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Metabolic insights of lactic acid bacteria in reducing off-flavors and antinutrients in plant-based fermented dairy alternatives

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Abstract

Multiple sensorial, technological, and nutritional challenges must be overcome when developing plant-based fermented dairy alternatives (PBFDA) to mimic their dairy counterparts. The elimination of plant-derived off-flavors (green, earthy, bitter, astringent) and the degradation of antinutrients are crucial quality factors highlighted by the industry for their effect on consumer acceptance. The adaptation of plant-derived lactic acid bacteria (LAB) species into plant niches is relevant when developing starter cultures for PBFDA products due to their evolutionary acquired ability to degrade plant-based undesirable compounds (off-flavors and antinutrients). Some plant-isolated species, such as *Lactiplantibacillus plantarum* and *Limosilactobacillus fermentum*, have been associated with the degradation of phytates, phenolic compounds, oxalates, and raffinose-family oligosaccharides (RFOs), whereas some animal-isolated species, such as *Lactobacillus acidophilus* strains, can metabolize phytates, RFOs, saponins, phenolic compounds, and oxalates. Some proteolytic LAB strains, such as *Lacticaseibacillus paracasei* and *Lacticaseibacillus rhamnosus*, have been characterized to degrade phytates, protease inhibitors, and oxalates. Other species have also been described regarding their abilities to biotransform phytic acid, RFOs, saponins, phenolic compounds, protease inhibitors, oxalates, and volatile off-flavor compounds (hexanal, nonanal, pentanal, and benzaldehyde). In addition, we performed a blast analysis considering antinutrient metabolic genes (42 genes) to up to 5 strains of all qualified presumption of safety-listed LAB species (55 species, 240 strains), finding out potential genotypical capabilities of LAB species that have not conventionally been used as starter cultures such as *Lactiplantibacillus pentosus, Lactiplantibacillus paraplantarum*, and *Lactobacillus diolivorans* for plant-based fermentations. This review provides a detailed

understanding of genes and enzymes from LAB that target specific compounds in plant-based materials for plant-based fermented food applications.

KEYWORDS
antinutrients, fermentation, lactic acid bacteria, off-flavors, plant-based alternatives

1 | INTRODUCTION

Milk fermentation processes have been used due to their preservation and sensorial characteristics, contributing to the safety and quality of final fermented food products such as yogurt, cheese, and kefir. In the last decade, the plant-based dairy-fermented market has increased due to the growth of consumers' demand and awareness toward more sustainable, healthier, and more ethical food production processes and products (Engels et al., 2022; Harper et al., 2022; Ma et al., 2022; Tangyu et al., 2019). The plant-based milk industry utilizes raw materials that require less energy, emit less greenhouse gas emissions, and need less water and land usage to be produced compared to the processing of bovine milk (Harper et al., 2022). The main challenges of the plant-based fermented dairy alternatives (PBFDA) industry in replacing dairy products are mimicking dairy-like flavors, color, and texture properties characteristic of dairy-fermented products, and developing products without off-flavors and antinutrients to improve their acceptance (Genet, Molina, et al., 2023; Sedó Molina et al., 2022; Sedó Molina, Shetty, et al., 2024).

The terms "antinutrients" and "off-flavors" refer to multiple and physiochemically different undesirable compounds that affect a food product's nutritional and sensory profiles, in this case, PBFDAs. On the one hand, there are several antinutrients present in different plant-based matrices that either decrease the digestibility of proteins, such as protease inhibitors, reduce the bioavailability of nutrients (minerals, vitamins, and proteins) such as phytates, polyphenolic compounds, and saponins, or cause diverse health effects such as plant oligosaccharides (raffinose, stachyose, and verbascose) that are attributed to result in flatulence (Gemede & Ratta, 2014; López-Moreno et al., 2022; Popova & Mihaylova, 2019). On the other hand, off-flavors are classified into volatile, such as specific plant aldehydes, alcohols, ketones, furans, and pyrazines, and non-volatile, such as phenolic compounds, particular peptides, and saponins (Leonard et al., 2022). Volatile compounds provide "green," "grassy," "earthy," and "mushroom" notes, whereas non-volatile are defined as "bitter" and "astringent" (Mittermeier-Kleßinger et al., 2021). Different plant-based matrices are characterized to have chemically different antinutrients and off-flavors that need to be removed to produce high-quality PBFDAs.

The transition from dairy to plant-based milk also implies a change in the physical and chemical composition perspective, influencing the subsequent fermentation process (Sedó Molina, Shetty, et al., 2024). Overall, bovine milk is mainly composed of protein (3.2%–3.4%), in which casein accounts for 82%, fat (3.2%–3.7%), and lactose (4.6%) as the main carbohydrate. In comparison, plant-based milk offers a more diverse composition depending on the plant-based substrate utilized, its processing conditions, and the formulation when producing the product. The most common plant substrates, such as soybeans, almonds, and coconut, are composed of 7.3%, 4.4%, and 6.2% sugars, without considering fibers, 19.9%, 49.9%, and 33.5% fat, and 36.5%, 21.2%, and 3.3% protein, respectively, in raw form (Gorissen et al., 2018; Vanga & Raghavan, 2018). Moreover, plant-based fermentable sugars present in plant-based milk differ from glucose, maltose, fructose, sucrose, raffinose, and starch, among others, depending on the plant-based material used (Elango et al., 2022; Sedó Molina, Shetty, et al., 2024). Moreover, plant-based proteins differ in structure, sequence, and amino acid composition but generally are characterized by their large size and multimeric and globular structures in comparison to casein (Christensen et al., 2022; Mittermeier-Kleßinger et al., 2021; Sedó Molina, Shetty, et al., 2024). The differences between bioavailable carbon and nitrogen sources and the presence of certain minerals and vitamins in each type of milk will affect the fermentation and metabolism of microorganisms, thus influencing the overall sensory properties of the final PBFDAs (Merzlov et al., 2022; Samtiya et al., 2021; Sedó Molina, Shetty, et al., 2024).

Traditionally, some lactic acid bacteria (LAB) species, which have been inhabiting dairy milk niches, have been extensively used throughout the fermentation of dairy products. Historically, dairy fermentation procedures have moved from using spontaneous and back-slopping fermentation techniques in small or medium batches to employing specific starter cultures in large-scale production to generate more controllable, predictable, and safe final fermented products and processes. Milk-isolated LAB strains have been demonstrated to be useful as starter cultures due to their evolutionarily adapted ability to consume

milk substrates, such as lactose and casein, and mainly produce lactic acid, among other secondary metabolites, which fast acidifies milk and generates specific flavor, texture, and other characteristics to the desired final product (Alemayehu et al., 2014; de Vos & Vaughan, 1994; Fontana et al., 2018; Szutowska, 2020). LAB species are ubiquitous in nature and have been found in multiple sources, such as plants, fruits and vegetables, insects, and meat (Filannino et al., 2016; Konings et al., 2000; Wu et al., 2017). LABs are characterized by genetically adapting to their inhabiting niches, resulting in a diverse genotype among species and strains that have acquired or lost genes through evolutionary events in specific environments (Bachmann et al., 2017; Bačun-Družina et al., 2009; Makarova & Koonin, 2007; Ventura et al., 2009). Thus, LAB evolution is essential when selecting LAB strains to be used as starter cultures, specifically in PBFDAs. Some LAB species and strains from plant-based niches have acquired genes and encode enzymes that are useful for the degradation, transformation, or removal of such antinutrients and off-flavors (Gaur & Gänzle, 2023; Sedó Molina, Shetty, et al., 2024). Thus, it may be relevant to redirect the use of conventional milk LAB starter cultures to the utilization of plant LAB isolates that phenotypically express those genes, thereby reducing the concentrations of unwanted compounds while increasing the quality of PBFDAs.

Multiple studies have shown the successful removal of undesirable compounds by physicochemical and biological approaches such as germination, dehulling, soaking, and fermentation (Das et al., 2022). This review focuses on the key metabolic machinery characterized in LAB strains involved in removing those compounds through fermentation. Thus, we explore the state-of-the-art genes, enzymes, and pathways that have been described to be present in LAB species and relevant to the degradation of antinutrients and off-flavors present in different plant-based matrices, including a homology-based analysis with all qualified presumption of safety (QPS)-listed LAB species. Our focus is on several antinutrients, including phytates, plant oligosaccharides, saponins, phenolic compounds, protease inhibitors, and oxalates, as well as several volatile off-flavors, including aldehydes such as hexanal, pentanal, and nonanal, and furans such as 2-pentylfuran and others.

2 | METHODS

2.1 | Blast analysis of genes involved in the degradation of antinutrients

A homology-based analysis has been conducted in 240 LAB strains from 55 LAB species (considered QPS) blasting 42 different genes (accession numbers found in File S1) found in LAB. These genes have been characterized to be involved in the biochemical transformation of phytate, raffinose-family oligosaccharides (RFOs), saponins, phenolic compounds, enzyme inhibitors, and oxalates. The annotated ".faa" files (translated gene-based protein sequences) of 240 LAB strains, generated using Prokka, were retrieved from the National Center of Biotechnology Information database according to the QPS list. These files were used as templates for the BLAST analysis of the targeted protein sequences. Positive matches were considered if there was a ≥50% amino acid homology and *E*-value < 0.0005. Genes, LAB strains, and the number of positive blast matches can be found in File S1. Two graphs were generated from the blast outcome using OriginLab Pro 2021 (OriginLab Corporation), as shown in Figure 2. Figure 2a is a hierarchical clustering heatmap generated based on the average number of genes present in each LAB species, considering all the strains tested from each species. The clustering was generated based on Pearson correlation distance matrix, and the linkage was based on each species' average number of genes. In the heatmap, only rows (LAB species) were clustered, and the color scale was from red (lowest values) to dark blue (highest values), passing through light yellow (medium values). Figure 2b is a PCA biplot graph with loadings visually representing closely related species based on their genetic similarities linked to their genetic capabilities to metabolize the different categories of antinutrients. The PCA considers 49.7% of the variation (between both components). The number of LAB strains from each species was included as follows: *Bifidobacterium* spp.: *adolescentis* (4), *animalis* (4), *bifidum* (3), *breve* (5), *longum* (5), *Carnobacterium divergens* (4), *Companilactobacillus* spp.: *alimentarius* (4), *farciminis* (4), *Fructilactobacillus sanfranciscensis* (5), *Lacticaseibacillus* spp.: *casei* (5), *paracasei* (5), *rhamnosus* (3), *Lactiplantibacillus* spp.: *argentoratensis* (4), *paraplantarum* (5), *pentosus* (5), *plantarum* (5), *Lactobacillus* spp.: *acidophilus* (4), *amylolyticus* (4), *amylovorus* (4), *crispatus* (5), *delbrueckii* (5), *gallinarum* (4), *gasseri* (3), *helveticus* (5), *johnsonii* (5), *kefiranofaciens* (5), *Lactococcus lactis* (4), *Lapidilactobacillus dextrinicus* (3), *Latilactobacillus* spp.: *curvatus* (5), *sakei* (4), *Lentilactobacillus* spp.: *buchneri* (4), *diolivorans* (4), *hilgardii* (5), *kefiri* (5), *parafarraginis* (3), *Leuconostoc* spp.: *citreum* (5), *lactis* (5), *mesenteroides* (5), *pseudomesenteroides* (5), *Levilactobacillus brevis* (4), *Ligilactobacillus* spp.: *animalis* (5), *aviarius* (4), *salivarius* (3), *Limosilactobacillus* spp.: *fermentum* (5), *mucosae* (5), *panis* (3), *pontis* (5), *reuteri* (5), *Loigolactobacillus coryniformis* (4), *Oenococcus oeni* (5), *Pediococcus* spp.: *acidilactici* (5), *parvulus* (5), *pentosaceus* (5), *Secundilactobacillus collinoides* (2), *Streptococcus thermophilus* (4).

3 | IMPORTANCE OF THE EVOLUTION OF LAB: FROM MILK TO PLANT NICHE ADAPTATION

LAB is a group of gram-positive bacteria widely used in multiple areas, including biotechnological, medical, and food applications (Kandler, 1983). In the food industry, some LAB species have been mainly used in food fermentation processes as starter cultures to produce safe and high-quality fermented products in robust, replicable, and controlled fermentation processes. Other LAB species can spontaneously grow during fermentation without being added (nonstarter LABs), influencing the final fermented product outcome. In the food fermentation industry, some LAB species benefit from a generally recognized as safe (GRAS) status in the United States and/or QPS in Europe, allowing them to be applied and considered safe for consumption as technological adjuvants.

LAB species are metabolically divided into obligate homofermentative (OHOM), facultative heterofermentative (FHET), and obligate heterofermentative (OHET) based on their carbohydrate metabolic pathways. OHOM genera, such as *Lactococcus*, *Pediococcus*, *Enterococcus*, *Streptococcus*, and some other *Lactobacillaceae* species (*L. acidophilus*, *L. delbrueckii*, and *L. helveticus*), utilize the Embden–Meyerhoff pathway for glucose metabolism, producing lactic acid as the main metabolic product, predominantly use phosphotransferase (PTS)-based transport systems, and are not (with some exceptions) majorly able to ferment pentoses (Batt, 2014; Kandler, 1983; Lonvaud-Funel, 2014). FHET genera, such as some *Lactobacillaceae* genera (*L. casei, L. plantarum*, and *L. sakei*, e.g.), metabolically behave as OHOM under excess of hexose concentrations but switch their metabolism to OHET under hexose-limiting conditions, producing acetic acid, and ethanol and CO_2 (apart from lactic acid) using the pentose-phosphate pathway. OHET genera such as *Leuconostoc, Oenococcus*, and some other *Lactobacillaceae* genera such as *L. brevis, L. fermentum*, and *L. reuteri* only utilize the pentose-phosphate pathway for hexose metabolism and usually permeases for sugar transport. They can ferment pentoses into mainly lactic and acetic acids (Batt, 2014; Kandler, 1983; Lonvaud-Funel, 2014).

The evolution of *Lactobacillales* has been characterized as reflecting more gene loss rather than acquisition events, mainly regarding biosynthetic genes due to niche adaptation (Makarova & Koonin, 2007). It is suggested that 600–1200 genes have been lost, whereas less than 100 genes have been gained after the evolutionary divergence from the *Bacilli* ancestor (Makarova & Koonin, 2007). Differences have been observed among LAB species and strains and specific niche isolates. Milk, considered a nutrient-rich substrate, has influenced the genetic niche-specific adaptation of milk-isolated LAB strains toward substantial gene loss events. For instance, *S. thermophilus*, which is mainly found in milk and has been used as a starter culture in yogurt and specific cheese production, is an example of an ongoing process of genome decay with an average genome size of 1.8 Mb in comparison to an average *Bacilli* such as *Bacillus subtilis*, which has a size of 4.2 Mb (Cavanagh et al., 2015; Makarova & Koonin, 2007). Moreover, specific milk-isolated *L. lactis* strains have been characterized to possess plasmid complements that provide a phenotypic advantage in milk, generally involved in bacteriophage resistance, lactose utilization, bacteriocin production, and proteolytic activities. These genes could have been acquired through horizontal gene transfer (HGT) events such as conjugation, which has been the most probable HGT mechanism through LAB (Cavanagh et al., 2015). Other mobile elements, such as transposons that formed genomic islands and gene duplication events, have played an advantageous role for some *L. casei* strains throughout evolution and niche adaptability in milk and plant-based niches (Cai et al., 2009). Group A *L. casei* strains in milk have mainly been through genome decay as they became "dairy adaptative specialists." In contrast, Group B *L. casei* strains have acquired new genes through HGT, becoming "niche generalists" an environmental adaptative group of *L. casei* strains (Cai et al., 2009).

In the plant-based niche, *L. plantarum*, which is mainly associated with living in plant-based environments, is characterized by counterbalancing its ancestral gene loss with acquiring new genes throughout gene duplication and HGT primarily carried out by bacteriophages or conjugative pathways, having an average genome size of 3.3 Mb (Makarova & Koonin, 2007). For instance, genetic and phenotypical variation has also been found among different isolates of *L. plantarum* from olive brine, tomatoes, and grain fermentations. Yu et al. (2021) showed how only *L. plantarum* strains that were isolated from olive-brined sources were able to degrade raffinose to some extent, demonstrating their niche adaptation to raffinose-rich environments such as olives in comparison to the other sources. *L. plantarum* has been shown the ability to adapt and specialize in different plant-based niches while at the same time sustaining intraspecific diversity as a way of promoting genetic stability in various environments (Yu et al., 2021).

Most of the intraspecific traits investigated to compare different niche isolates from the same species have focused on carbohydrate, protein, and amino acid metabolisms, which are crucial due to their high impact on the quality, flavor, and texture profiles of fermented products such as cheese (Buron-Moles et al., 2019; Cai et al., 2009; Cavanagh et al., 2015; Okoye et al., 2022). Nevertheless, fewer stud-

ies have been made on the inter- and intraspecific genetic traits acquired by LAB strains related to the degradation of antinutrients and off-flavor molecules present in plant-based matrices. Understanding genetic variations, evolutionary events, and adaptability of LAB species in plant niches may also help select LAB strains as starter cultures for producing high-quality PBFDAs.

4 | ANTINUTRIENTS AND OFF-FLAVORS

4.1 | Antinutrients in plant-based food matrices

Plant-based food matrices used for the development of PBFDAs are usually divided into five main different categories: legumes (soybeans, peas, chickpeas), grains (oats), pseudograins (quinoa), drupes (cashew, almonds, coconut), and tubers (potato). These raw materials have been used as substrates to develop commercial plant-based yogurts and cheese (Grasso et al., 2021). For example, yogurts made of soymilk and/or soybeans (Alpro) and oats (Oatly AB) (Fazer Oy), sometimes supplemented with potato protein isolate and/or starch, have been found in commercial retail (Grasso et al., 2020; Montemurro et al., 2021). On the other hand, pea, potato, soy, and cashew protein isolates have been some of the most used plant-based matrices to produce plant-based cheeses (Grasso et al., 2021). Based on those sources, phytic acid, saponins, phenolic compounds, lectins, protease inhibitors, RFOs, and oxalates are the antinutrients that mainly influence the nutritional (and sometimes sensorial) value of PBFDAs (Harper et al., 2022; Popova & Mihaylova, 2019; Pua et al., 2022; Samtiya et al., 2020, 2021).

Each raw material contains different macro- and micronutrients and antinutrients that affect the overall nutritional value of PBFDAs (Samtiya et al., 2020). Generally, the adverse effects of plant antinutrients are divided into two main antinutritional properties, which are the reduction of bioavailability of nutrients (amino acids, minerals, vitamins, and lipids) and the decrease of protein digestibility, apart from others that specifically have health adverse effects (Harper et al., 2022; Popova & Mihaylova, 2019; Pua et al., 2022; Samtiya et al., 2020, 2021). Moreover, plant metabolites that are considered antinutrients differ in their physicochemical nature, composition, and structure; for example, proteins (protease inhibitors), carbohydrates (RFOs), glycosylated compounds (saponins and phenolic compounds), and organic (oxalate and phytate) acids (Table 1). The removal, biotransformation, and/or degradation through microbial metabolism involve different pathways and specific enzymes for each compound. Furthermore, antinutrients that belong to the same physicochemical metabolic family might be structurally different from plant-to-plant family, leading to a more complex understanding of their degradation pathways and enzymatic hetereospecificity variability. As an example, steroidal saponins are secondary metabolites that are composed of sugar moieties (mono- and oligosaccharides) and aglycone structures, present in multiple plant sources such as legumes (soybean, peanuts, and chickpeas), tea, and cereals (oats). Soybean saponins, such as soyasapogenol A, have a different sugar moiety and aglycone than oat saponins, such as avenacoside A (Oleszek & Oleszek, 2020); thus, different enzymatic degradation complexes and/or different enzyme heterospecificity substrate affinity might be needed to be able to degrade them.

Some secondary plant metabolites are considered antinutrients for human consumption but play an essential role, among others, in plant metabolisms, influencing plant–microbiome, plant–plant, and microbiome–microbiome communications, the regulation of abiotic and biotic stresses, antibacterial and antifungal activities, and defense mechanisms (Cid-Gallegos et al., 2022, Li et al., 2022, Pang et al., 2021). For example, phenolic compounds such as flavonoids, present in some legumes, bind to specific plant proteins to regulate the symbiosis between rhizobia species, attracting nitrogen-fixing bacteria. In contrast, terpenoids regulate the growth of peculiar root-associated bacteria, increasing *Arenimonas* proliferation and inhibiting *Arthrobacter* growth in *Arabidopsis* sp. (Pang et al., 2021). Other phenolic compounds, such as chlorogenic acid, act as herbivore-resistant agents against aphids such as *Aphis pomi* and other insects such as Western thrips (X. Liu et al., 2017). Protease inhibitors are found in storage plant tissues and deplete insect digestive system functionality as a plant protection mechanism (Cid-Gallegos et al., 2022). Oxalic acid influences plant metabolisms, such as ion homeostasis, pH regulation, metal detoxification, and plant defense (Li et al., 2022). RFOs serve as carbon storage sources for anticipating fluctuations in environmental conditions, providing energy and carbon in the seed germination period, and diminishing seed desiccation by water replacement and vitrification mechanisms (Elango et al., 2022). Phytic acid is the central phosphorus storage in seeds (López-Moreno et al., 2022).

Although those plant compounds have been considered antinutrients in the last decades, few studies have started focusing on health-promoting positive effects that some specific metabolites might have. For instance, flavonoids such as quercetin, which are phenolic compounds, have shown health-promoting benefits in vivo by reducing the risk of cardiovascular diseases (Bravo, 1998). For instance, phenolic compounds have been associated with binding

TABLE 1 List of the main plant antinutrients, their composition and structure nature, health adverse effects, and the primary sources relevant when developing plant-based fermented dairy alternatives (PBFDAs).

Antinutrient	Types/forms	Nature of the compound	Sources	Main adverse effects
Phytic acid	Inositol with 1-6P, bound to Zn^{2+}, Fe^{2+}, Mg^{2+}, Ca^{2+}	Myoinositol is bound to 6 phosphate molecules bound to minerals.	Legumes, grains, pseudograins, drupes, tubers	Decrease plant mineral bioavailability
Saponins	Avenacosides, avenacins, soysaponins, α-chaconine, α-solanine, etc.	Triterpenes or steroidal hydrophobic aglycones attached to sugars (Glu, Ara, Gal, Rha, GlucA)	Legumes, grains, pseudograins, and tubers	Inhibition of digestive enzymes, intestinal inflammation
Phenolic compounds	Flavonoids, phenols, hydroxycinnamic acids, coumarins, stilbenes, xanthones, etc.	Monomeric or oligomeric phenol-based compounds are sometimes attached to sugars (Glu, Gal, Rha, Xyl, Gluc and GlucA acids), organic acids, lipids, amines, etc.	Legumes, grains, drupes, and tubers	Some bind and precipitate proteins and bind minerals (Fe^{3+}, Cu^{2+}, Zn^{2+}, Na^{+}, Al^{3+}) lowering the bioavailability of minerals and digestibility of proteins
Protease inhibitors	Trypsin, chemotrypsin, elastase, aspartic, serine protease inhibitors	Small tertiarily structured proteins with disulfide bonds	Legumes, grains	Inhibition of digestive enzymes decreases the digestibility of plant protein and other nutrients
Oligosaccharides (RFOs)	Raffinose, stachyose, verbascose	Tri, tetra-, and penta-oligosaccharides (Glu, Gal, Fru)	Legumes, tubers	Flatulence and abdominal discomfort
Oxalates	K^{+}, Na^{+}, Ca^{2+}, Mg^{2+}, Fe^{3+} bound oxalates	Organic acid (oxalic acid) bound to minerals	Legumes, grains, nuts, tubers	Decrease of mineral bioavailability

Abbreviation: RFO, raffinose-family oligosaccharide.

and precipitating proteins, thus reducing their digestibility and sometimes the action of digestive enzymes. However, this has only been shown for phenolic compounds with at least three flavonol monomers, such as polymeric tannins (Bravo, 1998). Conversely, some phenolics, such as *ortho*- and *para*-diphenolics, have shown health-promoting capabilities such as antioxidant and scavenging effects on free and peroxyl radicals, sometimes only effective in their aglycone (non-glycoside) forms. Metabolite classification (Table 1) is based on physicochemical properties, not their nutritional health effect; hence, different compounds from the same family might have different antinutritional side effects. For instance, saponins from lentils, beans, and peas have been shown to inhibit digestive enzymes. In contrast, saponins from tea (*Camellia sinensis*) have been demonstrated to have anti-inflammatory and antioxidant properties. In addition, saponins from garlic (*Allium sativum*) and oats (*Avena sativa*) were found to show antifungal and antimicrobial effects against specific microorganisms (Oleszek & Oleszek, 2020). Saponins from oats exert antioxidant activity but increase intestinal permeability when consumed (Oleszek & Oleszek, 2020). Although RFOs are mostly considered antinutrients because they cause flatulence and abdominal discomfort, they have lately been associated with some positive attributes, such as prebiotic, anti-allergic, anti-obesity, and anti-diabetic properties (Elango et al., 2022).

4.2 | Volatile off-flavors in plant-based food matrices

Plant volatile organic compounds (VOCs) consist of a wide range of secondary metabolites generally characterized by their lipophilic and low molecular weight nature with high vapor pressure at ambient temperatures (Dudareva et al., 2013; Picazo-Aragonés et al., 2020). There are multiple classes of VOCs, differing from their biosynthetic origin in plants and physicochemical properties, such as amino acid derivates, fatty acid derivates, terpenoids, and phenylpropanoid/benzenoid compounds (Dudareva et al., 2013; Picazo-Aragonés et al., 2020). VOC production and regulation in plants is a complex multifactorial process that involves multiple factors such as specific activities of certain biosynthetic enzymes, the concentration of substrate, precursor availability, epigenetics, and environmental factors such as plant nutrient concentration, uptake, and availability, temperature, humidity, light intensity, among others (Dudareva et al., 2013; Picazo-Aragonés et al., 2020). Interestingly, VOCs have been considered relevant for plant evolution and environmental adaptation because their involvement in defense and pollinator attraction explains their primary production in flowers. However, VOCs are also produced in leaves, fruits, and stems. They play an essential molecular role in plant–plant, plant-pollinator, and plant-herbivore inter-

actions (Dudareva et al., 2013; Picazo-Aragonés et al., 2020).

Apart from their influence on plant metabolism and biology, plant VOCs affect the overall flavor profiles of plant-based foods, consequently affecting consumer acceptance of certain food products. It is considered one of the significant consumer drawbacks when producing PBFDAs, along with appearance and texture (Gupta et al., 2022; Short et al., 2021; Yilmaz-Ersan & Topcuoglu, 2022). As in milk products such as yogurts and fresh, hard, and mold-based cheeses, plant-based dairy alternatives have different flavor profiles due to their difference in the raw material used, ingredients used, fermentation process, starter cultures (if inoculated), and the overall production processes employed. Nevertheless, based on flavor and Western consumer acceptance studies of PBFDAs, some flavor attributes have generally been associated with off-flavor traits, such as "beany," "green," and "earthy" notes (Sedó Molina, Shetty, et al., 2024). VOCs denoting those flavor attributes differ depending on the plant-based raw material used, processing, and formulation. In addition, the presence of VOCs alone does not entirely explain the flavor profile of such food because flavor is a multifactorial and often subjective phenomenon. VOC concentration is crucial to be considered due to its direct influence on perception (Spence & Kilcawley, 2021).

Although the current analytical chemical techniques can detect the presence of hundreds of VOCs in each food and beverage product, the average human nose can detect 30–40 VOCs that are considered to significantly contribute to the overall flavor perception (Spence & Kilcawley, 2021). VOCs mainly considered off-flavors in PBFDAs belong to aldehydes, alcohols, ketones, acids, pyrazines, furans, and sulfur compounds (Saffarionpour, 2023). They belong to different VOC classes and mainly originate from lipid oxidation through lipoxygenase pathway (LOX), autooxidation, and amino acid derivatives generated by decarboxylation, aminotransferase, deamination, and aldehyde synthesis (Dudareva et al., 2013). VOCs with the highest impact on flavor perception have lower perception odor thresholds (the compound's lowest concentration that humans can smell), such as aldehydes, furans, and pyrazines.

Table 2 lists the VOC off-flavors typically found in plant-based raw materials, such as peas, soybeans, oats, almonds, cashews, walnuts, and potatoes used to generate PBFDA. Aldehydes are the most common off-flavors found in PBFDA and are usually generated from Strecker degradation, autooxidation, or LOX-mediated oxidations. Alcohol and ketones are typically generated from aldehydes through alcohol dehydrogenase (ADH) reactions in plants. Moreover, ketones might be produced through aldol condensations of aldehydes or from decarboxylation reactions of 3-oxo-acids. Furans and pyrazines are typically produced through Maillard reactions from polyunsaturated fatty acids (among others) and α-aminocarbonyl, respectively. Sulfur compounds are mainly produced from methanethiol oxidation, a compound formed from Stecker degradation of methionine (Fischer et al., 2022; Leonard et al., 2022; Saffarionpour, 2023; Wang et al., 2023; C. Zhang et al., 2020). It has been demonstrated how off-flavor molecules, such as aldehydes, pyrazines, alcohols, ketones, and furans, can interact with plant proteins through multiple interactions such as hydrophobic, hydrogen, or covalent bonds. Degradation of plant proteins through fermentation might cause an increase in protein solubility and a decrease in hydrophobicity surface, thus releasing off-flavor compounds (Leonard et al., 2022; Saffarionpour, 2023; C. Zhang et al., 2020).

Some VOCs could be used as chemical signatures influencing off-odor perception due to their high concentrations in plant bases and low odor thresholds, such as hexanal, 2-pentylfuran, nonanal, heptanal, octanal, 1-octen-3-ol, 1-octen-3-one, (*E*, *E*)-2,4-nonadienal, 2,4-*E*, *E*-decadienal, pyrazines, and sulfur compounds that are associated with "green," "beany," and "earthy" notes. Commonly, hexanal, (*E*, *E*)-2,4-nonadienal, and (*E*, *E*)-2,4-decadienal have been considered to contribute, majorly, to the off-flavor notes in pea and soy (C. Zhang et al., 2020) and oat milk (McGorrin, 2019), based on combining analytical and sensory analyses. Additionally, pyrazines and 1-octen-3-one were also associated explicitly with off-odors in pea and soy milk, respectively (C. Zhang et al., 2020), and (*E*, *E*, *Z*)-2,4,6-nonenal and 2-methyl-3-furanthiol mainly contributed to the oat characteristic aroma in oat milk (McGorrin, 2019). In nut-based milk, hexanal, heptanal, and nonanal were found to be present at significantly higher concentrations in walnut, peanut, and almond (Type 1) milk, respectively (Manousi & Zachariadis, 2019). Differences in VOCs prevalence in plant-based milks are associated with different activities of LOX-1, -2, -3, ADH, and hydroperoxide lyase (C. Zhang et al., 2020). Moreover, other parameters, such as crop varieties, processing, and the different vegetable-based oils used for milk formulations, influence the concentration and presence of the different VOCs. The metabolic involvement of LAB in degrading off-flavor VOCs present in PBDA milk through fermentation is discussed in Section 6.

5 | METABOLIC INSIGHTS OF LAB: BIOTRANSFORMATION OF PLANT-BASED ANTINUTRIENTS

Genes and enzymes involved in the transport and degradation of phytates, RFOs, saponins, phenolic compounds, enzyme inhibitors, and oxalates, documented in LAB

TABLE 2 Volatile organic compounds (VOCs) list that contribute to off-flavor attributes in the production of plant-based fermented dairy alternatives (PBFDAs) (CAS number, thresholds, "odor description").

Group of VOCs	Compound	CAS number	Odor description	Odor threshold in water (ppb)
Aldehyde	2-Heptenal	18829-55-5	Green, spicy, hazelnut, apple	13
	(*E*)-2-Hexenal	505-57-7	Leafy, apple, cheesy, vegetable, fat, banana, rancid, fatty, sweet, plum, fruity, aldehydic, almond, green	17
	Nonanal	124-19-6	Citrus, lime, orange peel, rose, fat, green, fishy, waxy, fresh, fatty, aldehydic, orris, grapefruit	1
	Benzaldehyde	100-52-7	Cherry, almond, sweet, burnt sugar, sharp, strong, bitter	350–3500
	Hexanal	66-25-1	Leafy, grass, sweaty, tallow, fat, fresh, fatty, fruity, aldehydic, green	4.5–5
	Octanal	124-13-0	Lemon, citrus, soap, orange peel, fat, waxy, fatty, aldehydic, green	0.7
	Heptanal	111-71-7	Citrus, ozone, fat, herbal, fresh, wine-lee, rancid, fatty, aldehydic, green	3
	Pentanal	110-62-3	Almond, bitter, malt, oil, pungent	12–42
	2,4-Decadienal (*E*, *E*)	25152-84-5	n.a.	0.07
Alcohols	1-Penten-3-ol	616-25-1	Butter, fish, green, oxidized, wet earth	400
	1-Octen-3-ol	3391-86-4	Raw, fishy, oily, earthy, fungal, chicken, mushroom, green	1
	1-Pentanol	71-41-0	Oil, balsamic, vanilla, fusel, sweet, balsam	4000
	1-Hexanol	111-27-3	Oil, alcoholic, ethereal, resin, fuel, sweet, fruity, flower, green	2500
	1-Heptanol	111-70-6	Leafy, coconut, herbal, peony, strawberry, chemical, musty, sweet, woody, violet, green	3
	1-Nonanol	143-08-8	Fat, floral, green, oil	90
	2-Ethyl-1-hexanol	104-76-7	Green, rose	270,000
Carboxylic acids	Hexanoic acid	142-62-1	Cheese, oil, pungent, sour	3000
Esters	Ethyl acetate	141-78-6	Pineapple, ethereal, sweet, anise, fruity, balsam, weedy, green	5–5000
Furans	2-Pentylfuran	3777-69-3	Green, bean, vegetable, earthy, beany, fruity, metallic, green	6
	2-Ethylfuran	3208-16-0	Earthy, sweet, burnt, malty	–
Ketones	3-Hexanone	589-38-8	Grape, fruity	n.a.
	5-Methyl-2-hexanone	110-12-3	n.a.	2.1
	2-Nonanone	821-55-6	Fragrant, fruit, green, hot milk	5–200
	1-Octen-3-one	4312-99-6	Herbal, earthy, metal, musty, mushroom, dirty	0.005
	2-Octanone	111-13-7	n.a.	50
	2-Hexanone	591-78-6	Ethereal, ether	76–3000
	2-Heptanone	110-43-0	Coconut, soap, herbal, sweet, woody, fruity, spicy, cinnamon	140–3000
Pyrazines	2-Isobutyl-3-methoxypyrazine	24683-00-9	Spice, pepper, green pepper, bell, earth, galbanum, pea, green	0.002–0.016
	2-Isopropyl-3-methoxypyrazine	25773-40-4	Earthy, beany, pea, earthy	0.0002
	2-Methoxy-3-isopropyl-5-methylpyrazine	32021-41-3	Green, pea, earthy	–

(Continues)

TABLE 2 (Continued)

Group of VOCs	Compound	CAS number	Odor description	Odor threshold in water (ppb)
Sulfur compounds	Dimethyl sulfide (DMS)	75-18-3	Sulfurous, cabbage, onion, vegetable, sweet corn, tomato, radish, wild, green	0.3–1
	Dimethyl disulfide (DMDS)	624-92-0	Citrus, cabbage, sulfurous, putrid, onion, vegetable, fatty, floral, earthy, woody, fruity, herbaceous, nutty, green	0.16–12
	Dimethyl trisulfide (DMTS)	3658-80-8	Cabbage, fish, onion, sulfur	0.005–0.01
	Dibutyl disulfide (DBDS)	211-091-3	Sulfurous	0.21

Source: Data on odor description and thresholds were extracted from FlavorDB, FEMA Flavor (Flavor and Extract Manufacturers Assoc.), and Leffingwell and Associates. Part of the data was extracted from Table S2 by Sedó Molina et al. (2024).

species and strains, are discussed in depth and summarized in Figure 1 and Table 3.

5.1 | Phytates

Phytic acid (myoinositol hexaphosphate) is a crucial plant metabolite responsible for 50%–80% phosphorus storage in plants, particularly cereals, seeds, and legumes. This compound is often considered an antinutrient due to its biochemical ability to chelate minerals such as Zn^{2+}, Fe^{2+}, and Mg^{2+}, affecting their solubility, absorption, and bioavailability in the GIT (López-Moreno et al., 2022; N. Sharma et al., 2020; Vats & Banerjee, 2004). Its negative charge facilitates the chelation reaction with positively charged divalent and trivalent cations. Furthermore, phytic acid has been associated with binding proteins and carbohydrates, impacting their digestibility and diminishing the nutritional value of phytate-containing foods (Popova & Mihaylova, 2019). Degradation of phytic acid by microbial fermentation has been mainly associated with a phytase (myoinositol hexakisphosphate phosphohydrolase), encoded by a gene *phy*, a histidine acid phosphatase that catalyzes the hydrolysis of phosphomonoester bonds of phytates (IP6) into myoinositol phosphate derivatives (IP5, IP4, IP3, IP2, IP) releasing myoinositol and six inorganic phosphates, depleting the ability to chelate metal ions (Figure 1) (Vats & Banerjee, 2004).

There are two main types of phytases: 3-phytase (EC 3.1.3.8) and 6-phytase (3.1.3.26), depending on the position of the ester bond hydrolyzed (Vats & Banerjee, 2004). This enzyme is also found in plants (*phyt1, phyt2*) such as soybean, oats, canola seeds, spelt, and maize, which might be activated through the lactic acid fermentation with optimal activities at pH between 4.5 and 5 (Vats & Banerjee, 2004). Furthermore, differences in the origin of phytase synthesis, food matrix, pH, temperature, metal ions present, and the type of phosphoric ester bonds of the target molecule might influence phytase activities. Apart from phytases, other non-specific phytate phosphatases that were able to dephosphorylate phytates thereof having phytase activities, such as tyrosine phosphatase-like phytase (Phylf), described in *L. fermentum* NKN51, have been characterized (R. Sharma et al., 2018). Phenotypical studies in LAB strains have also been performed in cereal and legume-based fermentations, demonstrating their ability to decrease phytate content. LAB species such as *L. plantarum*, *L. buchneri*, *P. pentosaceus*, *L. brevis, Bifidobacterium* spp., *L. reuteri, L. fermentum, C. alimentarius, L. acidophilus, L. casei, L. amylovorus, L. rhamnosus, F. sanfranciscensis*, among others, have been characterized to express this phenotype in specific conditions (Andrabi et al., 2016; De Angelis et al., 2003; García-Mantrana et al., 2015; Haros et al., 2005; Lee et al., 2013; Sandez Penidez et al., 2020; R. Sharma et al., 2018; Sreeramulu et al., 1996; Sumengen et al., 2013; Sümengen et al., 2012; Zamudio et al., 2001). For instance, phytase from *Fructilactobacillus fructivorans* DA106 showed the second-highest phytase activity (295.3 U/mL) among 13 LAB strains tested, whereas the one from *F. sanfranciscensis* 22E did not show high phytase expression (De Angelis et al., 2003). Other studies have demonstrated a substrate multispecificity of the phytases within LAB strains. *F. sanfranciscensis* CB1 phytase (50 kDa) had a substrate multispecificity toward acetyl phosphate and adenosine-phosphate derivatives, among others, also showing higher activities with other substrates such as *p*-nitrophenyl phosphate (De Angelis et al., 2003). *L. pentosus* CECT 4023 acid phosphatase (69 kDa) showed multispecificity towards other phosphate-bound molecules such as *p*-nitrophenyl phosphate, D-fructose-6-phosphate, and D-glucose-6-phosphate, with higher activities than toward phytate (Palacios et al., 2005). Phytase from *L. plantarum* CRL1964 (55 kDa) showed higher substrate specificity towards sodium phytate than to other substrates (Sandez Penidez et al., 2020). Other factors can influence LAB's phytase activity, as seen with the selection of carbon

source and growth phase. For instance, *F. sanfranciscensis* CB1, a species mainly found in traditional sourdough fermentation, intracellularly produced phytase with an activity of 420.8 U/mL when sodium phytate was present. Its expression was increased by 35% when this strain was grown with maltose and fructose in comparison to other carbohydrates (maltose with glucose or sucrose), which was correlated by the cell counts reached after fermentation (De Angelis et al., 2003). Its highest peak of phytase activity was during the stationary phase. In addition, *L. pentosus* CECT 4023 intracellularly produces an acid phosphatase with phytase activity at maximum rates during its stationary growth phase. This was reduced by high concentrations of glucose (2% w/v) and optimal at 0.5% glucose-MRS (Palacios et al., 2005). However, *L. amylovorus* B4552 showed the highest phytase activity extracellularly (125–146 U/mL) with glucose preferably and during the exponential growth phase (Sreeramulu et al., 1996). *L. plantarum* CRL1964 was determined to express significantly higher specific phytase (*pLhyLP*) activity when growing in raffinose, maltose, and xylose in comparison to glucose, fructose, sucrose, and galactose (Sandez Penidez et al., 2020). Phytase relative activity was increased by the presence of raffinose and lactose (20 g/L) in comparison to glucose (20 g/L) in *L. casei* 40 W and *L. fermentum* DSM 20052 and the presence of fructo-oligosaccharides in *L. plantarum* JBPRS (Damayanti et al., 2017). In all strains tested, phytase activity was severely reduced when inorganic phosphate was added to the growth media, although growth yields were unaffected (Damayanti et al., 2017). Finally, metal ions and other chemical compounds enhance or deplete phosphatase and phytase activities. *L. pentosus* CECT 4023 phosphatase activity was increased by adding 1 mM of $CoCl_2$ (15× factor) and L-ascorbic acid (1.25× factor) (Palacios et al., 2005), whereas in *L. fermentum* NKN51 was increased by 5 mM Ag^+ (1.5× factor) (R. Sharma et al., 2018). Intracellular phytase relative activity was increased in *L. brevis* with 1 mM of $HgCl_2$, $MnCl_2$, $MgCl_2$, $CuCl_2$, and $FeCl_2$ by 1.4, 1.4, 1.3, 1.3, and 1.2 factors, respectively, whereas extracellular phytase activity was decreased by all compounds tested (Sümengen et al., 2012). In another study, PhyLP was increased by 10 mM ascorbic acid and Co^{2+} (Sandez Penidez et al., 2020). Even though an acid phosphatase from *L. plantarum* DPC2739 had a considerable range of substrate specificity (hydrolyzing phospho-ester bonds from α-phospho-DL-serine/threonine/tyrosine, D-glucose-6-phosphate, and D-fructose-6-phosphate, among others), no phytate specificity was tested (Magboul & McSweeney, 1999). Moreover, based on the blast analysis (Figure 2), *phyLf* was found homologous in all *L. fermentum* and *L. brevis* strains, setting the positive hit threshold on 50% sequence homology and *E*-value < 0.0005. No hits were found with *phyLP* in any strains analyzed (Section 2.1—data not shown).

5.2 | Raffinose-family oligosaccharides (RFOs)

Raffinose-family oligosaccharides (RFOs) are soluble oligomeric carbohydrates in the plant kingdom that are considered α-galactosyl derivatives of sucrose. They are particularly abundant in the legume family (*Fabaceae*), such as soybean (0.1–19.9 g/kg), lentil (4.5–5.5 mol/100 g), chickpea (1.2–48.5 g/kg), and peas (22.6–63.4 g/kg) (Elango et al., 2022). The most common antinutritional attributes associated with RFOs are indigestion and flatulence caused during its transition in the upper intestine. The lack of RFOs-degrading enzymes in the human gut triggers their accumulation in the large intestine and finally ferments them, producing hydrogen, methane, and CO_2 (Elango et al., 2022; Kanwal et al., 2023). There are five major RFO di- and oligosaccharides: melibiose, raffinose, stachyose, verbascose, and ajugose. Their main difference is their polymeric length, in which melibiose (Gal–Glu), raffinose (Gal–Glu–Fru), stachyose (Gal–Gal–Glu–Fru), and verbascose (Gal–Gal–Gal–Glu–Fruc) are constituted by two, three, four, and five monosaccharides, respectively. Structurally, they differ in the number of galactose monomers linked to sucrose (α-D-glucose and β-D-fructose) through glycosidic bonds to the glucose monomer.

Several microorganisms have shown the ability to degrade RFOs through the action of two main enzymes: α-galactosidases (*galA, melA*) (EC 3.2.1.22), which hydrolyze the α-1,6 bond between Gal–Glu and Gal-Gal releasing galactose and sucrose (from raffinose) or galactose and glucose (from melibiose), and levansucrases (EC 2.4.1.10) such as *evS* (*F. sanfransciscensis*) and FtFA (*L. reuteri*), which are cell-wall glycosylases that degrade RFOs cleaving β-1,2 (Glu–Fru) and transferring the fructose monomer to a fructosyl acceptor, generating fructose and melibiose (Figure 1) (Gänzle & Follador, 2012). Other genes participate in RFO metabolism, especially in sucrose, such as sucrose phosphorylase (EC 2.4.1.7) (*ScrP, GftA*) and fructofuranosidase (EC 3.2.1.26) (*SacA/SacB, BfrA*), which break down sucrose through phosphorylation or hydrolysis, respectively (Gänzle & Follador, 2012).

In Figure 2, the homology-based analysis considered two different protein sequences of MelA (*L. fermentum* and *L. mesenteroides*) and LevS (*L. salivarius* and *L. mesenteroides*). On average, *L. plantarum*, *L. aviarius*, and *L. mucosae* encoded the highest number of genes involved in RFO metabolism. In contrast, *C. divergens*, *Companilactobacillus* spp., *Lacticaseibacillus* spp., *L. gasseri, L.*

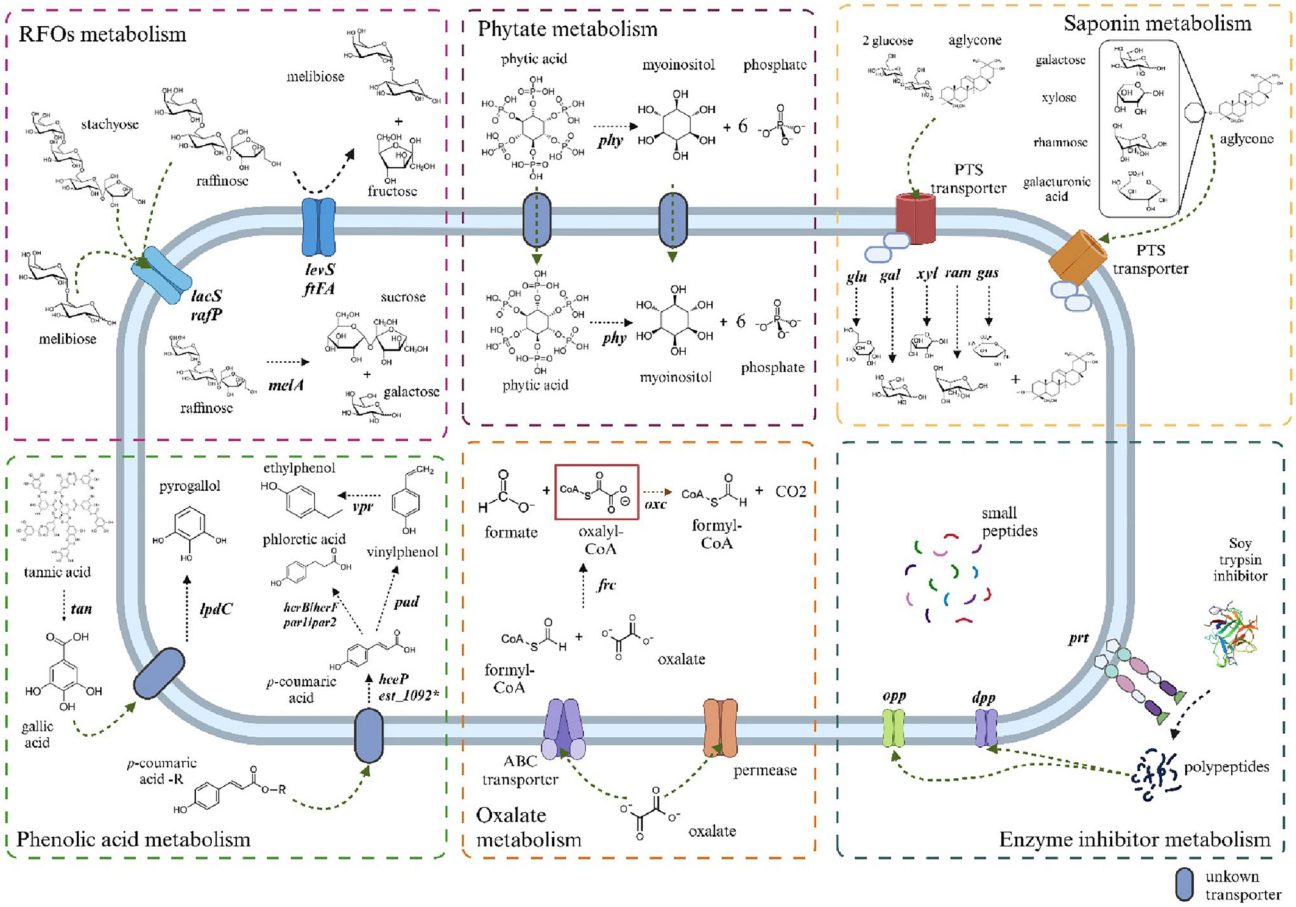

FIGURE 1 Lactic acid bacteria (LAB) metabolic pathways involved in raffinose-family oligosaccharides (RFOs), phytate, saponin, phenolic acid, oxalate, and enzyme inhibitor metabolisms. All enzymes are marked in bold. *LacS* (sugar transport permease), *rafP* (raffinose permease), *levS* (levansucrase), *ftfA* (levansucrase), *melA* (α-galactosidase), *phy* (phytase), *glu* (β-glucosidase), *gal* (β-galactosidase), *xyl* (β-xylosidase), *ram* (α-rhamnosidase), *gus* (β-glucuronidase), *tan* (tannase), *lpdC* (gallate decarboxylase), *est_1092* (*estA*, feruloyl esterase), *pad* (phenolic acid decarboxylase), *hcrB* (flavocytochrome c), *hcrF* (FAD-dependent oxidoreductase), *par1/par2* (FAD-binding reductases), *frc* (formyl-coA transferase), *oxc* (oxalyl-coA transferase), *prt* (envelope-proteinase), *opp* (oligopeptide transport system), *dpp* (di-/tripeptide transport system). *Source*: Created with BioRender.

amylolyticus, L. sakei, L. curvatus, L. lactis, L. dextrinicus, L. coryniformis, S. thermophilus, and *P. parvulus* did not encode for any gene or only one from the ones considered in RFO metabolism. *B. bifidum* showed the highest average gene number from *Bifidobacterium* spp. encoding for two copies of *BfrA* in each strain. Specific strains encoded multiple copies of the same gene, such as one *L. aviarius*, two *L. plantarum*, and one *L. mesenteroides* strains encoded 13, 7, and 4 copies of *levS* in their genome. Moreover, the highest copies of *melA* were found in *L. mucosae* DSM 13345, *L. gallinarum* DSM 10532, and *L. acidophilus*, with 6, 3, and 4 copies. Levansucrases (FtfA) were highly present in *F. sanfranciscensis* (1–2 copies), *L. pentosus* (0–4 copies), *L. helveticus* (up to 6 copies), and *L. fermentum* (1–2 copies).

RFOs are transported in LAB through specific transport systems such as PTS, ABC, and permeases, among others, and subsequently hydrolyzed intracellularly by the action of glycolytic enzymes mentioned (Kanwal et al., 2023; Zhong et al., 2018). Based on the proteomic and transcriptomic analysis, OHOM LAB strains, such as *L. acidophilus* CICC 22162, have been shown to use PTS systems and ECF-type transporters to transport stachyose intracellularly. Moreover, higher expression of M6PI isomerase (EC 5.3.1.8) that converts β-D-mannose-6-phosphate (M6P) to D-fructose-6-phosphate (F6P) was observed in comparison to the control grown in glucose, indicating fructose as one of the products of stachyose degradation (Zhong et al., 2018). In OHET LAB, such as *L. reuteri*, extracellular levansucrase activities are preferred due to a facilitated transport of less complex oligosaccharides (Gänzle & Follador, 2012). Nevertheless, *L. reuteri* has also been suggested to transport raffinose through LacS and has also shown broad carbohydrate specificity to lactose and melibiose and consecutively cleaved by GalA intra-

cellularly, releasing galactose, melibiose, and/or sucrose oligosaccharides. Galactose might be catabolized by the expression of the *gal* operon (*galM*, *galK*, *galT*, *galE*, and *galU*) to glucose-1-P and enter the phosphoketolase pathway. Sucrose might be degraded into glucose and fructose by invertase and follow the same metabolic pathway (Zhao & Gänzle, 2018). In FHET LAB, such as *L. plantarum*, raffinose transport has been associated with *rafP*, located in the upstream part of the *melA* gene, and has high homology with *lacS* from *S. thermophilus*. However, the latter has a low affinity to raffinose (Silvestroni et al., 2002).

LAB species such as *L. mesenteroides* and *L. pseudomesenteroides*, *L. paracasei* ssp. *paracasei*, *S. thermophilus*, *L. plantarum*, *L. fermentum*, *L. brevis*, *L. reuteri*, *L. casei*, *L. curvatus*, and *L. acidophilus* have been documented to be able to degrade raffinose, stachyose, and/or verbascose during fermentation of plant-based raw materials, such as soy milk (Garro et al., 1993; Hati et al., 2014; Oguntoyinbo, 2007; Sedó Molina, Shetty, et al., 2024; Yoon & Hwang, 2008). *Bifidobacterium* spp. also showed α-galactosidase activity (Carević et al., 2016; Tsangalis & Shah, 2004). As the structural complexity of RFOs increases, fewer LAB strains can metabolize them; for example, only a limited number of strains such as *L. reuteri*, *P. pentosaceus*, *L. mesenteroides*, and *Bifidobacterium lactis* HNO19 have been able to degrade verbascose, a pentasaccharide (Kahala et al., 2023; Kanwal et al., 2023), among 14 LAB strains RFOs-degrading tested.

α-Galactosidase is a glycosyl hydrolase that belongs to the GH36 glycosidase family and binds to unbranched oligosaccharides such as melibiose, raffinose, and stachyose, hydrolyzing α-1,6 bond between Gal and Glu (Kanwal et al., 2023). They are classified into two groups (Groups I and II); the first hydrolyzes RFOs, and the second hydrolyzes higher polymer galactomannans (Zartl et al., 2018). Carević et al. (2016) showed how *L. reuteri* ATCC 23271 was the most promising strain among those tested due to its high α-galactosidase activity (1.27 IU/mL), followed by *L. acidophilus* ATCC 23271 (0.25 IU/mL) and *S. thermophilus* S3 (0.181 IU/mL). *L. rhamnosus* ATCC 7469, *Lactobacillus bulgaricus* ATCC 11842, and *L. helveticus* ATCC 15009 did not show activity. Furthermore, in a study conducted by Kahala et al., 2023, *P. pentosaceus* (AM173) and *L. mesenteroides* (PM173), both isolated from pulses, showed the highest consumption rates of raffinose, stachyose, and verbascose present in fava bean and pea after 48 h of fermentation. In this study, some LAB strains, such as *L. fermentum* (LF314), showed high abilities to degrade raffinose and stachyose but lower when degrading verbascose. This case is an example of substrate specificity of α-galactosidase, even though the last galactosyl monomer in verbascose is attached with the same type of bond as the galactosyl monomer in stachyose. Moreover, *Weisella cibaria* (AM3) showed a high ability to degrade all RFOs in fava beans but low performance in pea fermentation, suggesting plant-matrix dependency influenced by the ability to metabolize fermentable nutrients provided by the specific raw material (Kahala et al., 2023). Additionally, certain LAB strains, such as *B. lactis* HNO19, have demonstrated better growth on stachyose than on raffinose. This may be due to a preference for consuming galactose over glucose or fructose, as stachyose contains an extra galactose monomer in its structure (Zartl et al., 2018).

Several studies have considered *L. pseudomesenteroides* strains (NFICC 99 and 2004) as RFOs high-degrading candidates in soy milk (Sedó Molina et al., 2022; Sedó Molina, Shetty, et al., 2024; Wätjen et al., 2023) as well as promising candidates for plant-based fermentations due to their high proteolytic capabilities toward plant proteins (Christensen et al., 2022; Sedó Molina, Shetty, et al., 2024). Among QPS *Leuconostoc* species, over 95% of *L. pseudomesenteroides* strains can ferment raffinose, whereas only a few *L. mesenteroides* strains are capable; however, neither *Leuconostoc lactis* nor *L. citreum* can ferment raffinose (Lonvaud-Funel, 2014). Generally, dairy-derived *L. lactis* species cannot ferment raffinose, although the *galA* gene has been found in some strains (Batt, 2014; Sedó Molina, Shetty, et al., 2024), although larger genome-sized plant-derived lactococci might be able to degrade plant complex sugars (Khayatt et al., 2020). Raffinose consumption was also detected in a hybrid soy drink (Madsen et al., 2021).

5.3 | Saponins and glycoalkaloids

Saponins are a vast and diverse group of molecules found in plants chemically characterized by glycoside compounds attached to their aglycone structure (Oleszek & Oleszek, 2020). Different mono- and oligosaccharides forming diverse sugar chains can be found depending on the different saponins' type, source, and chemical structure. Some glycosidic bonds between sugars are similar to the ones found in some phenolic compounds with sugar moieties attached (Bravo, 1998).

Various plant saponins have been found in PBFDAs, influencing the fermented products' nutritional and non-volatile flavor attributes. In soybeans, for example, three main types of saponins are found: soyasapogenol A (A1 and A2), B (I, II, III, IV, V, V1), and E. In soyasapogenol A, there are multiple variations of sugar chains in C-3 (aglycone) containing specific chains of Glu, Gal, Rha, Ara, and glucuronic acid (GluA) and chains of Glu, Ara, and Xyl in C-22 (Oleszek & Oleszek, 2020). In oats, the major saponins found are triterpene saponins, such as avenacins, and steroidal saponins, such as avenacosides. Avenacosides (A,

B, C) and 26-deglucoavenacosides (A, B) are characterized by containing sugar chains of Glu and Rha disposed of in different distributions in C-3 and a Glu monomer in C-26 (only in avenacosides) (Oleszek & Oleszek, 2020; Yang et al., 2016). In potatoes, glycoalkaloids, such as α-solanine and α-chaconine, are characterized by their toxicity and bitter taste. They contain mono-, di- and tri-saccharide molecules attached in their aglycone structure, which can vary from Rha, Glu, and Gal, forming different types of glycosidic bonds and structures (Baur et al., 2021; Hennessy et al., 2018; Oleszek & Oleszek, 2020).

In general, multiple structures of aglycones attached to numerous chains of sugars can be found depending on the plant-based raw material source used. Nevertheless, specific glycosidic bonds are found throughout the different saponins. For instance, Glu–Rha, Gal–Glu, Rha–Gal, Ara–Glu, Gal–Ara, and GluA–Glu, among others, are recurrently found in the different plant saponins (Oleszek & Oleszek, 2020). In fact, hydrolyzing their glycosidic bonds reduces their toxicity (Hennessy et al., 2020). Here, the glycosidic hydrolases present in LAB might play a role in the degradation of saponins (Fu et al., 2020; Overney & Huang, 2020; Pham et al., 2023). Specific LAB strains that have been evolutionarily adapted to have high glycosidic activities toward specific glycosidic bonds might be useful as starter cultures to biotransform saponins into less toxic compounds.

Enzymes such as β-D-glucosidases (EC 3.2.1.21), β-galactosidases (EC 3.2.1.23), α-L-rhamnosidases (EC 3.2.1.40), α-L-arabinosidases (EC 3.2.1.55), β-D-xylosidases (EC 3.2.1.37), and β-glucuronidases (3.2.1.31) are present in specific LAB species but only phenotypically expressed in specific strains and conditions might be useful to investigate when selecting LAB strains for the generation of PBFDAs. Indeed, the substrate specificity of those enzymes toward saponin sugar moieties is relevant to consider due to the presence of multiple similar glycosidases in whole genome LAB sequences.

In the homology-based analysis presented in Figure 2a, different families of glycoside hydrolases (GH) characterized to have β-glucosidases (GH1, 2, 3, and 30), β-galactosidases (GH1, 2, 3, 30, 35, and 43), and α-glucosidases (31) activities as well as glucuronidases (Gus), L-α-arabinosidases (AraA), β-xylosidases (XynB), xylose isomerases (XylA), and L-α-rhamnosidases (RamA/L-ram) were considered to play an important role in degrading sugar moieties attached to aglycones. Those GH families for β-glucosidases and β-galactosidases were chosen based on the substrate specificity toward glucose or galactose-linked moieties. Overall, *L. diolivorans*, *L. pentosus*, *P. acidilactici*, *L. brevis*, and *L. rhamnosus* encoded for more variety and multicopy GH. On the other hand, *B. bifidum, B. breve, F. sanfranciscensis, L. amylolyticus, L. delbrueckii, L. gallinarum, L. gasseri, L. aviarius, L. salivarius*, and *S. thermophilus* encoded for 0 to 1 copies of all those genes. GH1 and GH2 families were more conserved in most of the LAB species tested compared to the other families, such as *Companilactobacillus, Lactiplantibacillus, Lacticaseibacillus*, and *Latilactobacillus* genera for GH1 and *Lactiplantibacillus, Lactobacillus, Lentilactobacillus, Leuconostoc, Limosilactobacillus, Loigolactobacillus*, and *Latilactobacillus* genera for GH2. Most of the strains of *L. pentosus* also encoded for GH3 and GH43, whereas some *Lacticaseibacillus* species blasted positive against GH35. Gus showed higher positive hits with *B. longum, L. rhamnosus, L. buchneri, L. diolivorans*, and *L. parafarraginis. AraA* was found in *B. breve* and *B. longum, L. buchneri, L. diolivorans*, and one strain of *L. hilgardii*; *xynB* was found in all strains of *B. adolescentis, B. animalis, L. lactis, L. diolivorans, L. pseudomesenteroides, L. brevis*, and *Pediococcus acidiilactici; xylA* was found in *B. adolescentis, B. animalis, L. lactis, L. diolivorans, L. pseudomesenteroides, L. brevis, L. mucosae, P. acidiilactici*, and *S. collinoides*. Finally, *ramA* was only found in specific strains of *C. alimentarius (1), L. pentosus (4), L. acidophilus (3), L. fermentum (1)*, and *L. coryniformis (1)*.

β-D-glucosidases are glycosidic hydrolases that have been widely characterized in LAB species. Enzymes from GH1, GH2, GH3, and GH30 have shown β-D-glucosidase activity in LAB. They have been associated with hydrolyzing sugar moieties (mainly glucose-based) present in different plant metabolites, including plant saponins (Michlmayr & Kneifel, 2014). Some glucosidases have shown additional activities toward pentose-based glycosidic bonds, such as xylose and arabinose (Michlmayr & Kneifel, 2014). They have been characterized to be either extracellularly (*L. plantarum* USC1) or intracellularly (*L. casei* ATCC 393*, O. oeni* ATC BAA-1163*, L. brevis* SK3, and *L. mesenteroides*) produced (Coulon et al., 1998; Gueguen et al., 1997; Michlmayr & Kneifel, 2014; Sestelo et al., 2004). β-glucosidase activities in plant-based fermented products, such as kimchi, were also studied in *L. pentosus* 6105 and *Companilactobacillus paralimentarius* LH4 about ginsenoside Rb1 saponin biotransformation (He et al., 2019).

Moreover, phosphor-β-glucosidases and phosphor-β-galactosidases, which are involved in the PTS-based sugar transport, mainly in OHOM and FHET LAB species, might be involved in the degradation of such moieties as it has been demonstrated for phenolic compounds (Acin-Albiac et al., 2021). Interestingly, *L. brevis* is one of the few OHET species that harbor those putative genes in their genome (Michlmayr & Kneifel, 2014) together with *L. pseudomesenteroides* DSM 20193 that encodes for one cellobiose phosphor-β-glucosidase PTS system (Acin-Albiac et al., 2021). The transport of plant glucoside metabo-

lites was studied in *L. acidophilus* NCFM, where different PTS transport systems were upregulated depending on the compounds in which they were grown. Nevertheless, some upregulated genes were shared within different compounds. For instance, the EIIABC component of the PTS system and a phospho-β-glucosidase that belonged to glycoside hydrolase Family 1 were upregulated when cells were grown in amylagdin, esculin, and salicin, in comparison to when they were grown in glucose (Theilmann et al., 2017). Moreover, β-glucosidase (*gluA*), β-galactosidase (*bgl*), and α-rhamnosidase (*rhaA*) expressed in *Arthrobacter* sp. S41 has been demonstrated to play an essential role in the degradation of glucose, galactose, and rhamnose moieties in α-chaconine and α-solanine glycoalkaloids from potatoes (Hennessy et al., 2020).

Furthermore, few studies have been conducted on β-galactosidase activities of LAB about saponin deglycosylation. β-galactosidase in LAB has been mainly studied for its function on the degradation of lactose into free glucose and free galactose, cleaving the β-1,4-glycosidic bond (Vasudha et al., 2023). In some plant saponins, this bond type (demissidine in potatoes) and similar bonds (β-1,2-glycosidic bond) between glucose and galactose are found in different plant saponins such as soyasaponins (Oleszek & Oleszek, 2020). High β-galactosidase activities have been characterized in *L. acidophilus, L. helveticus*, and *L. reuteri* based on the *o*-nitrophenol-β-D-galactopyranoside assay (Carević et al., 2016). *Lactobacillus bulgaricus* L3 β-galactosidase has been concluded to be involved in the glycosylation of steroidal saponins, used as sugar substrate acceptors using lactose as a sugar donor (J. Zhang et al., 2016).

Rhamnosidase activities have also been studied in LAB due to their relevance in the hydrolysis of rhamnose moieties attached to flavonoids, thus increasing their bioavailability and consequently performing their favorable biological properties as anti-inflammatory and antimutagenic compounds (Mueller et al., 2018). Although flavonoids are polyphenolic compounds, their sugar-attached bonds are si the ones found in some plant saponins, therefore suggesting that similar enzymatic activities might be important to correlate among different plant metabolites (Bravo, 1998; Oleszek & Oleszek, 2020). Strains of *L. plantarum, L. brevis, P. adidilactici*, and *L. fermentum* have shown correlations between in vitro rhamnosidase activity and the ability to hydrolyze rhamnose from specific flavonoids (hesperidin) (Mueller et al., 2018). Nevertheless, the hydrolysis of specific flavonoids has been shown to be substrate and strain-dependent. For instance, some strains showed high rhamnosidase activities but low flavonoid hydrolysis, whereas others showed different flavonoid hydrolysis toward different saponins within the same LAB strain (Mueller et al., 2018). Other rhamnosidases have been characterized in *L. plantarum* DSM 20205 and *L. acidophilus* DSM 9126, showing evolutionary differences among them, where the former seemed to be more closely related to *Aspergillus* genera, whereas the latter to *ramA* gene of *Clostridium stercorarium*, suggesting HGT events (Beekwilder et al., 2009). Although their presence and activity in those strains, their application in fruit juice was limited by their pH-dependent activity, which was close to none in pH < 4.5 (Beekwilder et al., 2009). More studies on the performance of rhamnosidases in the hydrolysis of rhamnose-containing saponins are needed to evaluate their promising activities.

Furthermore, it has been shown how some strains of *L. brevis* (*L. brevis* subsp. *coagulans*) and *Lactobacillus crustorum* encoded and expressed β-glucuronidase (*gus*) that demonstrated to hydrolyze glucuronic acid moiety attached to herbal and tea saponins attached to the C-3 of the aglycone (Qian et al., 2018; Sakurama et al., 2014). This enzyme belongs to the glycoside hydrolase Family 30 (GH30), and it has shown substrate specificity preferences toward some flavonoids (baicalin) in comparison to others (estrone) (Sakurama et al., 2014).

Future research on factors that affect glycoside hydrolase expression and their specificity toward sugar moieties attached to aglycone is needed. LAB strains capable of producing specific GH also need to be adapted to express them under specific fermentation conditions, considering pH, temperature, other C-sources, and coculture conditions with other LAB strains. Saponins might not necessarily up–downregulate the transcription of glycoside-related genes, but their expression has been demonstrated to influence saponin's degradation. Therefore, finding other ways to upregulate their expression might positively affect the degradation outcome.

5.4 | Polyphenolic compounds

Phenolic and polyphenolic compounds are widely present as plant metabolites, constituting an important factor in the human diet (Bravo, 1998). There are more than 8000 types of polyphenols differing in structure, chemistry, biological action, origin, and composition. However, they are all considered secondary metabolites originating through the shikimate or the acetate pathways in plants. Polyphenols are generally found in nature in conjugated forms, frequently bound to sugars (such as glucose, galactose, rhamnose, xylose, and arabinose), carboxylic and organic acids, lipids, and other phenolic compounds (Bravo, 1998). They are classified into multiple groups, including phenolic acid derivatives (acetophenones, coumarins, chromones, and hydroxycinnamic acids), flavonoids (flavonols, flavanones, isoflavonoids, etc.), stilbenes, and lignans, among others (Bravo, 1998; Rodríguez et al., 2009). A more recent

TABLE 3 Summary of transport systems, enzymes, and genes characterized in lactic acid bacteria (LAB) species and strains, including the specific target substrates tested and the factors influencing those phenotypes, for the degradation of phytates, raffinose-family oligosaccharides (RFOs), saponins, phenolic compounds, protease inhibitors, and oxalates.

Antinutrients	Transport systems	Relevant enzymes and genes	LAB species and strains (phenotypically and/or genotypically characterized)	Substrates	Factors influencing phenotypes	References
Phytates	Unknown	phytase (*phy, phyLP*), tyrosine-like phosphatase (p*hyLf*), putative phosphatases	*Lactiplantibacillus plantarum (CRL1964, JBPRS, DPC2739)*, *Lentilactobacillus buchneri*, *Pediococcus pentosaceus*, *Levilactobacillus brevis*[a], *Bifidobacterium* spp., *Limosilactobacillus reuteri, Limosilactobacillus. fermentum (DSM 20052, NKN51), Companilactobacillus alimentarius, Lactobacillus acidophilus, Lacticaseibacillus casei 40 W, Lactobacillus amylovorus (B4552*[b]*), Lacticaseibacillusrhamnosus, Fructilactobacillus sanfranciscensis 22E and CB1, Fructilactobacillus fructivorans DA106, Lactiplantibacillus pentosus CECT 4023*	Phytate, *p*-nitrophenyl phosphate, D-fructose-6-phosphate, and D-glucose-6-phosphate, sodium phytate, α-phospho-DL-serine/threonine /tyrosine	pH, temperature, metal ions, phosphoric ester bonds type, C-source, substrate specificity	Andrabi et al. (2016), Damayanti et al. (2017), De Angelis et al. (2003), García-Mantrana et al. (2015), Haros et al. (2005), Lee et al. (2013), Palacios et al. (2005), Sandez Penidez et al. (2020), N. Sharma et al. (2020), R. Sharma et al. (2018), Sreeramulu et al. (1996), Sumengen et al. (2013), Sümengen et al. (2012), Zamudio et al. (2001)
RFOs	PTS transporter (l*acS*), ABC transporter, ECF-type transporter (M6PI), permeases (*rafP*)	α-Galactosidases (*galA, melA*), levansucrase (*levS, ftFA*), sucrose phosphorylase (*scrP, gtfA*), fructofuranosidase (*sacA/sacB, bfrA*)	*Leuconostoc mesenteroides PM173* and *pseudomesenteroides NFICC 99* and *2004, Lacticaseibacillus paracasei* ssp. *paracasei, Streptococcus thermophilus S3, L. plantarum, L. fermentum LF314, L. brevis*, *L. reuteri ATCC 23271*, *L. casei, L. curvatus*, and *L. acidophilus ATCC 23271, B. lactis HNO19, P. pentosaceus AM173*	Raffinose, stachyose, verbascose, melibiose	Substrate specificity, plant food matrices	Carević et al. (2016), Gänzle and Follador (2012), Hati et al. (2014), Kahala et al. (2023), Kanwal et al. (2023), Oguntoyinbo (2007), Sedó Molina et al. (2022), Sedó Molina, Shetty et al. (2024), Silvestroni et al. (2002); Tsangalis and Shah (2004), Wätjen et al. (2023), Yoon and Hwang (2008), Zartl et al. (2018), Zhao and Gänzle (2018), Zhong et al. (2018)

(Continues)

TABLE 3 (Continued)

Antinutrients	Transport systems	Relevant enzymes and genes	LAB species and strains (phenotypically and/or genotypically characterized)	Substrates	Factors influencing phenotypes	References
Saponins	PTS systems (phospho-β-glucosidases and phospho-β-galactosidases)	β-D-Glucosidases (*gluA*, GH1,2,3, 30), β-galactosidases (*bgl*, GH1,2,3,30,35,43), α-L-rhamnosidases (*ramA*), α-L-arabinosidases (*araA*), β-D-xylosidases (*xynB*), xylose isomerase (*xylA*) and β-glucuronidases (*gus*, GH30)	*L. plantarum (USC1*[b] *and DSM 20205), L. casei ATCC 393, O. oeni ATC BAA-1163, L. brevis SK3 and L. mesenteroides, L. pentosus 6105, Companilactobacillus paralimenterius LH4, Lactobacillus bulgaricus L3, L. acidophilus (NCFM and DSM 9126), Lactobacillus crustorum*	ginsenoside Rb1 saponin, steroidal saponins, tea and herbal saponins, soysaponins	Substrate specificity, type of sugar moiety, growth C-source	Acin-Albiac et al. (2021), Carević et al. (2016), Coulon et al. (1998), Fu et al. (2020), Gueguen et al. (1997), He et al. (2019), Michlmayr and Kneifel (2014), Overney and Huang (2020), Pham et al. (2023), Qian et al. (2018); Sakurama et al. (2014), Sestelo et al. (2004), Theilmann et al. (2017), Ventura et al. (2009)
Phenolic compounds	Unknown, PTS systems (phospho-β-glucosidases)	Hydroxycinnamic acid esterases (*lP_0796, lj0536, lj1228, hceP, and est_1092*), phenolic acid decarboxylase (*padC*), hydrocinnamic acid reductases (*hcrB. hcrF, and par1/par2)*, tannases (*tanA*, t*anB*), vinyl phenol reductases (*vrpA*), hydroxybenzoic acid decarboxylases (*lpdC*), β-glucosidases (*gluA*), rhamnosidases (ram1), β-glucurunosidases (*lcGUS30*)	*L. plantarum (ATCC 14917, WCFS1, TMW1.460, DSM 1055, DSM 20205), L. fermentum FUA3589, L. johnsonii N6.2, Furfurilactobacillus millii FUA 83583, L. brevis, L. acidophilus NCFM, L. lactis, P. pentosaceus, and L. brevis FERM BP-4693, L. crispatus, L. helveticus*	ferulic acid, caffeic acid, *p*-coumaric acid, oleuropein, flavonoids, tannic acid, chlorogenic acid, rosmarinic acid, hydroxycinnamic methyl and ethyl esters, gallocatechin, epigallocatechin gallate	Substrate specificity, type of sugar moiety (glycosidases), cell physiological state, outcompeting gene regulation	Gaur et al. (2020, 2023), Gaur and Gänzle (2023), Jiménez et al. (2013, 2014), Landete et al. (2021), Michlmayr and Kneifel (2014), Sakurama et al. (2014), Santamaría et al. (2018)
Protease inhibitors	Di- and oligopeptide intracellular transporters (*opp, dpp*) (hydrolyzed peptides from protease inhibitors)	Proteinases (CEPs—*prt*) and proteases	*L. paracasei (Lpa4), L. pseudomesenteroides (Leps1), P. pentosaceus (Pp3), L. corynniformis (Lco4), L. plantarum (Lpl5 and NRRL B-4496), L. salivarius H32.1, L. mucosae D5a1, and L. rhamnosus LE3, L. brevis and L. lactis*	KTI and BBI inhibitors (soy, chickpeas, peas, wheat)	Substrate specificity and growth conditions (pH, redox balance)	Çabuk et al. (2018), Caminero et al. (2019), Fraberger et al. (2020), Gao et al. (2013), Sáez et al. (2022)

(Continues)

TABLE 3 (Continued)

Antinutrients	Transport systems	Relevant enzymes and genes	LAB species and strains (phenotypically and/or genotypically characterized)	Substrates	Factors influencing phenotypes	References
Oxalates	Putative permeases and ABC transporters.	Formyl coenzyme A transferase (*frc*) and oxalyl coenzyme A decarboxylase (*oxc*)	*L. acidophilus (NCFM), L. gasseri (ATCC 33323), L. plantarum, L. fermentum, L. murinus (1222, 3133, 5333), L. animalis (5323, 5241, 5342, 5121, 1221, 6331, 223C), L. reuteri, L. paracasei, Weissella confusa, W. cibaria, L. rhamnosus, Loigolactobacillus bifermentans, L. salivarius* and *Bifidobacterium animalis subsp. lactis BI07, Bifidobacterium dentium Bd1*	Oxalate	pH, oxalate intracellular transport	Azcarate-Peril et al. (2006), Cho et al. (2015), Gomathi et al. (2014), Kullin et al. (2014), Lewanika et al. (2007), Murphy et al. (2009), Tavasoli et al. (2022), Turroni et al. (2010), Ventura et al. (2009), Youssef (2024)

[a]Represents strains characterized to produce the corresponding enzyme/s extracellularly and intracellularly.
[b]Represents strains that have been characterized to produce the corresponding enzyme/s extracellularly.
Abbreviation: PTS, phosphotransferase.

classification separates phenolic compounds based on their negative or positive effect on human health. First, review articles have focused on their adverse action due to their participation in precipitating proteins, inhibiting digestive enzymes, and reducing the absorption of plant vitamins and minerals (Bravo, 1998; Rodríguez et al., 2009). Nevertheless, some other studies have postulated some beneficial health effects in specific types of phenolic compounds (flavonoids) due to their antioxidant and free-scavenging abilities (Bravo, 1998; Rodríguez et al., 2009). Apart from those attributes, phenolics contribute to the volatile and non-volatile flavor profiles (bitterness and astringency) and color of specific food products (Gaur & Gänzle, 2023; Rodríguez et al., 2009).

Tannins, which are the polyphenolic compounds mainly studied due to their antinutritional effects, are high molecular weight multimeric phenolic compounds that are highly hydroxylated and form insoluble complexes with carbohydrates and proteins and are responsible for the astringency of tannin-rich food products (Bravo, 1998). Hydrolysable tannins are constituted by gallic acid monomers (gallotannins) and/or hexahydroxydiphenic acids bound to glucose (usually) (ellagitannins). In contrast, insoluble condensed tannins are multimeric flavan-3-ol (catechin, etc.) polymers. In cereals, hydroxycinnamic acids are the most abundant phenolic compounds, such as ferulic acid esterified to arabinoxylans (barley and rye) or ferulic, *p*-coumaric, and caffeic acid esterified to glycerol (oat and sorghum).

The metabolic effect of specific LAB species and strains on the biotransformation of different phenolic compounds has been extensively studied through the last decades toward specific phenolic compounds such as hydroxycinnamic, hydroxybenzoic, and tannic acids found in specific plant-based matrices such as fruits (mangoes, grapes, cherries, and pomegranate), vegetables (broccoli), cereals (oats, wheat), and legumes (soybeans). Specific esterases, reductases, and decarboxylases are important in degrading some phenolic compounds (Gaur & Gänzle, 2023). These authors have explained that hydroxycinnamic esters might be released by esterases such as *LP_0796, Lj0536, Lj1228, HceP*, and *Est_1092*, forming hydroxycinnamic acids, which can subsequently be decarboxylated by phenolic acid decarboxylases (Pad), producing vinyl phenol derivatives or reduced by HcrB. HcrF and Par1/Par2 reductase coding genes. Vinyl phenol derivatives can also be reduced through other reductase coding genes such as *vrpA*. In contrast, hydroxybenzoic esters can be transformed into hydroxybenzoic acids by other esterases, such as tannases (TanA or TanB), and subsequently decarboxylated to simple phenols throughout other decarboxylases such as LpdC. Furthermore, as mentioned in the saponin section, some LAB glycosidases, such

as β-glucosidases, phosphor-β-glucosidases, and rhamnosidases, have been demonstrated to be involved in the deglycosylation of flavonoids. For instance, *L. plantarum, L. pentosus, L. brevis*, and *P. pentosaceus* have been characterized to hydrolyze glucose moiety of oleuropein through β-glucosidase activities (Michlmayr & Kneifel, 2014).

The activities of the enzymes mentioned above have been characterized in specific strains of *L. plantarum* (TanA, TanB, HceP, Lp_2945, Lp_366, est_1092, Lp_0796, Est_1092, HcrB, Pad, VrpA, and Ram1), *L. fermentum* (HcrF), *L. johnsonii* (Lj0536), *Furfurilactobacillus millii* (EstR, Par1, Par2), *L. brevis* (LcGUS30), and *L. acidophilus* ($RamA_{LA}$) (Gaur et al., 2020, 2023; Jiménez et al., 2013, 2014; Sakurama et al., 2014; Santamaría et al., 2018). For instance, in some LAB strains such as *F. millii* FUA 83583, the reductase activity of Par1/Par2 was out-competing the decarboxylase activity of Pad, producing more dihydro-derivatives than vinyl derivatives out of ferulic, caffeic, and *p*-coumaric acids. However, more vinyl derivatives were produced when phenotypically testing *Δpar1/par2* mutants (Gaur et al., 2023) throughout decarboxylation pathways, suggesting overexpression of *pad* in reductive growth conditions. All the genes mentioned above have been documented to be produced intracellularly, thus requiring an intracellular transport system to be transformed, except TanA, which is extracellularly produced (Jiménez et al., 2014).

L. plantarum has been the LAB species primarily studied in the degradation of phenolic compounds (Barthelmebs et al., 2001; Jiménez et al., 2013, 2014; Landete et al., 2021; Pulido-Mateos et al., 2022; Santamaría et al., 2018). Some of their genes have been cloned to other LAB species to characterize their activity when heterologously expressed. Tannase genes were more expressed in *L. lactis* MG1363 than in *L. casei* BL23, *L. reuteri* CECT, or *S. thermophilus* INIA 468 when cloning the same gene from *L. plantarum* (Landete et al., 2021). Esterase activities toward feruroyl compounds (*est_1092*) have also been reported in *L. fermentum, L. crispatus, L. acidophilus*, and *L. helveticus*. Moreover, *pad* activity has been found in *L. lactis*, *P. pentosaceus*, and *L. brevis*, apart from *L. plantarum* species (Landete et al., 2021).

Niche adaptation of LAB into specific environments might explain the evolutionary events concerning phenolic acid degradation and HTS. For instance, fructophilic LAB (FLAB) that live in fructose-rich niches such as pollen and insect gastrointestinal tracts have demonstrated the advantage of using their genotypical characteristics to acquire metabolic benefits from phenolic compounds present in those environments (Filannino et al., 2016). Specifically, Filannino et al. (2016) suggested that heterofermentative *Lactobacillaceae* such as FLAB may use *p*-coumaric acid as a final external acceptor when others such as fructose, oxygen, or pyruvate are low or not present. Thus, the regeneration of NAD^+ from the reduction of *p*-coumaric to phloretic acid might enhance glucose intake by FLAB throughout glycolysis, increasing ATP yield in the phosphoketolase pathway (Filannino et al., 2016; Gaur & Gänzle, 2023). In contrast, decarboxylation pathways of phenolic compounds throughout the *pad* may be used by LAB as detoxification reactions of those compounds into less toxic derivatives. Moreover, decarboxylation reactions involve the consumption of H^+, which might contribute to the internal and external pH balance and the production of CO_2 that increases buffer capacity (Barthelmebs et al., 2000; Zuljan et al., 2016).

All genes and enzymes mentioned above were considered for generating the amino acid-based blast analysis (Figure 2). Strains from *C. alimentarius, L. argentoratensis, L. paraplantarum, L. pentosus, S. collinoides* (one strain), and *L. plantarum* encoded for more than 10 genes were analyzed. Most strains of *L. argentoratensis, L. paraplantarum*, and *L. plantarum* encoded for 3–4 copies of HcrB, finding up to 7 copies in one *L. plantarum* strain. LpdC was found in *S. collinoides* to have 3–4 copies. *TanA* coding genes were found not only in *L. plantarum* but also in three strains of *C. alimentarius*, two strains of *L. argentoratensis*, four strains of *L. paraplantarum* and *L. pentosus*, and four strains of *O. oeni*. PadC was found in most of the strains belonging to *L. lactis, Pediococcus spp., C. farciminis, L. helveticus, Latilactobacillus spp., L. brevis, L. aviarius, L. mucosae*, and *L. fermentum*, apart from the ones mentioned previously (not *O. oeni*). Par1 was only found in *Lactiplantibacillus* spp., and only specific strains of *C. farciminis* (1), *L. hilgardii* (3), *S. collinoides* (1), *L. coryniformis* (2), and *L. parafarraginis* (1). Furthermore, homologs of *estA* gene were found in more than 60% of strains belonging to *L. fermentum, P. parvulus, L. reuteri, L. aviarius, L. johnsonii, L. gallinarum, L. crispatus, L. plantarum, L. pentosus, C. farciminis*, and *C. alimentarius*. *EstA* was not found in any of *L. paraplantarum* strains.

5.5 | Protease inhibitors

Plant protease inhibitors are small proteins (5–70 kDa) found in storage and aerial plant tissues and are essential to them due to their function against insects and pathogens, interfering in their enzymatic digestive system. They are frequently classified into 12 families, including the 2 most studied families, which are Bowman–Birk inhibitors (BBI), which generally inhibit trypsin, chymotrypsin, and/or elastase, and Kunitz-type inhibitors (KTI), which act on serine, cysteine, and aspartic proteases (Cid-Gallegos et al., 2022). The former is typically found in plant families such as *Fabaceae* (soy, pea, chickpea,

lentils) and *Poaceae* (maize, wheat, rice, barley, millet, and oat), whereas the second also includes *Solanaceae* (potato), *Cruciferae*, among others, apart from the previously mentioned. Moreover, specific α-amylase and trypsin inhibitors from *Poaceae* belong to Family VI of protease inhibitors, as well as specific potato inhibitors (I and II) (Families III and IV) and carboxypeptidase inhibitors (Family X), which are mainly present in *Solanaceae* plant family (Cid-Gallegos et al., 2022). They are considered antinutrients due to their ability to bind digestive proteases, inhibiting their capability to break down proteins and limiting the absorption of peptides and amino acids during digestion (Cid-Gallegos et al., 2022). Structurally, they can form mono, di, and tetrameric protein structures, depending on their source (Boakye et al., 2022; Laatikainen et al., 2017).

Research studies on the degradation of protease inhibitors by LAB have focused on α-amylase and trypsin inhibitors (ATIs) degradation, mainly during legume and cereal-based fermentations (Caminero et al., 2019; Fraberger et al., 2020; Huang et al., 2020). It has generally been associated with pH-based ATI activity inhibition or proteolytic activities of LAB toward ATI hydrolysis. However, limited research has been conducted on the latter. LAB strains belonging to *L. paracasei* (Lpa4), *L. pseudomesenteroides* (Leps1), *P. pentosaceus* (Pp3), *L. corynniformis* (Lco4), and *L. plantarum* (Lpl5) have shown high abilities (40%–85%) of degrading wheat-extracted ATIs among 87 sourdough LAB isolates (Fraberger et al., 2020). Caminero et al. (2019) compared the high ATI-degrading ability of *L. salivarius* H32.1, *L. mucosae* D5a1, and *L. rhamnosus* LE3 with the low ATI-degrading ability of *L. fermentum* R39.3 and *L. reuteri* R12.22 in vivo, all isolated from human. ATI-degrading ability was demonstrated to be strain-specific. ATI-degrading ability has been studied phenotypically, but transcriptomic and genetic studies of LAB proteolytic enzymes involved in their degradation need further exploration. Nevertheless, interactions between serine-type endopeptidases (*prt* family) and KTI have been modeled, showing binding energy changes and high relative affinities in proteases encoded by *L. plantarum* and *L. lactis* (B7VFD1 and Q49SH0 UniProt accession numbers) toward three different KTI and BBI chickpea protease inhibitors. Peptidase from *L. plantarum* showed higher relative affinity to all three inhibitors in the model (Sáez et al., 2022). Cell envelope proteinases (CEPs) present in LAB are proteases that belong to the *prt* family and play an essential role in the primary degradation of extracellular proteins, such as milk or plant proteins, into oligopeptides that can be transported intracellularly by specific peptide transporters and serve as N-source for growth and metabolism. Six main types of CEPs have been identified based on protein sequences, including PrtP *(L. paracasei* subsp. *paracasei, L. lactis* subsp. *cremoris*, and subsp. *lactis, L. rhamnosus)*, PrtB *(L. delbrueckii* subsp. *bulgaricus)*, PrtH *(L. helveticus)*, PrtS *(S. thermophilus)*, PrtR *(L. rhamnosus)*, and PrtL *(L. delbrueckii* subsp. *lactis)* (Ji et al., 2021). Other *Leuconostoc* spp., such as *L. pseudomesenteroides* and *L. mesenteroides*, have also been characterized to encode for *prtP* genes (Christensen et al., 2022; Sedó Molina et al., 2024). Other species, such as *L. acidophilus (BGRAA3, CH2, V74), L. casei (HN14, IFPL731), L. plantarum (LP69)*, and *F. sanfranciscensis* (CB1), have also been characterized to encode for CEPs. The specificity of CEPs has been mainly studied toward milk proteins, and different cleavage sites have been found depending on the type of milk protein targeted, such as α_{s1}, α_{s2}, β, and κ-caseins (Ji et al., 2021). Moreover, different *prt* genes from LAB strains have been shown to cleave in specific sites in milk protein sequences (Ji et al., 2021). Although specificity, structure, and activity of CEP studies have mainly been conducted on milk proteins, more phenotypical, transcriptomic, and genetic studies might be relevant to assess their activity toward ATIs, as Sáez et al., 2022 modeled CEPs-ATI interactions.

Furthermore, studies investigating the decrease of trypsin inhibitory activities during and after fermentation have also been reported. Trypsin and chymotrypsin inhibitory activities in pea protein concentrate were reduced by 18% and 70%, respectively, after 11 h of fermentation with *L. plantarum* NRRL B-4496 (Çabuk et al., 2018). Moreover, cocultured solid-state fermentation (SSF) using *L. brevis* with *Aspergillus oryzae* in soybean meal reduced trypsin inhibitor content by 89.2% after 72 h, majorly contributed by the action of the filamentous fungi (Gao et al., 2013). Hoffmann et al. (2003) showed how soybean trypsin inhibitor was inactivated and degraded in an in vitro rumen incubation. Three different concentrations of trypsin inhibitor (2, 4, 10 mg/mL) were subjected to three different rumen incubations, being completely inactivated after 6, 9, and 12 h, respectively. In another context, the ATI content was significantly reduced (by 41%) after 12 h of sourdough fermentation using a Type 1 sourdough starter (Boakye et al., 2022). Interestingly, Laatikainen et al. (2017) compared ATI concentration in wheat after yeast-based and sourdough fermentation. Sourdough fermentation decreased the ATI polymeric (60 kDa) content while increasing the ATI monomeric forms (<14 kDa), significantly higher than upon yeast-based fermentation. This could mainly be due to the reduction of disulfide bonds between ATI monomers under the reductive redox conditions of sourdough.

Prt-based homologous genes were considered in the blast. The high presence of *prt* genes was found to be associated with *L. rhamnosus, L. delbrueckii, L. gallinarum, L. kefiranofaciens, L. panis*, and *S. collinoides. prtP* and

prtR were predominantly found in *Lacticaseibacillus spp*., whereas *prtP* and *prtB* were in *L. delbrueckii* and *L. gallinarum*. PrtM was found in two strains of *B. animalis* and one strain of *B. bifidum*, two strains of *C. alimentarius, L. reuteri, O. oeni, P. pentosaceus, L. mesenteroides*, and *L. panis*, and three of *L. citreum*, and one strain of *Companilactobacillus farciminis, F. sanfranciscensis, L. crispatus, L. sakei, L. diolivorans, L. coryniformis*, and *L. pentosus*. Two strains of *L. kefiranofaciens* were found to have one copy of *prtM, prtH, and prtB* each, whereas only *prtB* was found in the other three strains. *PrtH* was found in the same two strains of *C. farciminis, L. kefiranofaciens, L. panis, O. oeni*, and *P. pentosaceus*, and in one strain of *B. bifidum, L. pentosus, L. crispatus, L. citreum, L. diolivorans, L. sakei, L. mesenteroides*, and *L. reuteri*.

Further research is needed to understand the transcriptomic and protease substrate specificity factors behind the ability to degrade different protease inhibitors in multiple crops. Since proteinases target specific peptide bonds, proteomic studies could elucidate the protease expression patterns during fermentation under different pH levels and using different protease inhibitors as substrates. However, highly proteolytic LAB strains isolated from crops with high inhibitor content might be a promising LAB selection target for PBDA fermentations. The presence of other plant proteins that are more accessible and found at higher concentrations in plant-based matrices might influence the inhibitor degradation outcome.

5.6 | Oxalates

Oxalic acid is a dicarboxylic acid widely present in diverse families of plants, fungi, lichens, and algae involved as a secondary metabolite in the glycolate, oxaloacetate, and ascorbic acid pathways (Li et al., 2022). Oxalic acid is relevant for its participation in calcium regulation, photosynthesis, metal detoxification, and pH homeostasis in plants. Nevertheless, its increased intake and absorption might cause health diseases such as hyperoxaluria, which involves the formation of calcium oxalate stones in humans (Li et al., 2022; Mogna et al., 2014; Tavasoli et al., 2022). There are two main types of oxalic acid in plants: soluble and insoluble oxalic acid. Soluble oxalic acid is usually bound to sodium (Na^+), ammonium (NH_4^+), or potassium (K^+), whereas the insoluble forms complexes with calcium (Ca^{2+}), magnesium (Mg^{2+}), and iron (Fe^{2+}) (Li et al., 2022). In plants, oxalic acid degradation mainly involves three enzymes: oxalyl-CoA synthase (EC 6.2.1.8) (Aae3), oxalate oxidase (EC 1.2.3.4) (Oxo), and oxalate decarboxylase (EC 4.1.1.2) (Oxdc). Aae3 is essential in the oxalate acetylation pathway, which is ATP-dependent. Oxalate degradation through this pathway involves four different enzymes that catabolize consecutive reactions until producing CO_2 after decarboxylase, transferase, and dehydrogenase transformations. Both Oxo and Oxdc are Mn-dependent enzymes that catalyze the oxidation of oxalate into CO_2 and H_2O_2 and into CO_2 and formate, respectively. Oxdc is also pH-dependent (Li et al., 2022).

Some species have been genetically and phenotypically evaluated in bacteria to encode for oxalate degradation enzymatic machinery. For instance, *Oxalobacter formigenes* has been studied for its metabolic mechanism of using oxalate as the main C-source in the GIT (Kullin et al., 2014; M. Liu et al., 2021; Mogna et al., 2014). Because oxalate is found in the GIT due to its uptake from oxalate-rich foods, specific strains of *L. acidophilus* (NCFM), *L. gasseri* (ATCC 33323), *L. plantarum, L. fermentum, L. murinus, L. animalis, L. reuteri, L. paracasei, Weissella confusa, Weissella cibaria, L. rhamnosus, Loigolactobacillus bifermentans, L. salivarius*, and *Bifidobacterium* spp. have been tested for the presence of oxalate-degrading phenotypes as well as their potential to be used as probiotic strains to avoid oxalate derived adverse health effects (Azcarate-Peril et al., 2006; Cho et al., 2015; Gomathi et al., 2014; Kullin et al., 2014; Lewanika et al., 2007; Murphy et al., 2009; Tavasoli et al., 2022; Turroni et al., 2010; Youssef, 2024). Based on genetic and transcriptomic studies, two critical genes in LAB are involved in positive oxalate-degrading LAB strains: formyl coenzyme A transferase (EC 2.8.3.16) (*frc)* and oxalyl coenzyme A decarboxylase (EC 4.1.1.8) (*oxc*). The former is involved in transferring CoA moiety from formyl-CoA to oxalate, producing oxalyl-CoA and formate. The latter decarboxylates oxalyl-CoA into formyl-CoA and CO_2, resulting in one molecule of formate and CO_2 per molecule of oxalate (Figure 1) (Azcarate-Peril et al., 2006; Kullin et al., 2014). In some LAB strains, such as *L. gasseri* ATCC 33323 and *L. acidophilus* NCFM, *frc* and *oxc* appear to form an operon because both genes have been analyzed to have terminators (Azcarate-Peril et al., 2006; Lewanika et al., 2007).

Transport systems encoding genes are in the same cluster as those that encode oxalate degradation in some LAB strains. *L. gasseri* ATCC 33323 showed a putative predicted permease, *L. acidophilus* NCFM had a putative predicted ABC transporter, and *L. reuteri* encoded for a xanthine, uracil, and vitamin C putative permease next to *frc* locus (Azcarate-Peril et al., 2006; Lewanika et al., 2007). Differently, *O. formigenes* encodes for an antiport transport system of oxalate and formate (*oxIT*), which belong to the major facilitator superfamily of transporters (Iyalomhe et al., 2015).

Interestingly, Youssef (2024) stated that among five positive oxalate-degrading LAB strains screened, all encoded for the *frc* gene, while only three encoded for both *frc* and *oxc* genes, which were *L. bifermentans* SA5, *L. para-*

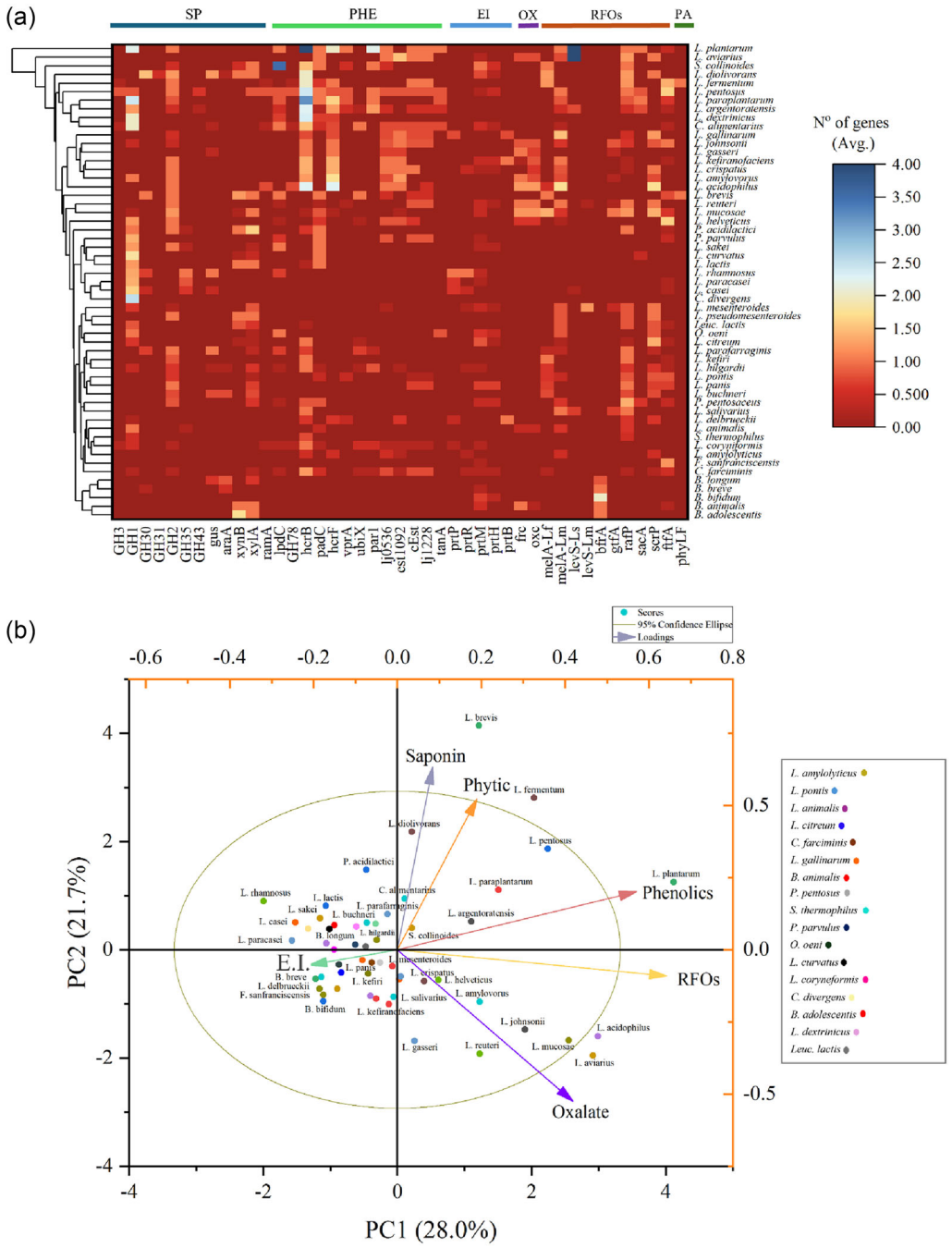

FIGURE 2 Homology-based blast analysis of genes (42) involved in the degradation of antinutrients to all QPS-listed LAB species (240 strains). Gene and species abbreviations are included in File S1. (a) Species-based clustered heatmap representing the average number of copies of genes found in the different LAB strains from each LAB species. (b) PC-biplot (PC2 = 21.7% and PC1 = 28.0%) of the average number of genes found in each LAB species standardized to a scale of 0–1 based on the maximum LAB species representative of each antinutrient category. The five antinutrient categories were included as loadings, whereas each species was included as a score with a colored-based dot scale. The closer the score (dot) is to the loading, the higher the number of species' genes as an average of the representative strains analyzed from that species. EI, enzyme inhibitors; OX, oxalates; PA, phytate; PHE, phenolic compounds; RFOs, raffinose-family oligosaccharides; SP, saponins. *Source*: Plots were created using OriginPro 2021.

casei SA9, and *L. plantarum* SA37. In *L. reuteri* 100-23C, both genes were present, but no phenotype was observed. This fact might be explained by the lack of an oxalate transport mechanism in this strain (Kullin et al., 2014). *Bifidobacterium animalis* subsp. *lactis* BI07, which encoded for *oxc* and *frc* genes, showed a pH dependency of the gene expression based on transcriptomics. The oxalate degradation rate was increased when this strain was exposed to pH 4.5, supporting that *frc* and *oxc* genes require mildly acidic conditions to be expressed (Turroni et al., 2010). Moreover, an ORF encoding a putative permease (*ORF-1*) flanking *oxc* gene was found and might be involved in intracellular oxalate transport and counteracting pH changes (Turroni et al., 2010). Similarly, both strains *L. gasseri* ATCC 33323 and *L. acidophilus* NCFM showed higher oxalate-degrading gene expression when cells were adapted to sodium oxalate and transferred to pH = 5.5 growth media (Azcarate-Peril et al., 2006; Lewanika et al., 2007). Furthermore, *Bifidobacterium dentium* Bd1, a LAB strain isolated from dental plaque, upregulated both *frc* and *oxc* when the strain was exposed to acidic conditions (pH = 4), suggesting their influence under acidic-based stress conditions (Ventura et al., 2009). Phenotypical-based studies performed in *L. acidophilus* ATCC5344 and *L. acidophilus* (probiotic 1) have shown a decrease in oxalate concentrations by 21.7% and 41.2%, respectively. In contrast, *L. plantarum* (probiotic 2) increased its concentration significantly (Cho et al., 2015). Some *L. animalis* (5323, 5241, 5342, 5121, 1221, 6331, 223C) and *L. murinus* (1222, 3133, 5333) showed oxalate-degrading phenotype in vitro, but only 223C and 5323 were active in vivo (Murphy et al., 2009).

Only the presence of homologs of *frc* and *oxc* was tested throughout the blast analysis. *B. animalis* was the only *Bifidobacterium* spp. that encoded for at least one of both genes (*frc*), although there was only one strain that encoded for both. *L. acidophilus, L. amylovorus, L. gasseri, L. helveticus, L. johnsonii, L. kefiranofaciens, L. aviarius, L. mucosae*, and *L. reuteri* strains were 100% positive in at least one of both genes. Only all the strains belonging to *L. acidophilus* and *L. mucosae* tested positive for both genes. However, one strain of *L. acidophilus* and *L. mucosae* had two copies each, and one strain of *L. helveticus* had three copies of each gene. All *L. reuteri* strains had both genes, but one strain, although there was another strain with two copies of *frc* and one copy of *oxc*.

However, there are still some challenges to overcome. The regulation of *frc* and *oxc*, particularly dependent on pH, could change over fermentation time because pH is decreased. Moreover, most oxalate-degrading strains are particularly associated with being isolated from the gastrointestinal tract, perhaps limiting their application to plant-based fermentations because their *frc* and *oxc* expression might be adapted to the gut conditions.

6 | METABOLIC INSIGHTS OF LAB: BIOTRANSFORMATION OF OFF-FLAVOR VOCS

VOCs considered off-flavors for the generation of PBFDAs display undesired flavor attributes such as green, beany, and earthy notes that negatively influence the consumer acceptance of plant-based fermented products that mimic their milk-based counter products (Table 2). As discussed previously, they usually have low odor thresholds that make them perceivable at low concentrations.

However, associating a VOC with a particular note is often challenging because a high or a low concentration can affect the perceived notes. This also applies when VOCs are found in combination with other odorant and non-odorant volatiles (Fischer et al., 2022). For instance, hexanal displays "beany" notes when it is present at low concentrations (1–10 ppm), although it does not have this attribute by itself. Similarly, 1-octen-3-one displays sweet-green notes at 100 ppm, whereas it is beany at lower concentrations (1–10 ppm) and 1-octen-3-ol is perceived as earthy at low (1–10 ppm) and high (>1000 ppm), but "beany" in between those concentrations. The binary combinations of 1-octen-3-one (10 ppm) and hexanal or (*E, E*)-2,4-decadienal (2 ppm) display a higher "beany" concentration range (from 1 to 1000 ppm) than others such as hexanal (10 ppm) with (*E*)-2-nonenal (2 ppm) that are perceived as "beany" at <100 ppm (Trindler et al., 2022).

Multiple studies have investigated the potential of LAB strains to remove aldehydes, ketones, pyrazines, furans, and sulfur-based VOCs, some of those off-flavors via fermentation. Still, the underlying mechanisms of specific enzymes involved remain to be understood. Tangyu et al. (2023) analyzed the transformation of VOCs in four different plant-based milks (oat, sunflower seed, faba, and pea milk) using 14 single-strain LAB different fermentations. Although other types of milk contained various VOCs, "green" and "earthy" off-flavor compounds were consistently present across all types, including hexanal, benzaldehyde, nonanal, heptanal, 2-pentylfuran, and 1-octen-3-ol, at varying concentrations. Interestingly, certain LAB strains could transform these compounds into their respective reduced or oxidized forms. For instance, hexanal, nonanal, and heptanal may be reduced to *n*-hexanol, *n*-nonanol, and *n*-heptanol or oxidized to hexanoic, nonanoic, and heptanoic acids (Figure 3). Less is known about the biological transformation products of furans and pyrazines in LAB. However, it has been studied in other

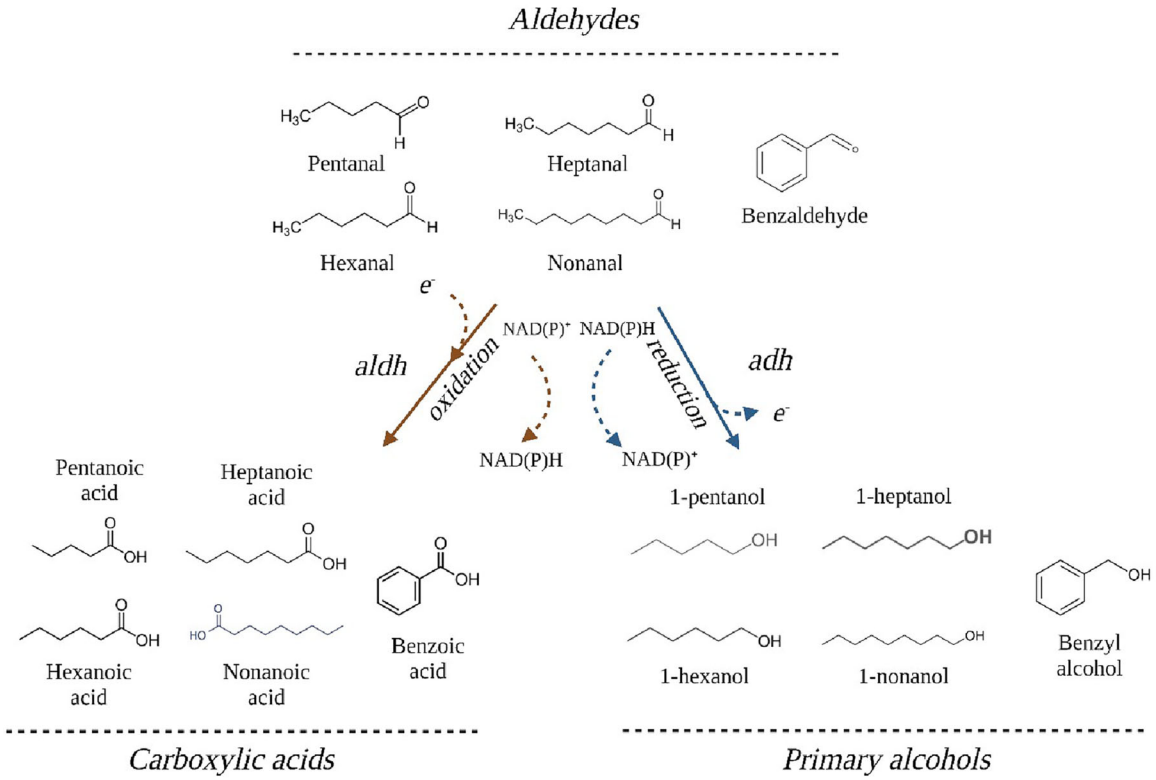

FIGURE 3 Reductive–oxidative reaction of aldehyde volatile organic compound (VOC) off-flavors to their carboxylic acids and primary alcohol forms through lactic acid bacteria (LAB) aldehyde (*aldh*) and alcohol (*adh*) dehydrogenases, respectively. NAD(P)H might mediate those reactions by acting as an electron donor or acceptor molecule. *Source*: Created with Biorender.

bacteria, such as *Stenotrophomonas* sp. and *Mycobacterium* sp. (Rajini et al., 2011). Moreover, the biotransformation of sulfur compounds in LAB has been more focused on the production of dimethyl sulfide, dimethyl disulfide, and dimethyl trisulfide throughout L-methionine and L-cysteine metabolisms than to its degradation (Landaud et al., 2008). Furthermore, OHET LAB species, such as *L. mesenteroides*, showed a higher reduction of aldehyde-based off-flavor rates than other OHOM LAB species, such as *S. thermophilus* strains, in most of the plant-based milk (sunflower, faba, and pea). Aldehydes were mainly transformed into their alcohol forms, although carboxylic acid forms were also present in pea and oat milk. Similarly, Sedó Molina et al. (2024) demonstrated how the removal of aldehyde-based off-flavors was higher when fermenting with *L. pseudomesenteroides* NFICC 2004 than with *L. lactis* NFICC 2005 in soy, oat, and pea milks. That phenotype was conserved when both were cocultured.

Fischer et al. (2022) stated that aldehyde (Aldh) and alcohol (Adh) dehydrogenases are the most important enzymes involved in the transformation of aldehyde and ketone-based VOCs into their alcohol and carboxylic acid respective forms through redox reactions; thus, decreasing off-flavor note's perception (Figure 3). In the central LAB carbon metabolism, the *adh* and *aldh* genes play an essential role in establishing redox balance through $NAD(P)^+$ production, depending on the type of metabolism a LAB species has. There have been classified three types of $NAD(P)^+$ dependent ADH in LAB: long-chain zinc-type ADH (Group I—around 350 amino acids), short-chain metal-free ADH (Group II—250 amino acids), and iron-containing ADH (Group III—around 385 amino acids per subunit) (Chen et al., 2016). It has been suggested that Group III ADHs could have been primarily involved in reducing aldehydes (Elleuche & Antranikian, 2013). Some Group III ADHs homologues of YqhD (NADPH-dependent ADH) in *E. coli* and DhaT (1,3-propanediol dehydrogenase) in *Klebsiella pneumoniae*, have been phenotypically involved in reduction of aldehydes with broad substrate specificity, and have been found in genomes of specific LAB species such as *O. oeni* (Elleuche & Antranikian, 2013). Conversely, the bifunctional aldehyde/alcohol dehydrogenase gene (*adhE*), present in the genomes of most LAB species (except specific fructophilic LABs and some OHOM strains), encodes an iron-containing ADH that is constitutively expressed in OHET species during mixed-acid fermentation of carbohydrates (phosphoketolase pathway) (Fischer et al., 2022; Verce et al., 2020). It catabolizes the reduction of acetyl-CoA (ALDH domain) into acetaldehyde and then

to ethanol (ADH domain), present in the phosphoketolase pathway (Pony et al., 2020). Microbial strains that constitutively produce ALDH and/or ADH are suggested to display better capabilities in removing aldehyde-based off-flavor molecules. Interestingly, LAB species, such as *Fructobacillus fructosus, Apilactobacillus kunkeei*, and *Apilactobacillus apinorum*, which are considered fructophilic LAB, have naturally lost either the ADH or both domains from the *adhE* through adaptation to fructose-rich niches (Endo et al., 2014; Maeno et al., 2019; Sedó Molina et al., 2022). Vermeulen et al. (2007) studied how *F. sanfranciscensis* used hexanal as a hydrogen acceptor to regenerate NADH, producing hexanol and higher levels of acetic acid when hexanal was present. Thus, OHET LAB strains might use the reduction of aldehydes such as hexanal, pentanal, and nonanal, mediated by the oxidation of NAD(P)H to $NAD(P)^+$, to produce additional ATP through acetyl-P dephosphorylation reaction to acetate. This fact suggests that OHET species have developed their competitiveness in nature by utilizing alternative electron acceptors to increase growth and outcompete other microbial strains in specific environments (Gänzle, 2015); therefore, they are more metabolically prone to utilize aldehydes as electron acceptors than OHOM LAB species.

It has been observed that other enzymes, such as glutamate aldehyde dehydrogenase and aspartate aldehyde dehydrogenase, can present alcohol and/or aldehyde dehydrogenase activities in LAB (Chen et al., 2016; Fischer et al., 2022; Hu et al., 2019). In *L. reuteri* DSM 20016, five different ADHs were identified, cloned, and characterized (Hu et al., 2019). They showed substrate heterospecifity on the different *adh* where the highest activities of ADH-1, -2, -3, -4, and -5 were demonstrated on heptanal (heptaldehyde), butyraldehyde, propionaldehyde, heptanal, and 3-methyl butanal, respectively. On the one hand, they showed that ADH-2 and ADH-3 could not reduce benzaldehyde, a key aldehyde-based VOC. On the other hand, ADH-2 and 4 had the highest relative activity toward pentanal (valeraldehyde) (82.6% and 81.1%) and hexanal (76.2% and 85.1%), whereas ADH-1 showed the highest with benzaldehyde (49.8%) (Hu et al., 2019). Finally, all ADH activities were stimulated with the presence of Zn^{2+}, suggesting them as zinc-dependent dehydrogenases. A benzyl ADH was characterized in *L. plantarum* WCFS1 to have substrate specificity to oxidize aliphatic and aromatic alcohols such as benzyl alcohol, which could be involved in benzaldehyde metabolism (Landete et al., 2008). Benzaldehyde can also be produced from phenylalanine through non-enzymatic reactions (Russo et al., 2021). Moreover, benzoic acid produced by *L. casei* has been found to have an inhibitory effect on soybean LOX, thereby reducing the oxidative action toward plant fatty acids (Sekhar Rao et al., 2002).

Moreover, higher concentrations of aldehydes such as (*E*, *E*)-2,4-decadienal have been reported after fermentation due to the LAB strains and conditions that could lead to creating an oxidizing environment (ex: H_2O_2), hence promoting lipid oxidation in the matrix toward aldehyde production (Vermeulen et al., 2007). Little is known about the biotransformation of 2-pentylfuran by LAB, although it has been characterized in *Saccharomyces cerevisiae* (Xu et al., 2022). In this, 2-pentylfuran is transformed into acetic acid hexyl ester and *o*-cymene through consecutive enzymatic reactions that involve epoxide hydrolase, *adh*, aldo-keto reductases, dehydrogenases, oxidases, acyltransferases, and ester synthases (Xu et al., 2022). Interestingly, *o*-cymene was increased in sunflower seed fermentation by *L. johnsonii* and *L. plantarum*, although 2-pentylfuran concentration was kept equal after fermentation (Tangyu et al., 2023). Most yeast species used in food fermentations have higher esterase activities than LAB species, which are usually characterized by low esterase expression. Therefore, alcohol and carboxylic forms of VOCs might be frequently transformed by yeast to ester derivatives by ester synthases and acyltransferases to produce ethyl ester derivatives (Xu et al., 2022). In LAB, some strains have one or more esterase-coding genes, typically having preferences with substrates such as acetate (Katz et al., 2002).

7 | DISCUSSION

The high demand for adequate nutritional, sensorial, and technological PBFDAs, such as plant-based cheeses and yogurts, leads to investigating the microbial-based transformation of plant compounds that might affect quality attributes in the final fermented products. Here, we described the state-of-the-art genes, enzymes, and metabolic pathways involved in the biotransformation of antinutrients (phytic acid, RFOs, polyphenols, saponins, enzyme inhibitors, and oxalic acid) (Table 3) and off-flavor VOCs (Table 2) by LAB fermentation. LAB is the most important group of bacteria that has been used for centuries for food fermentation, especially for the generation of milk-based fermented products (Harper et al., 2022; Smit et al., 2005). Most LAB species are ubiquitous in nature and have genetically evolved differently depending on the environment, abiotic and biotic conditions, and microbial diversity, where they have been inhabiting and adapting, among others (Makarova & Koonin, 2007). Some LAB species have lost or gained relevant competence genes through genetic transfer events during their environmental adaptation, thereby increasing or reducing their microbial fitness (Bačun-Družina et al., 2009). Most LAB strains used in dairy-fermented products have been adapted to grow in milk, allowing them to uti-

lize lactose, milk proteins, and other nutrients for their growth and metabolism (de Vos & Vaughan, 1994; Fontana et al., 2018). Therefore, the adapted dairy starter cultures may not be optimal in producing fermented plant-based alternatives where different nutritional compositions and physicochemical properties have been observed.

The development of PBFDAs, derived from legumes, cereals, and nuts, may require the use of other LAB species and/or strains that will be better equipped (both genetically and enzymatically) to thrive in those new environments and cope with the undesired plant metabolites present (Gaur et al., 2020; Zartl et al., 2018). This review suggests the importance of selecting specific LAB species for detailed research when screening and characterizing strains for targeted plant-based applications involving LAB fermentation. It emphasizes the use of particular species, such as *L. plantarum, L. fermentum, L. acidophilus, L. paracasei*, and *L. rhamnosus*, which have been characterized to encode relevant genes in multiple antinutrient categories based on research studies. On the other hand, the blast analysis genotypically validates the potential of employing those species while showing the promising capabilities of other unconventional QPS-listed LAB species such as *L. pentosus, L. diolivorans, S. collinoides*, and *L. paraplantarum* as suitable candidate species to be used as starter cultures for plant-based fermentations.

Genetic annotation, gene and enzyme expression, and enzymatic substrate specificity have been the most critical factors when evaluating promising LAB strains to be used as starter cultures for plant-based fermentations. The evaluation of the presence of relevant genes in a pool of LAB strain genomes might be helpful as a primary genotype screening tool when the genes have been functionally characterized and are not highly conserved genes among LAB species. For example, *tanA* has been mainly described in specific strains of *Lactiplantibacillus* spp. (Jiménez et al., 2014), although found in other species such as *O. oeni* (this study), and involved in the degradation of tannic acid (Figure 1). In addition, genetic annotation and analysis of upstream and downstream regions of relevant genes might provide information on the presence of other non-homologous genes involved in the transport of target molecules, such as an ABC transporter found in *L. acidophilus* NCFM, a putative permease found in *L. gasseri* ATCC 33323, and a putative permease found in *L. reuteri* 100-23C participating as analogous oxalate LAB transport systems, in the vicinity of the *frc* locus (Azcarate-Peril et al., 2006; Kullin et al., 2014; Lewanika et al., 2007). Nevertheless, genetic annotation might not be useful in highly conserved genes such as *adhE*, which is suggested to be involved in reducing aldehyde-based off-flavor compounds in OHET LAB species (Fischer et al., 2022; Sedó Molina, Shetty, et al., 2024).

The gene expression analysis under certain environmental conditions could be highly interesting when selecting LAB strains as starter cultures. However, genes might be present but not necessarily expressed under specific growth and environmental conditions, or expressed but having low activities. In fact, this might be a problem when phenotyping LAB strains using minimal media, where switching to complex media such as plant-based drinks might influence the output expression of targeted phenotypes, resulting in an undesired product quality. Variable growth and physicochemical conditions such as pH, temperature, carbohydrate and mineral composition, growth phase, and redox balance are some of the most relevant. Experimental and fermentation variables such as temperature and salt addition also might affect targeted LAB gene expression when fermenting plant bases. Moreover, some antinutrients, such as polyphenolic compounds, can be metabolized by multiple parallel enzymatic pathways, where gene expression plays an important role in which metabolic route outcompetes the others as occurred with *F. millii* FUA 83583 (Gaur et al., 2023).

Third, substrate enzymatic specificity is key when characterizing LAB strains relevant to biotransform specific antinutrients and volatile VOCs. Some key enzymes have been demonstrated to have substrate multispecificity towards different compounds belonging to the same category. Alcohol dehydrogenases, phytases, RFO transporters, galactosidases, and saponin glycosidases are some examples. The combination of substrate specificity studies linked with protein structure modeling might be relevant to predict multispecificity characteristics of target enzymes toward common plant metabolites present in different plant kingdoms.

Moreover, the degradation rate of antinutrients and off-flavors by LAB fermentation is influenced by many variables such as the plant-based matrix, LAB stains fitness and metabolism, bacterial physiological state, fermentation conditions, and synergistic interactions within strains (Sedó Molina et al., 2024). Nevertheless, Nugroho et al. (2024) demonstrated that the removal of off-flavor aldehydes could be performed under 1 h of biological activity by limiting the amounts of fermentable sugar conditions.

There is still a lack of knowledge of the transport systems involved in the transfer of the discussed compounds intracellularly, such as phytic acid, polyphenols, and oxalates, regulatory pathways involved in balancing the expression of the different enzymes mentioned, and paralogous enzymatic studies that prove similar activities in phylogenetically distant genes. Moreover, the considerable amount of structurally and chemically different compounds that are classified in the same category but are treated as similar, although found in various matrices, makes the applicability of the metabolic study limited. For

instance, strains that might specifically hydrolyze specific sugar moieties attached to oat saponins might not apply to the same sugar moieties attached to other aglycone structures found in soybeans because of substrate specificity. Another limitation is the assumption that different plant-based matrices are similar, leading to attempts to use the same starter cultures. This overlooks that these cultures exhibit distinct phenotypic performances depending on the specific matrix.

The increasing demand for plant-based products might lead to the discovery of new safety challenges that the milk industry has been evaluating for a long time. New and unexplored safety hazards found in plant-based matrices may be considered risk-associated compounds that could also be eliminated by fermentation, such as biogenic amines, allergenic compounds, pesticide residues, mycotoxins, and bacterial heat-resistant toxins generated from spoilage, and pathogenic agents such as *Aspergillus* sp. and *Bacillus cereus* (Bartula et al., 2023; Lin et al., 2023). Developing plant-based products requires reestablishing food processing methods distinct from those used in the milk industry. These new approaches could reduce those associated risks. Pre-processing and processing methods such as plant protein extraction methods or pasteurization might affect the fermentation performance of starter cultures in plant-based matrices, affecting protein, carbohydrate, and/or nutrient bioavailability and changing their metabolic outcome. Nevertheless, some methods, such as soaking and heat treatment, might help to reduce the antinutrient and off-flavor concentrations, such as phytates and trypsin inhibitors, in plant bases, facilitating the antinutrient degradation outcome after fermentation. A deeper understanding of how methods such as salting in cheese processing influence the metabolic activity of LAB during ripening could shed light on their role in the reduction of antinutrient compounds. This could help clarify how such processes affect the breakdown or removal of undesirable compounds during cheese ripening (Hickey et al., 2017).

Figure 2 represents the results of blasting multiple protein sequences to multiple LAB strains on the QPS list. Figure 2 is divided into a and b, in which the blast results are differently represented. Figure 2a analyzes the average number of copies of each gene in all strains from the same species. In contrast, Figure 2b shows that species have a higher number of genes from each antinutrient category, standardizing the presence of all genes from the same category on a scale from 0 to 1. Figure 2b helps to decide, which species to select when searching for a specific application based on the genes analyzed. For instance, *L. pentosus* strains showed high scores in the glycosidases considered relevant for degrading saponins but also a high number of genes in the phenolic metabolism, considering it a good candidate for those two phenotypes. The biplot adds extra information on the correlation between antinutrient categories and species, showing genetically similar species by the scores in relation to each loading. The PCA plot represents around 50% of the exposed data, and species such as *L. plantarum, L. aviarius*, and *L. brevis* highly contribute to the phenolic, oxalate, and saponin degrading phenotypic variables. Moreover, the PCA plot might provide a starting point when selecting LAB species for synergistic purposes, in strain mixture designs, and when selecting the best candidates from each category for combining them when developing starter cultures.

Figure 2 reveals that species from the *Lactiplantibacillus (L. argentoratensis, L. paraplantarum, L. pentosus*, and *L. plantarum)* genus encoded for multiple genes and copies of the same involved in the degradation of phenolic acid compounds where *L. plantarum* is the species with higher number of genes involved in this metabolism (Figure 2b). Moreover, tyrosine-like phosphatase (phytase) found in *L. fermentum* was blasted against all genomes, only finding homologous genes in all strains of *L. brevis* and *L. fermentum*. Gut and animal-derived LAB species such as *L. johnsonii, L. acidophilus, L. mucosae, L. aviarius*, and *L. reuteri* showed a higher presence of *frc* and *oxc* genes mainly involved in oxalate metabolism. For instance, one strain of *L. acidophilus, L. mucosae*, and *L. helveticus* species was determined to encode 2, 2, and 3 copies, respectively, of both genes in their genome. Furthermore, β-glucosidase, β-galactosidase, β-glucuronosidase, α-L-arabinosidase, β-xylosidase, and α-L-rhamnosidases were blasted in the form of GH families due to their heterospecific enzymatic activities showing *L. diolivorans, L. brevis*, *L. pentosus*, and *P. acidilactici* as the species with higher number of homologous genes involved in the degradation of glycoside bonds present in saponins (Figure 2a,b). Higher presence of envelope-based proteinase coding genes possibly involved in the enzyme inhibitor degradation was found in *L. rhamnosus, L. gallinarum, L. delbrueckii*, and *L. kefiranofaciens* having *prtP* and *prtB* as the primary proteolytic genes present. Finally, a higher number of genes and copies of genes involved in RFOs degradation were present in *L. plantarum, L. aviarius*, and *L. mucosae* mainly due to the high presence of *levS* transporters, *melA*, and *ftfA* high-copies in some the strains. Figure 2a presents the mean values of genes detected in each strain from the evaluated species without indicating variability within strains. In certain instances, some genes were highly conserved across strains within the same species, while in other cases, the presence of genes depended on the specific strain. For instance, the five *L. plantarum* strains evaluated showed 6, 7, 7, 0, and 0 copies of *levS* transporter genes, as an example of a species with high genetic variability due to its adaptability throughout gene transfer events

to its living environment. Moreover, *S. collinoides* and *L. helveticus* showed three copies of *hcrB* and GH1 in one strain, respectively, but no presence or one copy of the gene in the other strains analyzed. Thus, LAB-conserved genes within species might suggest the importance of those in ancestral evolutive genetic fitness and surveillance of the LAB species. In contrast, strain-based genetic variability might be related to specific niche-adaptation events. New knowledge on uncharacterized paralogous genes involved in identical phenotypes or similar substrate heterospecificities might be relevant for future research. Moreover, this genetic analysis can inspire the selection of unconventional LAB species that have not yet been used as starter cultures or investigated in spontaneous fermentations, such as *L. diolivorans, L. pentosus*, and *S. collinoides*.

8 | CONCLUSIONS

The genetic evolution of LAB strains is crucial when selecting LAB strains as starter cultures for fermentation. With the high demand for PBFDA food products with good nutritional and sensory attributes, other, perhaps unconventional, LAB species and strains might have genetic traits that could provide desired phenotypes for that purpose. We evaluated the state-of-the-art of relevant LAB genetic tools that are characterized to be associated with the degradation of antinutrients (phytates, RFOs, saponins, phenolic compounds, oxalates, and enzymatic inhibitors) and volatile off-flavors (aldehydes, pyrazines, furans, sulfur compounds, and ketones) present in legumes, cereals, tubers, and nuts. Genetic characterization, enzymatic expression and activity, and enzymatic substrate heterospecificity are important characteristics when genotyping and phenotyping LAB strains for fermented food applications. The homology-based gene analysis of all QPS-listed LAB strains has provided genetic information on unconventional species with promising genetic tools for each phenotype and strain-dependent genetic variabilities of target genes, functional for future starter culture selections and microbial characterization. Future work on linking protein sequences and structures to enzymatic expression and specificity through modeling might be required to speed up the starter culture selection process and design mixtures of LAB strains with different genetic tools to be used as starter cultures for developing PBFDAs.

AUTHOR CONTRIBUTIONS

Guillermo Eduardo Sedó Molina: Conceptualization; investigation; writing—original draft; methodology; visualization; writing—review and editing; formal analysis; data curation. **Geoffrey Ras**: Conceptualization; validation; visualization; writing—review and editing; supervision; formal analysis. **Denise Felix da Silva**: Conceptualization; validation; visualization; writing—review and editing; formal analysis; supervision. **Lene Duedahl-Olesen**: Conceptualization; validation; visualization; writing—review and editing; formal analysis; supervision. **Egon Bech Hansen**: Conceptualization; validation; visualization; writing—review and editing; formal analysis; supervision. **Claus Heiner Bang-Berthelsen**: Conceptualization; funding acquisition; methodology; validation; writing—review and editing; formal analysis; project administration; supervision; resources.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

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