillus plantarum</i>
<i>Fructilactobacillus sanfranciscensis</i>	<i>Lacticaseibacillus paracasei</i>	<i>Lentilactobacillus hilgardii</i>
<i>Lentilactobacillus kefir</i>	<i>Lactiplantibacillus pentosus</i>	<i>Levilactobacillus brevis</i>
<i>Lactococcus lactis</i>	<i>Liquorilactobacillus mali</i>	<i>Fructilactobacillus lindneri</i>
<i>Enterococcus faecium</i>	<i>Fructilactobacillus lindneri</i>	<i>Limosilactobacillus frumenti</i>
<i>Enterococcus avium</i>	<i>Fructilactobacillus fructivorans</i>	<i>Lactococcus</i> sp.
<i>Enterococcus durans</i>	<i>Lactobacillus delbrueckii</i>	<i>Pediococcus parvulus</i>
<i>Enterococcus hermanniensis</i>	<i>Lactococcus lactis</i>	
<i>Leuconostoc mesenteroides</i>	<i>Leuconostoc citreum</i>	
<i>Pediococcus damnosus</i>	<i>Leuconostoc fructosum</i>	
<i>Pediococcus parvulus</i>	<i>Leuconostoc mesenteroides</i>	
<i>Weissella paramesenteroides</i>	<i>Enterococcus faecium</i>	
	<i>Pediococcus damnosus</i>	
	<i>Pediococcus parvulus</i>	
	<i>Weissella paramesenteroides</i>	

Note: AF, alcoholic fermentation; MLF, malolactic fermentation.

The *O. oeni* species has ellipsoidal-to-spherical cells typically present in pairs or short chains. It is an asporogenous and nonmotile bacteria with an optimal growth range between pH 4.8–5.5 and 20–30 °C. The *O. oeni* population typically raises during the AF, and it often becomes the only species found in wine at the end of MLF [26,27]. *O. oeni* is the principal

LAB species of choice for winemakers because it can tolerate the harsh environment for bacterial survival after the completion of the AF [28]. Three different decarboxylation pathways are responsible for the conversion of L-malic acid to L-lactic acid (Figure 1).

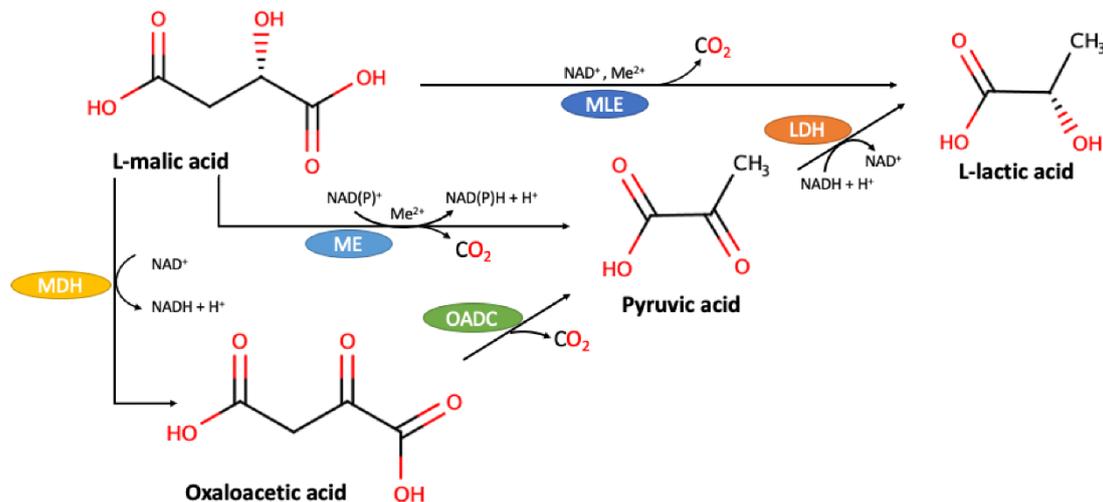


Figure 1. Possible biochemical routes responsible for the decarboxylation of L-malic acid to L-lactic acid. Image reproduced from Acevedo et al. [29]. MDH, malate dehydrogenase; ME, malic enzyme; MLE, malolactic enzyme; OADC, oxaloacetate decarboxylase; LDH, lactate dehydrogenase.

Lactobacilli have elongated shapes with rod-like forms, and they are facultative heterofermentative. These bacteria's taxonomy has been recently rewritten using a holistic approach that considered ecological, genetic, metabolic, and physiological criteria [30]. The previously genus denoted as *Lactobacillus* has been reorganised into 25 novel genera, and the previous *Lactobacillaceae* and *Leuconostocaceae* families have been merged to form the new *Lactobacillaceae* family [30]. Lactobacilli have shown that they successfully withstand winemaking conditions and possess many advantageous properties that make them appropriate for MLF management [31,32]. Besides their malolactic activity, these LAB detain complex secondary metabolisms that can positively influence a wine's final aroma and flavour, including synthesis or catalysis of citrates, amino acids, polysaccharides, aldehydes, and esters [33,34]. In particular, *Lactiplantibacillus plantarum* strains can promote MLF under high pH conditions, avoiding acetic acid synthesis due to their facultative heterofermentative features, and modifying wine aromas because of a more composite enzymatic profile when compared to *O. oeni* [31,32]. Together with the properties mentioned above, the significant oenological features of *L. plantarum*, i.e., the elevated tolerance to high both ethanol and SO₂ concentration and to pH conditions, make strains belonging to this species the source of the novel generation of MLF starter cultures [18,25,31].

Pediococcus damnosus, *P. parvulus*, *P. pentosaceus*, and *P. inopinatus* belong to the genus *Pediococcus* that has oenological importance [35]. They have a spherical or ellipsoidal form and possess a homofermentative glucose metabolism. *Pediococcus* spp. are commonly considered spoilage bacteria in wine because some strains can cause viscosity in wine due to their production of exopolysaccharides, produce a high amount of acetic acid, and synthesise biogenic amines [36]. However, species/strains belonging to the *Pediococcus* genus can positively influence the production of volatile compounds by synthesising a large number of secreted enzymes [36,37].

The huge microbial diversity of LAB associated with natural consortia (Table 1), together with the evolution of *L. plantarum* and pediococci significance in oenology, underlines the continuous interest in exploring the potential role of bacterial biodiversity in wine.

It is interesting to point out that for numerous LAB strains worldwide that are isolated from the oenological environment, their complete genome has been already sequenced

(Table 2), promoting knowledge improvements, molecular advances, and the application of “omics” approaches.

Table 2. Information about literature on the complete genome sequences of wine LAB strains.

Strains	Place of isolation	Reference
<i>Oenococcus oeni</i> PSU-1	United States of America	[38]
11 <i>O. oeni</i> strains (6 commercial and 5 environmental isolates)	Commercial starter cultures and Australia	[39]
<i>Oenococcus oeni</i> OM27	Italy	[40]
5 <i>O. oeni</i> strains isolated from the same <i>terroir</i>	Italy	[41]
14 <i>O. oeni</i> strains isolated from different wines	France	[42]
28 <i>O. oeni</i> strains isolated from different wines	Several countries (mainly from France and Australia)	[43]
<i>Oenococcus oeni</i> X2L	Argentina	[44]
About 135 <i>O. oeni</i> wine strains	Several countries (mainly from France and Australia)	[45]
<i>Oenococcus oeni</i> UNQOe19	Patagonia	[46]
<i>Lactiplantibacillus plantarum</i> Lp90	Italy	[47]
<i>Lactiplantibacillus plantarum</i> XJ25	China	[48]
<i>Lactiplantibacillus plantarum</i> UNQLp 11	Patagonia	[49]

2. Impact of Wine Environment on LAB Metabolisms

After the ending of the AF, the concentration of LAB populations does not usually change for 10 to 15 days, since bacterial multiplication is likely to be impaired by the residual yeast metabolic activity. Then, the LAB initiate to grow, and MLF occurs when the bacterial concentration in wine roughly corresponds to 10^6 CFU/mL. However, the physical and chemical factors of wine that can affect LAB’s malolactic performances are numerous [28]. Indeed, bacterial multiplication is enhanced by sulfur dioxide and ethanol concentrations lower than 20 mg/L and 14% (v/100 mL), respectively, relatively high pH values (>3.5), and a wine temperature ranging from 19 to 26 °C. The above stress factors possess different cellular targets, and they can affect different bacterial metabolisms, and thus are able to exert strong effects on cellular growth and viability [50]. Sulfur dioxide (SO₂) is routinely added to must and wines during the winemaking process because its antimicrobial and antioxidant action preserves the chemical and microbiological quality of wine. SO₂ is detectable in wine in both a free and bonded form: the former is available and able to carry out its protective action, whereas the latter cannot play an active role since it is bonded to several wine-related compounds (acids, anthocyanins and acetaldehyde). Even though LAB can exert cellular mechanisms for adaptation to SO₂ [51], high additions (>20 mg/mL) of SO₂ can inhibit the bacterial malolactic performances, thus suggesting that a strict monitoring of the additive concentration is required during the MLF. Ethanol concentrations over 14% (v/100 mL) can affect growth and metabolism of LABs and this toxic action is enhanced by the increase of temperature and lowering of pH [52,53]. Indeed, pH and alcohol content of wine have demonstrated that they are fundamental oenological factors to regulate bacterial viability and, subsequently, their malate-degrading ability [53,54]. High ethanol concentrations also impair cellular mechanisms devoted to maintaining pH homeostasis, increasing the passive proton flux into bacteria [55]. However, LAB’s capacity to survive at elevated ethanol concentrations is a strain-dependent property among different species [25]. Temperature is a parameter that disturbs the growth rate and, in particular, the length of the lag phase of LAB [56]. Previous microbiological observation emphasised the stress exercised by high temperatures on LAB metabolism [57]. The authors indicated that temperatures above 30 °C prejudiced bacteria’s capacity (in particular, *O. oeni*)

to degrade the malic acid and potentially enhanced acetic acid production. These findings have been recently confirmed by Guzzon and coworkers [58]. They showed that the *L. plantarum* strain more efficiently carried out the MLF compared to *O. oeni*, since the latter species was inhibited by a high fermentation temperature with subsequent incomplete malic acid degradation.

3. Plus Effects: Influence of MLF on Wine Organoleptic Properties, Bioprotection and the Removal of Undesired Compounds

In recent years, the metabolism of lactic bacteria that carry out MLF has been thoroughly investigated [25,59,60]. In addition to the decarboxylation of malic in lactic acid, which is the principal outcome of MLF, this biological process also produces a significant number of metabolic by-products. Most of these compounds are strain-specific, and they can positively modulate the volatile aroma profile and aroma perception of a wine [61,62]. In addition to the benefits for sensory quality, other important targets regarding the innovative use of LAB in oenology, are the biocontrol of undesired microbes (e.g., spoilers) and the degradation of toxic compounds. In fact, LAB have been proposed as part of potential sustainable solutions to enhance wine safety and reduce relevant economic losses.

3.1. Esters

Esters are secondary or tertiary compounds that considerably contribute to a wine's aromatic profile. They can be synthesised by yeast and bacteria throughout the AF and MLF, and their qualitative and quantitative profile can be modified by wine ageing [63,64]. Esters are formed through the esterification process or via ester hydrolysis [64]. LAB's contribution to the ester detectable in wine has been underlined by several investigations [12,63]. LAB's ability to affect or enhance the amount of esters in wine is strain-specific, and it is modulated by the MLF inoculation procedure [9,65,66]. In general, MLF is associated with increases in ethyl fatty acid esters' concentration, such as ethyl acetate, ethyl lactate, ethyl octanoate, and ethyl hexanoate [61,67]. This class of volatile molecules is responsible for the desired fruity aroma of wines. The LAB esterases have been recently investigated [17,68]. Costello and coworkers [69] have shown that *O. oeni* is able to produce relevant amounts of ethyl octanoate, propyl octanoate, and ethyl hexanoate due to the significant activity of intracellular esterases throughout the fermentation process. *L. plantarum* strains have been recently proposed as malolactic starters, since this species is a significant source of esterase enzymes [70]. In fact, Lerm et al. [18] highlighted that *L. plantarum* strains, due to their enzymatic activity, can modulate wines' volatile profiles more efficiently than *O. oeni*. These results have been further confirmed by investigating lactobacilli isolated from South African wines [33].

3.2. Carbonyl Compounds

Acetaldehyde is the main carbonyl compound present in wine that can add to wines' aromatic profile, such as notes of "nutty" and "bruised apple." Lactic bacteria can metabolise acetaldehyde when linked to sulfur dioxide, thus increasing the final concentration of this inhibitory compound [71]. However, the decrease in the acetaldehyde concentration caused by LAB can influence the colour and modulate the final wine's sensorial impression [72]. One of the major aroma compounds associated with LAB is diacetyl (2,3-butanedione), which originates from citrate fermentation and gives buttery and nutty notes to wines [59]. The citric acid is enzymatically transformed into pyruvate that can be converted to acetolactic acid. The decarboxylation of this last compound produces 2,3-butanediol and acetoin and their the oxidation gives rise to diacetyl during the occurrence of the MLF. When found in the range of 1–4 mg/L, diacetyl usually gives a wine positive aromatic notes, whereas when it is detected at concentrations higher than 5–7 mg/L, it is considered an undesired spoilage feature. Consequently, winemakers modulate diacetyl concentrations in order to enhance a wine's aroma through microbiological management during the winemaking process [73,74]. However, a number of other different factors, such

as the wine type, as well as oxygen and sulfur dioxide concentrations, determines the final concentration of diacetyl in wine.

3.3. Thiols

Volatile thiols are compounds of specific relevance to the composition of the varietal character [75]. In fact, they give tropical fruit notes to wine obtained from Sauvignon Blanc, Riesling, Cabernet Sauvignon, and Merlot grapes [76]. These molecules do not exist in grape juice, and are released during fermentative processes. However, wine yeasts do not synthesise volatile thiols *de novo*, but they promote thiol release from its precursor. Recently, Takase and coworkers [11] demonstrated that *L. plantarum* carry out the cleavage of 3-Sulfanylhexan-1-ol (3SH) from its precursor 3SH from S-3-(hexan-1-ol)-l-cysteine (3SH-S-cys) and S-3-(hexan-1-ol)-l-cysteinylglycine (3SH-S-cysgly), which contribute to varietal aromatic profiles, with notes of grapefruit and passionfruit. Even though the enzymes for the pathway and the specific enzyme in charge of this conversion have not yet been characterized, the above findings indicate that MLF guided by enzymatically active lactobacilli can improve the varietal aroma of produced wines. However, other volatile sulfur compounds, such as methanethiol, methionol, and dimethyl disulfide, when present in the opportune amounts, can enhance a wine's bouquet and sensorial quality [77].

3.4. Monoterpenes

The varietal compounds specific to each grape variety have great importance in the composition of the wine's aromatic profile. They can be present in the berry as free volatile molecules or mainly linked to sugars, these being the aroma precursors. The glycol-conjugates are not odorous and volatile, but they are a source of odorant molecules in wines, with a varietal, microbial, or technological origin. Volatile monoterpenes are released at the early stage of winemaking, directly or after the adding of oenological enzymes [78]. The microbial conversion from the precursors of free volatile monoterpenes necessitate the secretion of active β -glucosidase (in the case of monoglycosides) or exoglycosydases (active on disaccharides) [79]. Numerous investigations have demonstrated that *O. oeni* possesses a detectable β -glucosidase activity [80,81]. Recently, Michlmayr and coworkers [82] identified numerous LAB glycosidases with potential in the release of grape-derived aroma precursors. The authors described a glucosidase and an arabinosidase from *O. oeni* able to produce high concentrations of monoterpenes. The above evidence highlights that these bacterial enzymes can play an important role in the hydrolysis of aroma precursors during malolactic fermentation, since they were active in grape must and displayed wide substrate specificities. Hydrolytic enzymatic activity has also been detected in other oenological LAB genera, i.e., lactobacilli and pediococci [83]. Other authors have compared several malolactic starter cultures' performances in the releasing of specific volatile odorant molecules [84]. *Levilactobacillus brevis* and *Lacticaseibacillus casei* strains demonstrated that they were differentially capable of enhancing the amount of C13-norisoprenoides and monoterpenes in wine after completing the MLF. Recent investigations have indicated that several *L. plantarum* strains show a peculiar enzymatic profile when compared to other LAB, thus proposing that this species can perform a significant action in contributing to a wine's aromatic profile [10,18].

3.5. Degradation of Toxic Compounds

Two main classes of contaminants of microbial origin can affect wine safety: mycotoxins (mainly ochratoxin A, OTA) and BAs [85].

Mycotoxins are secondary metabolites produced by filamentous fungi, with relevant carcinogenic, teratogenic, nephrotoxic, and hepatotoxic properties [86]. Ochratoxin A, produced on grape berries by several *Aspergillus* and *Penicillium* species, is the most frequently mycotoxin found in wine samples [87]. Several phases in winemaking can influence OTA reduction, including microbes. Both alcoholic and malolactic fermentation can reduce OTA in wine [88]. In effect, selected yeasts and LAB demonstrated this capability [89,90].

Del Prete et al. [91] showed OTA removal by five LAB species of interest in wines, suggesting a cell-binding activity [91]. In *O. oeni*, heat-inactivated cells also were capable of removing OTA in synthetic media [92]. Abrunhosa et al. [93] highlighted the OTA biodegradation by *P. parvulus* strains isolated from Douro wines, as well as in grape must.

BAs are low molecular weight, organic bases, frequently occurring in wine, in which up to 25 different amines could be detected [94]. Although they can be found in wine in very low amounts compared to other fermented foods, BAs can exert a dangerous effect on consumer health because the ethanol can strengthen their noxious action by affecting human action on amine-oxidases accountable for their inactivation [95]. Enzymatic removal of BAs may represent a functional and cost-effective method to eliminate these harmful compounds in wine production. Capozzi and coworkers [96], during the physiological characterization of a *L. plantarum* population, selected two strains capable of degrading tyramine and putrescine. Callejón and collaborators [97] also identified new BAs-degrading activities of LAB in wine. The authors studied the enzymatic activities in charge of BAs degradation in 76 lactobacilli, pediococci, and enterococci strains isolated from wine. The enzymes accountable for BAs conversion were identified as multicopper oxidases, were isolated and purified from *L. plantarum* and *P. acidilactici* strains. Other lactobacilli were recently described as capable of BAs degradation, such as *Latilactobacillus curvatus* G-1, *L. plantarum* CAU3823, and *L. plantarum* PP02 [98,99]. Taken together, the above results indicate the possible use of wine *L. plantarum* strains as candidates for the design of starter cultures that can degrade biogenic amines during MLF.

3.6. Bioprotection

One emerging trait of lactic acid bacteria on grapes and wine is their potential in bioprotection [100]. The reduction of the chemical intake in wine, from the farm to the fork (from grape cultivation up to winemaking) is rising due to increasing consumer concerns about the toxicological problems of its residues [101] and the emerging evidence of undesired side-effects associated with fermentative performances [102]. This has led producers and researchers to orientate toward more sustainable and eco-friendly approaches. In this light, the selection of microbial strains with potential as bioprotective cultures and/or biological control agents is an emerging trait that is still poorly explored among lactic acid bacteria isolated from grapevine and wine environments [103]. In fact, LAB were already described as promising bioprotective cultures in other food supplies [104,105]. They produce a wide range of active antimicrobial compounds, such as organic acids, hydrogen peroxide, fatty acids, acetoin, diacetyl, cyclic dipeptides, and bacteriocins [106–108]. In the grape sector, these microbes could be used for in-field applications and post-harvest diseases, as well as during wine fermentation. In particular, *L. plantarum* strains have been proposed for the biocontrol of the filamentous fungus *Botrytis cinerea*, the microorganism responsible for grey mold formation and the main grape spoiler in both pre- and post-harvest conditions [109], as several strains have shown a strong competition and a rapid colonisation of wound space in other fruit crops [110–112]. In winemaking, LAB ensure a rapid implantation of malolactic fermentations when used as starter cultures, thus limiting the residual nutrients for the microorganisms that cause wine spoilage, such as *Brettanomyces bruxellensis* [113], which produce detrimental volatile compounds that affect the organoleptic quality of the final product, leading to important economic losses [114]. Besides, malolactic strains (belonging to both *O. oeni* and *L. plantarum* species) co-inoculated with yeasts demonstrated a potential in enhancing bioprotection [115,116]. In this light, LAB could be a concrete alternative to synthetic protectants, including sulfur dioxide [116].

4. Minus Effects: Production of Off-Flavours and Other Undesired Compounds

As described in the last paragraph, selected LAB can enhance global quality in oenological production. However, some species/strains belonging to the heterogeneous group of LAB can also depreciate wines, with substantial economic losses and/or possible undesired consequences for human health.

4.1. Production of Off-Flavours by Lactic Acid Bacteria

Numerous secondary compounds synthesised by lactic acid bacteria can affect a wine's sensorial profile, such as volatile phenols, and N- heterocyclic and sulfur volatile compounds [72]. Several phenolic compounds are present in wine; in particular, hydroxycinnamic acids (caffeic, ferulic, and p-coumaric acids) can be a substrate for LAB-mediated enzymatic conversions [117]. The feraric, cutaric, and caftaric esterified forms of hydroxycinnamic acids can be released into wine due to the cinnamoyl esterase activities promoted by bacterial enzymes. Phenolic acids can be decarboxylated into 4-vinyl derivatives and then converted to 4-ethyl derivatives, two classes associated with undesired odorous properties described as "wet dog," "sweaty horse," and "band-aid" [113]. Different investigations have described numerous LAB species' ability to synthesise these detrimental volatile phenols during the vinification process. Couto and collaborators [118] tested the ability of 35 strains of lactic acid bacteria belonging to 20 different species in converting phenolic acids into the corresponding volatile phenols. The reduction stage of the above pathway was detected in *L. brevis*, *L. collinoides* and *L. plantarum*. In contrast, strains belonging to the genus *Pediococcus* demonstrated the production of 4-vinylphenol but not 4-ethylphenol from p-coumaric acid. *O. oeni* and *L. mesenteroides* strains were unable to produce p-coumaric acid derivatives. LAB's capacity to carry out the conversion of volatile phenols in wine has been investigated by applying a novel molecular method able to identify strains that have this ability. The obtained data indicated that *L. plantarum* strains produced the corresponding vinyl and ethyl derivatives from hydroxycinnamic acids, whereas *L. brevis* and *P. pentosaceus* strains only produced the vinyl ones. A recent study confirmed the above results, indicating that all the species belonging to the *L. plantarum* group are genetically able to produce ethylphenol from vinylphenol [119]. Indeed, the authors highlighted the possible significance of lactic acid bacteria in volatile-phenol spoilage of wine after showing a faster ethylphenol synthesis by these bacteria than by yeasts.

The production of detrimental flavours in wine has been associated with the LAB catabolism of lysine and ornithine, which implicates the formation of numerous very strong and smelly nitrogen-heterocycle "mousy" compounds [120]. These compounds are detected on the back portion of the buccal region as a persistent aftertaste reminiscent of a mouse cage. *O. oeni*, *Leuconostoc mesenteroides*, and some lactobacilli can produce three nitrogen-heterocycle compounds relevant at the sensorial level, i.e., 2-ethyltetrahydropyridine (ETPY), 2-acetyl-1-pyrroline (ACPY), and 2-acetyltetrahydropyridine (ACTPY) [120]. High pH levels (>3.5) or low sulfur dioxide concentration during the winemaking process are likely to promote the growth of heterofermentative lactobacilli and pediococci strains capable of synthesizing the above-mentioned nitrogen-heterocycle compounds. However, very little is known about this defect's physiological basis and its effective consequence on wine quality [121].

Volatile sulfur compounds are produced during the MLF by the bacterial metabolism that utilises cysteine and methionine as substrate, these being the two sulfur-containing amino acids. *O. oeni* and lactobacilli can convert methionine to dimethyl sulfide, 3-(methylsulfanyl) propan-1-ol, methanethiol, and 3-(methylsulfanyl)-propanoic acid; whereas *O. oeni* strains can use cysteine to produce thiazoles, thus resulting in aroma descriptors such as "sulfury," "roasted," or "toasted" [122]. Investigations have recently examined the potential enzymes in depth, and codified the genes for the catabolic pathway of methionine in LAB during the MLF process [122,123]

4.2. Production of By-products Harmful to Consumer Health (i.e., BAs, EC)

Even though LAB are considered fundamental to the completion of wine fermentation, they also can represent a cause of alarm for human health, since they can synthesise harmful compounds such as BAs and ethyl carbamate (EC) [124,125].

Histamine, putrescine, and tyramine are the BAs most frequently detected in contaminated wine. They are formed after enzymatic decarboxylation of their respective amino acid precursors, histidine, ornithine, and tyramine [126]. Tyramine and histamine are the

most harmful to human health. The concomitant presence of other BAs, such as putrescine and cadaverine, can enhance this dangerous action [127]. LAB's role in biogenic amines' biosynthesis has been widely reported [125], with relevant cases also in the oenological field (Table 3).

Table 3. A nonexhaustive list of biogenic amine (BAs)-producing LAB species in wine.

Microbial Species	Produced BAs	References
<i>Enterococcus faecium</i>	tyramine	[128]
<i>Levilactobacillus brevis</i>	tyramine, putrescine, phenylethylamine	[129–132]
<i>Lentilactobacillus hilgardii</i>	histamine, tyramine, putrescine, phenylethylamine	[130,131,133,134]
<i>Lactiplantibacillus plantarum</i>	tyramine	[135]
<i>Lacticaseibacillus rhammosus</i>	histamine	[136]
<i>Oenococcus oeni</i>	histamine, putrescine	[137,138]
<i>Pediococcus parvulus</i>	histamine	[139]

Note: BAs, biogenic amines.

The ability to synthesise BAs is likely to be strain-dependent and not a species-specific property, and it is enhanced by favourable conditions for bacterial growth (availability of nutrients) and decarboxylating activity (low pH of wine) [140,141]. Several studies have documented *O. oeni* strains' contribution to the histamine content in wines and the presence of putrescine and cadaverine contaminated grape musts [142,143]. Strains of the genus *Pediococcus* can also be responsible for producing BAs in wines [144]. Concerning lactobacilli, strains belonging to different species demonstrated the ability to synthesise histamine and tyramine [138,145]. The lack of BAs production should thus be considered a pivotal parameter for the oenological selection of LAB, as demonstrated by recent investigations regarding the identification of autochthonous bacterial strains unable to form BAs during MLF [74,146]. Microorganisms capable of amino acid decarboxylation can be identified by applying a plate test with specific growth media [147], as well as specific molecular PCR-based approaches, including multiplex amplification or sensitive on-chip approaches [148]. To control BAs contamination in wine, the microbial management of MLF has been proposed by adopting starter cultures unable to produce BAs and able to dominate the indigenous microbiota that constitute the wine ecological niche [74,144]. No technological approaches are available to lower the amount of BAs in contaminated wine.

Ethyl carbamate (EC) is a carcinogenic molecule produced throughout the fermentation process by a non-enzymatic reaction between ethanol and a compound containing a carbamyl group. The principal carbamyl group implicated in EC synthesis is urea derived by the yeast metabolism of arginine, citrulline, and carbamyl phosphate [149]. Arginine deiminase promotes, by arginine deamination, the formation of citrulline, one of the main precursors for EC formation [124]. Heterofermentative LAB, such as *L. hilgardii*, *L. plantarum*, *L. buchneri*, and *O. oeni*, can actively catabolise arginine [150–152]. Several abiotic factors can enhance ethyl carbamate production, i.e., needless nitrogen adding in the vineyard, low wine pH, high storage temperature, elevated ethanol concentrations and relevant malic acid concentrations [31]. Moreover, EC's presence can be lowered by impairing the synthesis of its precursors, and this goal can be achieved through the employment of a LAB starter culture that produces low concentrations of citrulline [124].

5. Novel Inoculation Approaches to Enhance LAB Impact on Wine Quality

The simultaneous inoculation of selected strains of LAB species together with starter yeast directly into the must at the beginning of the alcoholic fermentation is considered a promising practice for improving the quality and safety of wine production [153,154]. This approach allows the simultaneous promotion of alcoholic fermentations (AF) and malolactic (MLF) fermentations [155] to avoid possible MLF arrests, generally caused by high ethanol concentrations, high acidity, and nutrient scarcity that characterize the wine at the end of AF [156]. Moreover, LAB and yeast co-inoculation demonstrated an

ability to reduce production time, improving the quality and the safety of the produced wine [156]. However, despite the above advantages, the yeast/lactic bacteria co-inoculation approach can be applied, subject to the preliminary study of the mutual influence and coexistence capacity between specific strains of *S. cerevisiae* and lactic acid bacteria when inoculated together [157]. Specific compatibilities have been observed between commercial yeasts and LAB strains, suggesting the importance of estimating different starters' microbial compatibility before their use in large-scale winemaking [157]. Recent studies have been conducted that investigated the interactions between yeast and commercial LAB strains after their inoculation into must [13]. All the evidence indicated that the two starters' simultaneous inoculation allowed for the rapid development of bacterial populations, resulting in a drastic reduction in the time required for MLF to take place and in the volatile acidity values in the wine produced. Another important advantage of the simultaneous yeast/bacteria inoculation is the reduction of the content of biogenic amines in wines produced in this way, compared to those obtained with the bacterium inoculation at the end of AF [158,159]. The co-inoculation approach was recently presented using selected strains of *Latiplantibacillus plantarum* as a malolactic starter [25]. Co-inoculation of *S. cerevisiae* and *L. plantarum* in grape must implemented the levels of adaptation of the bacterium to the harsh conditions of the wine, again reducing the time required for completion of MLF [18,32,160]. Increasing interest has been directed toward understanding the interactions between *S. cerevisiae* and non-*Saccharomyces* strains with different LAB species [161,162]. The species-specific impact in wineries has been recently assessed by studies that carried out vinification tests at the industrial scale [8,163]. The obtained results highlighted the impact of the different combinations of the strains on the "volatome" of produced wine, with specific attention paid to the effects of the concurrent inoculation of the LAB species, thus confirming that the aromatic complexity of the wine reflected the formulation of the starter cultures [164]. Increasing interest has been directed toward the use of immobilised cells for the production of fermented beverages. This strategy offers numerous technical and economic advantages and it can positively influence bacterial metabolism, affecting wine quality and aroma [165]. Immobilisation systems also benefit from recycling the biocatalysts numerous times, thus maintaining the fermentation activity [166]. Starter strains of *O. oeni* have also been immobilised with good results [167]. Malolactic starters included in plant waste (cobs, grape skins, and stems) have been used to promote MLF in white wine, showing a positive protective effect of immobilisation against stress caused by ethanol concentration and the presence of SO₂ on bacterial cells [168]. *S. cerevisiae* and LAB cells can be included on residues of vegetable origin or in calcium alginate spheres allowed the promotion of FA and MLF simultaneously. Recently, Blevé et al. [169] produced the co-immobilisation of *S. cerevisiae* and *O. oeni* cells in alginate drops, and they have used them in microvinifications. This mixed starter allowed for efficient AF and MLF fermentation processes, producing wines enhanced in their organoleptic properties compared with wines produced by the traditional sequential inoculation free cell starters.

6. Conclusions

The achievement of MLF depends on either the viability or metabolic performances of the LAB starter culture and the management of several physicochemical parameters of the fermentation process. MLF represents a fundamental step in winemaking that ensures microbial stability, reduced total acidity, and enhancement of aroma and flavour profiles in wines [5,59]. The continuous characterisation of the biodiversity associated with spontaneous fermentation will have, in the near future, a fundamental importance in selecting new starter cultures, designing tailored microbial resources for traditional/typical wines, and conceiving sustainable innovations in winemaking, including biotechnological solutions to the negative impact of climate change [18,27,62,101,170]. This up-to-date literature review summarises both the positive and negative influences of malolactic bacteria on wine

quality and safety, underlining species- and strain-dependent characteristics, and looking toward a more competitive and resilient wine industry.

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