



Conversion of (poly)phenolic compounds in food fermentations by lactic acid bacteria: Novel insights into metabolic pathways and functional metabolites

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ABSTRACT

Lactobacillaceae are among the major fermentation organisms in most food fermentations but the metabolic pathways for conversion of (poly)phenolic compounds by lactobacilli have been elucidated only in the past two decades. Hydroxycinnamic and hydroxybenzoic acids are metabolized by separate enzymes which include multiple esterases, decarboxylases and hydroxycinnamic acid reductases. Glycosides of phenolic compounds including flavonoids are metabolized by glycosidases, some of which are dedicated to glycosides of plant phytochemicals rather than oligosaccharides. Metabolism of phenolic compounds in food fermentations often differs from metabolism *in vitro*, likely reflecting the diversity of phenolic compounds and the unknown stimuli that induce expression of metabolic genes. Current knowledge will facilitate fermentation strategies to achieve improved food quality by targeted conversion of phenolic compounds.

1. Introduction

(Poly)phenolic compounds, subsequently referred to as phenolic compounds, are secondary plant metabolites with diverse chemical structure and function. They can be classified based on their structure. Major phenolic compounds in edible plants include flavonoids (C₆–C₃–C₆), phenolic acids (C₆–C₃ or C₆–C₁), and tannins (Del Rio et al., 2013; Tsimogiannis and Oreopoulou, 2019). Plants produce phenolic compounds for both structural and non-structural functions including the adaptation to environmental stress (Lattanzio et al., 2012). They possess antinutritive properties, precipitate proteins, inhibit digestive enzymes and are responsible for imparting astringency and/or bitter taste in many foods (Chung et al., 1998). Epidemiological and intervention studies also indicate a beneficial role in human health (Bordnave et al., 2014; Kim et al., 2016; Shahidi and Yeo, 2018). The majority of total phenolic compounds in plants are bound to other cellular compounds (Zhang et al., 2020).

Food fermentation has been a part of human culture since the neolithic period (Arranz-Otaegui et al., 2018). In fermented foods, microbial conversions determine and maintain food quality and food safety (Marco et al., 2021). *Lactobacillaceae* are major fermenting organisms frequently found in traditional fermentations (Gänzle, 2022; Hutkins,

2019). Metabolites of food fermenting organisms as well as the presence of live microbes in some fermented foods are increasingly recognized as contributors to human health (Gänzle, 2020; Marco et al., 2017, 2021; Wastyk et al., 2021). Recent comprehensive reviews have summarized microbial conversions of phenolic composition by intestinal microbial communities and their influence health (Chia et al., 2018; Leonard et al., 2021) but recent reviews of the metabolism of phenolic compounds by lactobacilli in food fermentations are not available. This communication outlines recent advances related to metabolic pathways in *Lactobacillaceae* that convert phenolic compounds in plant foods.

2. Overview of phenolic compounds that are metabolized in food fermentations

Several comprehensive reviews provide an overview on the structural diversity of phenolic compounds (Del Rio et al., 2013; Tsimogiannis and Oreopoulou, 2019) but a compilation highlighting those compounds that are metabolized in food fermentations is not available. Table 1 and the following sections provide an overview on those phenolic compounds that are known to be converted in food fermentations or by food fermenting lactobacilli.

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2.1. Phenolic acids

Phenolic acids (Table 1) account for almost one-third of the total dietary phenolic compounds in fruits and grains (Haminiuk et al., 2012). They comprise hydroxybenzoic acids (C₆–C₁) and hydroxycinnamic acids (C₆–C₃). The concentrations of free phenolic acids in plants is generally low in comparison to conjugated and bound phenolic acids. They are frequently linked to arabinoxylans and other cell wall polysaccharides via ester and ether linkages (Vitaglione et al., 2008) but also form covalent linkages with other molecules including monosaccharides and alcohols (Acosta-Estrada et al., 2014; Shahidi and Yeo, 2018).

Hydroxybenzoic acids are less abundant in cereals, fruits and vegetables when compared to hydroxycinnamic acids (Rashmi and Negi, 2020). Sinapic acid derivatives are particularly abundant in plants of the *Brassicaceae* family (Martínez-Sánchez et al., 2008). Cereals such as rye and barley are rich in hydroxycinnamic acids with ferulic acid esterified to arabinoxylans being most abundant (Rosa-Sibakov et al., 2015). Sorghum and oats also contain glycerol esters of ferulic, *p*-coumaric and caffeic acid (Svensson et al., 2010; Varga et al., 2018). Phenolic acid glycosides are frequently found in sinapic acid rich flaxseed, canola, and mustard (Engels et al., 2012; Khattab et al., 2010).

Table 1

Overview of common phenolic compounds metabolized by *Lactobacillaceae*.

Class of phenolic compounds	Basic chemical structure	Active or putative microbial enzymes ^{a)}
Hydroxybenzoic acids (C ₁ –C ₆) R = H, OH, OCH ₃		-Esterase (Tannase) -Decarboxylase
Hydroxycinnamic acids (C ₂ –C ₃) R = H, OH, OCH ₃		-Esterase -Decarboxylase -Reductase
Vinyl-derivatives of hydroxyl-cinnamic acids		-Reductase
Flavonoids (C ₆ –C ₃ –C ₆) C ring substitutions- Different flavonoid classes A and B ring substitutions- Different compounds		-Glycosyl hydrolase
Stilbenes (C ₆ –C ₂ –C ₆) R = H, OH, OCH ₃		- Putative activity of glycosyl hydrolases
Lignans (C ₆ –C ₃) ₂ R = C or O; R ₁₋₄ = OH, OCH ₃		- Putative activity of lycosyl hydrolases
Hydrolysable tannins A- Ellagitannins B- Gallotannins		-Tannase
Proanthocyanidins (C ₆ –C ₃ –C ₆) _n		- Tannase

^{a)} See Table 2 for more detailed information on the activity of enzyme active on phenolic compounds and the corresponding references for the biochemical characterization. References to the corresponding transformation in food fermentations is shown in Table 3.

2.2. Flavonoids

Flavonoids encompass more than 6000 known compounds (Vuolo et al., 2019). Alterations in the heterocyclic C ring of their basic C₆–C₃–C₆ carbon framework are classified in subclasses such as flavonols, flavanones and anthocyanidins. Flavonoids occur predominantly as glycosides. Among flavones, apigenin and luteolin glycosides are common in a variety of herbs and spices including peppers, watermelon, and Chinese cabbage (de la Rosa et al., 2019). Citrus fruits are rich in the flavanones hesperetin, naringenin and eriodictyol and polymethoxylated flavones such as tangeretin and nobiletin (Ho and Kuo, 2014). Sorghum contains flavanones as 7-O-glucosides along with apigenin and 3-deoxyanthocyanidins (Bai et al., 2014). Legumes are rich in isoflavones with genistein and daidzein being most abundant in soybeans (Liggins et al., 2000). Flavonols are one of the most widespread classes of flavonoids. Kaempferol, myricetin and quercetin and their glycosides are present in a variety of fruits and vegetables (Aherne and O'Brien, 2002; Barreca et al., 2021). Flavan-3-ols are abundant in tea, wine, cereals, chocolates and in various fruits and vegetables (de la Rosa et al., 2019). Monomeric flavan-3-ols including catechins, gallic acid esters along with oligomeric flavan-3-ols (proanthocyanidins) rarely exist as glycosides. The last major flavonoid group consists of anthocyanidins; their glycosylated derivatives anthocyanins are particularly rich in colored fruits including grapes, berries, cherry, and vegetables such as red cabbage, rhubarb and red onions (Manach et al., 2004).

2.3. Tannins

Tannins are polymeric polyphenolic compounds which form strong complexes with carbohydrates and proteins (Serrano et al., 2009). Based on the monomeric units, they can be further classified as water insoluble condensed tannins, proanthocyanidins, hydrolysable tannins and complex tannins. Gallotannins and ellagitannins are the most common hydrolysable tannins and are found in fruits such as berries, mangoes and grapes with a few legumes, vegetables and nuts being minor sources (Serrano et al., 2009). Proanthocyanidins are concentrated in peels of fruits with grapes the biggest source of condensed tannins in our diet (Haminiuk et al., 2012). Legumes, nuts, and certain cereals such as sorghum and barley also contain condensed tannins (Gu et al., 2004; Saura-Calixto et al., 2007).

2.4. Stilbenes, lignans and alkylresorcinols

Resveratrol is the only stilbene compound of interest in human diet with grape skins and subsequently wine being its primary source. Oilseeds, nuts, whole grain cereals and legumes are typically rich sources of lignans (Rodríguez-García et al., 2019). Alkylresorcinols are phenolic

compounds generally containing 15–25 carbon chain attached to a hydroxybenzene ring. Whole grain cereals such as rye followed by wheat are particularly rich dietary sources of alkylresorcinols (Mattila et al., 2005) but conversion of alkylresorcinols by lactic acid bacteria is not documented.

3. Enzymes involved in conversion of phenolic compounds in the *Lactobacillaceae*

3.1. Enzymes involved in conversion of phenolic compounds

Lactobacillaceae possess a broad spectrum of enzymatic activities for biotransformation of bioactive dietary phenolic compounds (Fig. 1 and Table 2). Recent studies demonstrate that conversion of hydroxycinnamic- and hydroxybenzoic acids is mediated by separate esterases, reductases, and decarboxylases (Fig. 1 and Table 2). Sinapic acid is the only hydroxycinnamic acid which is a substrate for hydroxycinnamic acid reductases but not for decarboxylases of *Lactobacillaceae* (Table 2).

Phenolic esterases are specific for the phenolic acid moiety of esters but have a more relaxed substrate specificity for the alcohol moiety of the phenolic acid esters (Table 2). To date, however, the characterization of the substrate specificity of esterases of hydroxybenzoic and hydroxycinnamic acids remains restricted to the use of few model compounds which do not reflect the diversity of phenolic acid esters in plants (Table 2) (de las Rivas et al., 2009; Esteban-Torres et al., 2015, 2013; Gaur et al., in press; Gaur, 2022; Iwamoto et al., 2008; Jiménez et al., 2014; Lai et al., 2009). For a majority of esters of hydroxycinnamic acids, hydroxybenzoic acids, or ellagic acid, it thus remains unknown whether they are substrate for any of the characterized enzymes (Table 2), or are hydrolyzed by uncharacterized enzymes. In addition, some enzymes including Est_1092, which shows highest activity on esters of hydroxycinnamic acids, also displayed weak activity on a broad range of other esters after heterologous expression in *E. coli* (Esteban-Torres et al., 2015) while it remains unclear whether this activity is relevant *in vivo* (Gaur, 2022). Moreover, mutational disruption of esterases of hydroxycinnamic esters in *Lp. plantarum* and in *F. mii* did not alter the phenotype in food fermentations (Gaur et al., in press; Gaur, 2022; Gaur et al., 2023), documenting that the activity of these esterases on the diversity of esters occurring in plants remains to be determined.

The substrate specificity of glycosyl hydrolases of lactic acid bacteria with activity on glycosylated phenolic compounds was tested with substrates that represent only a very small fraction of the diversity of glycosides of phenolic compounds or plant secondary metabolites. Mutational disruption of (phospho)- β -glucosidases in *L. acidophilus* provided proof of concept that one of the enzymes is active on glucosides of phenolic compounds but not on disaccharides (Theilmann et al., 2017). The presence of multiple copies of β -glucosidases in the genome of *Ff. mii* was also interpreted as an indication that one of the two

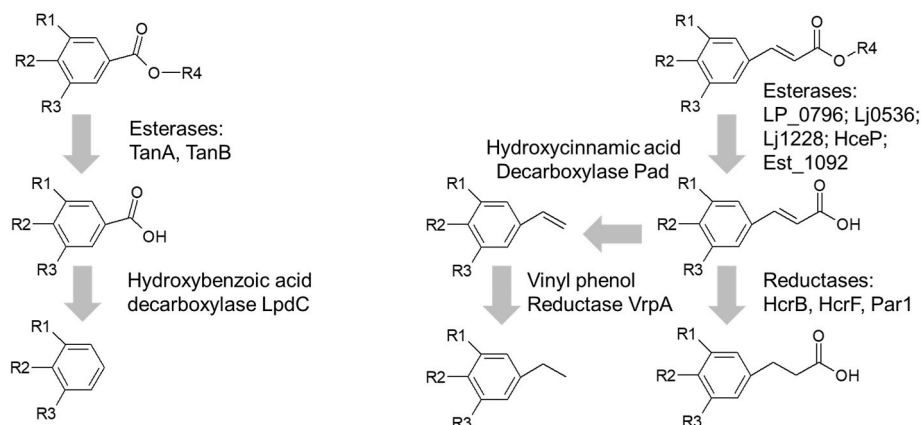


Fig. 1. Overview on enzymes of lactobacilli that convert hydroxycinnamic and hydroxybenzoic acids.

Table 2

Enzymes contributing to metabolism of phenolic compounds in the *Lactobacillaceae*.

Enzyme; Accession #	Known substrates	Source
Hydroxybenzoic acid esterases		
TanA; WP_003640628	Methyl gallate, ethyl gallate, propyl gallate, ethyl protocatechuate, gallic catechin gallate, epigallocatechin gallate, tannic acid	<i>Lp. plantarum</i> ATCC 14917 (Jiménez et al., 2014)
TanB; YP_004890536	Methyl gallate, ethyl gallate, propyl gallate, lauryl gallate, ethyl protocatechuate, gallic catechin gallate, epigallocatechin gallate, tannic acid	<i>Lp. plantarum</i> WCFS1 (Curiel et al., 2009 ; Iwamoto et al., 2008)
Hydroxycinnamic acid esterases		
Lj0536; WP_004898050	Chlorogenic acid, ethyl ferulate, rosmarinic acid	<i>L. johnsonii</i> N6.2 (Lai et al., 2009)
Lj1228; WP_011162057	Chlorogenic acid, ethyl ferulate, rosmarinic acid	
HceP; WP_011101978	Chlorogenic acid, methyl ferulate	<i>Lp. plantarum</i> TMW1.460 (Gaur, 2022 ; Gaur et al., in press)
Lp_0796; YP_004888771	Methyl ferulate, methyl caffeate, methyl p-coumarate, methyl sinapate	<i>Lp. plantarum</i> WCFS1 (Esteban-Torres et al., 2013)
Est_1092; WP_015825406	Methyl ferulate, methyl caffeate, methyl p-coumarate, methyl sinapate	<i>Lp. plantarum</i> DSM 1055 (Esteban-Torres et al., 2015)
Hydroxybenzoic acid decarboxylase		
LpdC; WP_003644796	Gallic acid, protocatechuic acid	<i>Lp. plantarum</i> WCFS1 (Jiménez et al., 2013 ; Landete et al., 2010)
Hydroxycinnamic acid reductases and decarboxylase		
HcrB; YP_004889276	Reductase; <i>m</i> -, <i>o</i> - and <i>p</i> -coumaric acid, sinapic acid, ferulic acid, caffeic acid	<i>Lp. plantarum</i> WCFS1 (Santamaría et al., 2018a)
Par1; WP_161000921	Reductase; <i>p</i> -coumaric acid, sinapic acid, ferulic acid, caffeic acid	<i>Ff. milii</i> FUA3583 (Gaur et al., 2020)
HcrF; WP_003682980	Reductase; <i>p</i> -coumaric acid, sinapic acid, ferulic acid, caffeic acid	<i>Lm. fermentum</i> FUA3589 (Gaur et al., 2020)
Pad; WP_003641609	Decarboxylase; <i>p</i> -coumaric acid, ferulic acid, caffeic acid	<i>Lp. plantarum</i> WCFS1 (Rodríguez et al., 2008)
VrpA; WP_011102053	Vinyl phenol reductase; vinyl catechol, vinyl phenol, vinyl guaiacol	<i>Lp. plantarum</i> WCFS1 (Santamaría et al., 2018b)
Flavonoid glycosidases		
Ram1; WP_011102176	Rutin, nicotiflorin, narirutin, hesperidin, pNP- α -l-rhamnopyranoside	<i>Lp. plantarum</i> DSM 20205 (Ávila et al., 2009 ; Beekwilder et al., 2009)
Ram2; WP_011102178		
RamA _{LB} ; WP_003548204	Naringin, rutin, nicotiflorin, narirutin	<i>L. acidophilus</i> NCFM (Beekwilder et al., 2009)
rBGLa; WP_007123550	Geniposide, pNP- β -D-glucopyranoside, daidzin, genistin, secoisolariciresinol diglucoside	<i>Lm. antri</i> DSM 16041 (Gaya et al., 2020 ; Kim et al., 2017)
LcGUS30; BAO73305	Baicalin, wogonoside, pNP- β -D-glucuronide	<i>Lv. brevis</i> FERM BP-4693 (Sakurama et al., 2014)

enzymes specializes on glucosides of phenolic compounds (Simpson et al., 2022).

Glycosyl hydrolases of *Lactobacillus melliventris* target the sugar molecules attached to flavonoids for growth, releasing the aglycons in the process (Brochet et al., 2021). Conversion of hydroxycinnamic acids by lactobacilli decreases the antimicrobial activity and was thus suggested to be a mechanism of detoxification (Sánchez-Maldonado et al., 2011). In addition, the reduction of phenolic acids is advantageous to heterofermentative *Lactobacillaceae* because the co-factor recycling increases the ATP yield in the phosphoketolase pathway (Filannino et al., 2014, 2016b).

With exception of TanA (Jiménez et al., 2014), all enzymes of lactobacilli with activity on phenolic compounds are intracellular; substrate conversion thus requires transport across the cytoplasmic membrane, or cell lysis. In *L. acidophilus*, transport of several glycosides of plant secondary metabolites including esculin and salicin is mediated by phosphotransferase systems, followed by hydrolysis by phosphor-glucosidases (Theilmann et al., 2017).

3.2. Distribution of enzymes for conversion of phenolic compounds in the *Lactobacillaceae*

The current taxonomic framework of the family *Lactobacillaceae* (J. Zheng et al., 2020) and the identification of lifestyles of many lactobacilli (Duar et al., 2017) allows *in silico* exploration of whether the ability for biotransformation of phenolic compounds by *Lactobacillaceae* is related to their phylogeny and ecology. The genomes of type strains in the *Lactobacillaceae* family that were available in February 2022 were screened for genetic determinants of conversion of phenolic compounds (Table 2) to determine associations of lifestyles or phylogeny to specific enzymatic activities (Fig. 2). Rarefaction of the genome database to type strains prevents over-representation of well-studied species, e.g. *Lp.*

plantarum and *Lm. reuteri*, and allows the determination of genus-specific metabolic preferences, but does not provide an assessment of the intra-genus variability of metabolism.

The most obvious association of lifestyle and metabolism of phenolic compounds is the low prevalence of genes coding for metabolism of phenolic compounds in insect-adapted *Lactobacillaceae* (Duar et al., 2017) (Fig. 2). Genomes of type strains in the species in the genera *Fructilactobacillus*, *Bombilactobacillus*, and *Apilactobacillus* encode for very few, if any, genes that would enable the organisms to convert phenolic compounds (Fig. 2). Because flowers that are rich in phenolic compounds are a hub for insect-associated microbes (McFrederick et al., 2017), this finding is counter-intuitive and may relate to niche-partitioning (Brochet et al., 2021) among the highly specialized insect-associated lactobacilli.

Vertebrate associated lactobacilli have a greater potential for conversion of phenolics than insect associated organisms (Fig. 2). In particular, hydroxycinnamic acid esterases, -reductases and -decarboxylases are relatively frequent in the genera *Lactobacillus*, *Ligilactobacillus* and *Limosilactobacillus*, indicating that bound hydroxycinnamic acids are relevant substrates in intestinal ecosystems (Fig. 2).

Free living lactobacilli are diverse with respect to their potential to convert phenolic compounds. Some genera including *Lapidilactobacillus*, *Liquorilactobacillus*, *Secundilactobacillus* and *Levilactobacillus* show a high prevalence of multiple enzymes for metabolism of phenolic compounds while others, e.g. *Agrilactobacillus*, *Schleiferilactobacillus* and *Lentilactobacillus* do not (Fig. 2). This may relate to the lack of knowledge on the diverse lifestyles of free living lactobacilli (Duar et al., 2017). For example, *Lentilactobacillus* species are known to grow in silage, pickles, or fermented cereals after other lactobacilli including *Lp. plantarum* and yeasts have depleted the substrate (Johanningsmeier and McFeeters, 2015; Krooneman et al., 2002; Zhang et al., 2010).

In addition to the enzymes for metabolism of phenolic compounds

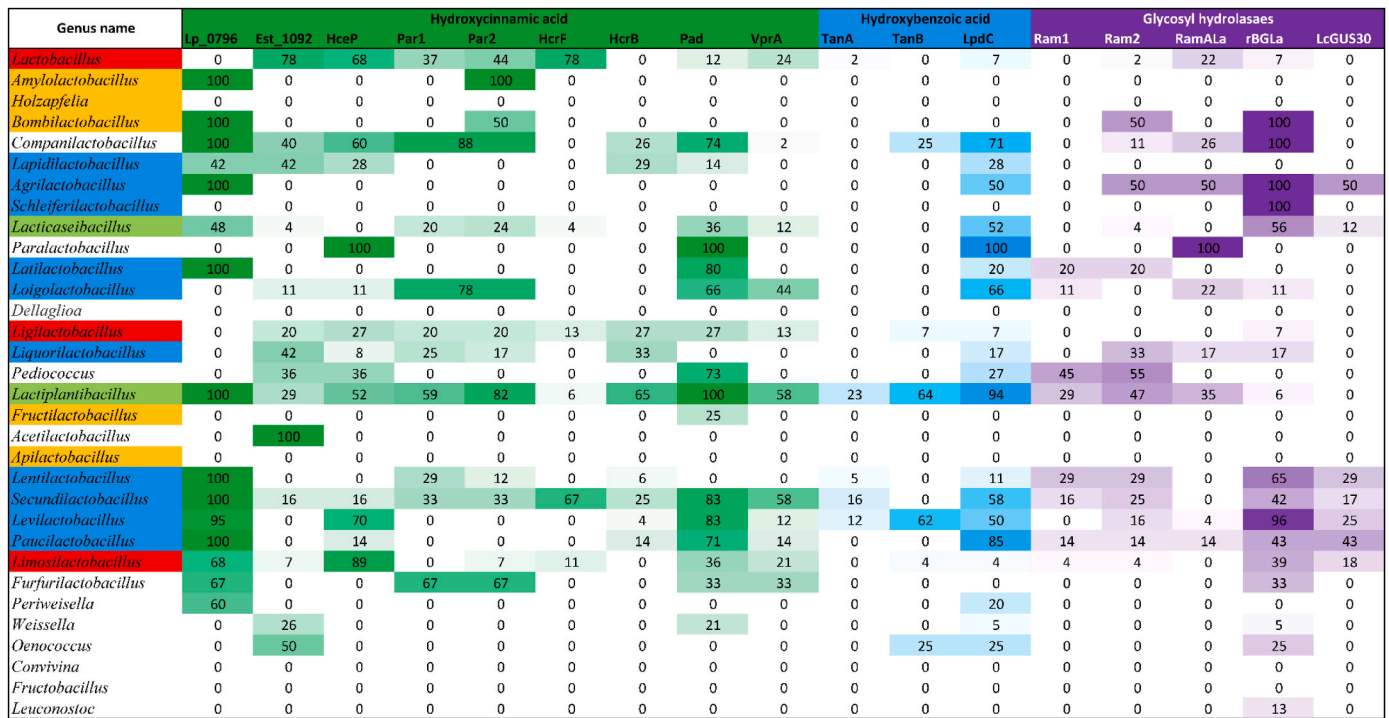


Fig. 2. *In silico* identification of presence/absence of phenolic metabolism genes across *Lactobacillaceae*. Query sequences of enzymes listed in Table 2 were used to perform protein BLAST on all *Lactobacillaceae* type strains (336) available in the NCBI database (February 2022) (Qiao et al., 2022), with cut-off values of 75% query cover and 35% amino acid identity. The heatmap represents the percentage of type species with a positive hit in each genus with white color representing absence in all type strains of a genus. The colors in genus name column represent lifestyles: red, vertebrate-adapted; orange, insect-adapted; blue, free-living; green, nomadic; white, unassigned (Duar et al., 2017; J. Zheng et al., 2020). *Blast hits cannot be differentiated for Par1 and Par2 (amino acid identities within 2% of each other). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

that were biochemically characterized, several enzymes remain unknown. *Weissella* species convert hydroxycinnamic acids (Gaur et al., 2020) and gallic acid (Sáez et al., 2017) but do not encode for homologues of any of the characterized decarboxylases or -reductases (Fig. 2). *Lactobacillaceae* have also been reported to reduce daidzein to equol (Heng et al., 2019). Conversion of anthocyanidins to chalcones has also been proposed (Ávila et al., 2009), with similar enzymatic activity reported for conversion of patulin to ascladiol (Wei et al., 2020). Proteins displaying moonlighting activity (Jeffery, 2018) may be responsible for various bioconversions including degradation metabolites of various phenolic compounds.

4. Transformation of phenolic compounds in food fermentations

Biotransformation of phenolic compounds during fermentation by *Lactobacillaceae* does not always match with the presence/absence of enzymes and the metabolic activity in laboratory media. *Limosilactobacillus fermentum* encodes the hydroxycinnamic acid decarboxylase Pad but nevertheless preferentially reduced hydroxycinnamic acids (Gaur et al., 2020). Conversely, strains of *Lp. plantarum* decarboxylated hydroxycinnamic acids in laboratory media but the same substrates were reduced to phenylpropionic acids in cherry juice and broccoli fermentations (Filannino et al., 2015). Decarboxylation of hydroxybenzoic acids by *Levilactobacillus hammesii* was observed in whole wheat sourdoughs but not in rye malt sourdoughs (Ripari et al., 2019). The composition of individual foods may be responsible for altering gene expression and enzyme production, affecting the behaviour of fermenting microbiota. The expression of genes coding for phenolic metabolism in *Lactiplantibacillus pentosus* was strain specific, in addition, differences in processing steps of olive extracts also led to differential expression of genes (Carrasco et al., 2018). Similarly, hydroxycinnamic acid esterase and reductase genes were expressed differentially in millet

and sorghum fermentations relative to gene expression in broth (Pswarayi et al., 2022). Thus, it is advisable to combine information of characterized enzymes and strain behaviour in laboratory media with model food fermentations to better predict the fate of phenolic compounds in fermented foods. An overview of past studies documenting conversion of phenolic compounds in food fermentations is shown in Table 3.

Current literature data remains inconclusive in the association of specific bacterial enzymes to esterase and glycosidase activities in food fermentation. Most studies rely on quantification of a decrease in concentration of specific compounds with corresponding increase in expected metabolites. Many strains, however, encode for multiple esterases or glycosyl hydrolases with complementary or overlapping substrate specificities (Gaur, 2022; Landete et al., 2021; Theilmann et al., 2017), which makes the unambiguous assignment of genotype to phenotype challenging or impossible. Only few studies used isogenic mutants to confirm the activity of specific enzymes in food fermentations (Gaur, 2022; Gaur et al., 2023) and data on the expression of genes in complex food substrates remains scarce. The identification of several genes related to metabolism of phenolic compounds since 2018 provides the necessary tools to address this limitation.

Table 3 and the subsequent sections provide an overview on current knowledge on the conversion of phenolic compounds in food fermentations. Because the content of phenolic compounds is specific for specific plant taxa, and because the food matrix impacts the metabolism of phenolic compounds by lactobacilli, the sections are organized first by plant substrate and then by metabolic activities.

4.1. Fruit and fruit products

Species in the genera *Lactiplantibacillus* and *Lactocaseibacillus* are frequently used for fermentation of various fruit substrates (Table 3).

Table 3Studies with biotransformation of phenolic compounds during fermentation of food substrates via *Lactobacillaceae*.

Food Matrix	Microorganisms	Putative microbial enzymes	Substrates; metabolites; references
Fruits and juices			
Cherry juice	<i>Lp. plantarum</i> , <i>Lm. fermentum</i> , <i>Lm. reuteri</i> , <i>Lv. spicheri</i>	Hydroxycinnamic acid reductase and -decarboxylase, vinyl phenol reductase	Protocatechuic acid, caffeic acid, <i>p</i> -coumaric acid; Catechol, dihydrocaffeic acid, phloretic acid, ethyl phenol; (Filannino et al., 2015; Ricci et al., 2019b)
Cloudy apple juice	<i>Lp. plantarum</i> , <i>Lm. fermentum</i> , <i>L. acidophilus</i>	Flavonoid glycosidase	Rutin; Quercitrin; (Han et al., 2021)
Apple juice	<i>Lp. plantarum</i> , <i>Lactocaseibacillus</i> spp., <i>Lactobacillus</i> spp.	Chlorogenic acid esterase, flavonoid glycosidase	Chlorogenic acid, quercetin-3-O-galactoside, phlorizin; Caffeic acid, quercetin, phloretin; (Z. Li et al., 2018; Wu et al., 2020)
Apple pomace	<i>Lactocaseibacillus rhamnosus</i>	β -glucosidase	Quercitrin, phlorizin; Quercetin, phloretin; (Liu et al., 2021)
Mulberry juice and pomace	<i>Lp. plantarum</i> , <i>Lc.</i> , <i>L. acidophilus</i>	Flavonoid glycosidase	Cyanidin-3-O-glucoside, peonidin-3-O-glucoside/peonidin-3-O-galactoside, quercetin-3-O-rhamnoside; Cyanidin, petunidin, quercetin, kaempferol; (Kwaw et al., 2018; Tang et al., 2021)
Mango and Papaya puree	<i>Lp. plantarum</i> , <i>W. cibaria</i>	Flavonoid glycosidase, tannase, chlorogenic acid esterase	Gallocatechin gallate, chlorogenic acid; Quercetin, ellagic acid; (Mashitoo et al., 2021a, 2021b)
Acerola cherry puree	<i>Lc. casei</i> , <i>L. acidophilus</i>	Flavonoid glycosidase, chlorogenic acid esterase	Hesperidin, rutin, chlorogenic acid; Caffeic acid; (de Assis et al., 2021)
Avocado puree	<i>Lp. plantarum</i>	Phenolic acid esterase, tannase, hydroxycinnamic acid reductase and -decarboxylase, vinyl phenol reductase	Rosmarinic acid, caffeic acid, ferulic acid, <i>p</i> -coumaric acid, sinapic acid; Caffeic acid, epicatechin, dihydroferulic acid, ellagic acid, ethyl catechol; (Filannino et al., 2020)
Pomegranate juice	<i>Lp. plantarum</i> , <i>L. acidophilus</i>	Tannase	β -punicalagin, punicalin; -; (Valero-Cases et al., 2017)
Bitter melon juice	<i>Lp. plantarum</i>	Hydroxybenzoic acid decarboxylase, hydroxycinnamic acid decarboxylase and -reductase	Gallic acid, caffeic acid, protocatechuic acid, <i>p</i> -coumaric acid; Pyrogallol, vinyl catechol, catechol, vinyl phenol, dihydrocaffeic acid phloretic acid, ellagic acid; (Gao et al., 2019)
Cactus cladodes	<i>Lp. plantarum</i> , <i>Lv. brevis</i>	Flavonoid glycosidase	-; Kaempferol, isorhamnetin; (Filannino et al., 2016a)
Cereals and pseudocereals			
Whole wheat and rye sourdough	<i>Lp. plantarum</i> , <i>Lv. brevis</i> , <i>Lv. hammesii</i>	Phenolic acid esterase, hydroxycinnamic acid decarboxylase, hydroxycinnamic acid reductase, vinyl phenol reductase	Ferulic acid; Vinyl guaiacol, dihydroferulic acid, ethyl guaiacol; (Ripari et al., 2019)
Wheat and rye sourdough	<i>Lp. plantarum</i> , <i>Lv. brevis</i>	Flavonoid glycosidase, hydroxycinnamic acid reductase	Isorhamnetin-3-O-hexoside, ferulic acid, caffeic acid, sinapic acid; Isorhamnetin, dihydroferulic acid, dihydrocaffeic acid, dihydrosinapic acid; (Koistinen et al., 2018)
Red sorghum sourdough	<i>Lc. casei</i> , <i>Lp. plantarum</i> , <i>Lm. reuteri</i> , <i>Lm. fermentum</i>	Flavonoid and phenolic acid glycosidase, hydroxycinnamic acid esterase, -reductase and -decarboxylase, vinyl phenol reductase	Naringenin-7-O-glucoside, eriodictyol-7-O-glucoside, coumaroyl-caffeoylglycerol, coumaroyl-feruloylglycerol, coumaroylglycerol, ferulic acid, caffeic acid, 3-deoxyanthocyanidins; Naringenin, eriodictyol, caffeic, <i>p</i> -coumaric acid, ferulic acid, dihydroferulic acid, vinyl catechol, ethyl catechol, pyrano-3-deoxyanthocyanidins, 3-deoxyanthocyanidin–vinylphenol adducts; (Bai et al., 2014; Svensson et al., 2010; Gaur et al., 2023)
Red quinoa	<i>L. acidophilus</i> , <i>Lc. casei</i> , <i>Lc. paracasei</i>	Flavonoid glycosidase	- ^{a)} ; Quercetin, kaempferol; (Zhang et al., 2021)
Vegetables and leafy plant substrates			
Kale	<i>Lc. paracasei</i>	Flavonoid glycosidase	Kaempferol-3-O-sophoroside; kaempferol; (Shimojo et al., 2018)
Curly kale juice	<i>Lp. plantarum</i> , <i>Lt. sakei</i>	Chlorogenic acid esterase	Chlorogenic acid; caffeic acid; (Szutowska et al., 2021)
Mulberry leaves	<i>Lp. plantarum</i>	Flavonoid glycosidase	- ^{a)} ; Quercetin, kaempferol; (N. K. Lee et al., 2015)
Broccoli puree	<i>Lp. plantarum</i> , <i>Lm. fermentum</i> , <i>Lm. reuteri</i> , <i>Lv. spicheri</i>	Chlorogenic acid esterase, hydroxycinnamic acid reductase	Chlorogenic acid; Caffeic acid, quinic acid, dihydrocaffeic acid; (Filannino et al., 2015)
Sweet Potato	<i>L. acidophilus</i>	Hydroxycinnamic acid esterase	4,5-dicaffeoylquinic acid; Caffeic acid, <i>p</i> -coumaric acid, ferulic acid; (Shen et al., 2018)
African nightshade	<i>Lp. plantarum</i> , <i>W. cibaria</i>	Flavonoid glycosidase, tannase	- ^{a)} ; Quercetin, luteolin, ellagic acid; (Degrain et al., 2020)
Chinese skullcap	<i>Lv. brevis</i>	β -glucuronidase	Baicalin, wogonoside; Baicalin, wogonin; (Xu and Ji, 2013)
Jussara pulp	<i>Lactobacillus</i> spp., <i>Lv. brevis</i> , <i>Lm. fermentum</i>	Flavonoid glycosidase, hydroxycinnamic acid reductase	Cyanidin 3-glucoside, cyanidin 3-rutinoside, pelargonidin 3-glucoside; Dihydrocaffeic acid; (Braga et al., 2018)
Cudrania tricuspidata leaves	<i>Lp. plantarum</i>	Flavonoid glycosidase	Quercetin-7-O-beta-glucopyranoside, kaempferol-3-O-beta-glucopyranoside, kaempferol-7-O-beta-glucopyranoside; Quercetin, kaempferol; (Y. Lee et al., 2015)
Legumes and oilseeds			
Soybean (Cheonggukjang)	<i>L. intestinalis</i>	Isoflavone reductase	Daidzein; Equol; (Heng et al., 2019)
Soy milk	<i>Lm. fermentum</i> , <i>Lp. plantarum</i> , <i>Lc. rhamnosus</i> , <i>L. delbrueckii</i> , <i>L. acidophilus</i> , <i>Lc. casei</i> , <i>Ln. kefir</i>	Flavonoid glycosidase	Daidzin, genistin, glycitin; Daidzein, genistein, glycitein; (de Queirós et al., 2020; Lodha et al., 2021)
Soybean flour	<i>Lc. casei</i>	Flavonoid glycosidase	Daidzin, genistin, glycitin and their malonyl and acetyl derivatives; Daidzein, genistein, glycitein; (S. Li et al., 2020)
Sunflower substrates	<i>L. gasser</i>	Chlorogenic acid esterase	Chlorogenic acid; Caffeic acid; (Fritsch et al., 2016)

^{a)} Information on the putative substrate or metabolites was not provided.

Fermentation increases the concentrations of free phenolic compounds including gallic acid, syringic acid, caffeic acid and catechins. Grape juice fermented with co-culture of *Lp. plantarum* and *Levilactobacillus brevis* significantly increased concentrations of procyanidin B1, B2, catechin and epicatechin after 12 h (Wu et al., 2021). Increases in anthocyanin and flavonoid glycoside content were also reported after fermentation of elderberry and cherry juice (Ricci et al., 2019a, 2019b).

However, many studies lack proper controls to account for the effect enzymes from the plant matrix or enhanced extractability after fermentation. This makes it difficult to assess the contribution of bacterial esterases and glycosidases to the increased total free phenolic acid content during fermentation.

Glycosyl hydrolases. Strains of *Lp. plantarum* increased kaempferol and quercetin concentrations in fermented apple and mulberry

substrates, likely via flavonoid glycosidase activity (Kwaw et al., 2018; N. K. Lee et al., 2015; Z. M. Li et al., 2018). This activity was strain specific in elderberry juice fermentation (Ricci et al., 2019a, 2019b). Fermentation of mulberry pomace with *Lp. plantarum* decreased cyanidin-3-O-glucoside concentrations with a corresponding increase in cyanidin levels, indicating anthocyanin glycosidase activity (Tang et al., 2021).

Conversion of hydroxycinnamic acids. *Lp. plantarum* and *Lc. casei* reduced chlorogenic acid concentration during fermentation (Lizardo et al., 2020; Zhou et al., 2020). In papaya puree fermented with *Leuconostoc pseudomesenteroides*, *Weissella cibaria* and *Lp. plantarum*, the chlorogenic acid content also increased after a 48 h fermentation and 7 d of storage at 4 °C (Mashitoa et al., 2021a). Esterase enzymes that are responsible for these conversions are frequently encoded by *Lp. plantarum* but are rarely present in *Leuconostoc* and *Weissella*. Strains of the genus *Lactobacillus* frequently encode hydroxycinnamic acid esterases with activity observed in fermented jujube and mulberry juice with *Lactobacillus helveticus* and *Lactobacillus acidophilus* (Kwaw et al., 2018; Li et al., 2021). Evidence of hydroxycinnamic acid esterase activity was observed in fermented avocado puree with *Lp. plantarum* AVEF17 where concentrations of caffeic acid increased with a corresponding decrease of the concentration of rosmarinic acid concentration when compared to a chemically acidified control (Filannino et al., 2020). *Oenococcus* strains typically lack the genes for phenolic acid metabolism; however, one out of six *Oenococcus oeni* strains significantly increased the hydroxycinnamic acid concentrations during model wine malolactic fermentation (Diez-Ozaeta et al., 2021).

Decarboxylation of hydroxycinnamic acids was observed during food fermentations but strains of *Lp. plantarum*, *Lc. rhamnosus* and *Lm. fermentum* predominantly reduced caffeic acid and *p*-coumaric acid to their respective dihydro-derivatives (Filannino et al., 2015; Gao et al., 2019; Ricci et al., 2019a). Strains of *Lp. plantarum* also produce ethyl derivatives of phenolic acids, such as ethyl phenol and ethyl catechol in fermented cherry juice and avocado puree by action of vinylphenol reductase on decarboxylated phenolic acids (Filannino et al., 2020; Ricci et al., 2019b).

Tannins and hydroxybenzoic acids. The content of ellagitannins such as β -punicalagin and punicalin was reduced after fermentation with *Lp. plantarum* and *L. acidophilus*, which is attributable to tannase or uncharacterized esterases (Valero-Cases et al., 2017). There was no corresponding increase in ellagic acid concentration which may indicate enzymatic conversions to unidentified ellagic acid derivatives (Valero-Cases et al., 2017).

Lu. pseudomesenteroides, *W. cibaria* and *Lp. plantarum*, also decreased galocatechin gallate in papaya fermentations (Mashitoa et al., 2021a). Fermentation with *L. helveticus* increased the gallic acid concentration in apple juice (Wu et al., 2020). Hydroxybenzoic acids were decarboxylated during elderberry and cherry juice fermentation (Filannino et al., 2015; Ricci et al., 2019a).

4.2. Cereal/legume fermentations

Increased free phenolic acids such as gallic acid, vanillic acid, *p*-coumaric acid and ferulic acid, epicatechin and procyanidin A2 were observed in fermented cereals (Guan et al., 2021; Ripari et al., 2019; Zhang et al., 2017, 2022) (Table 3). Fermentation of quinoa using a mixed culture of *L. acidophilus*, *Lc. casei* and *Lc. paracasei* after amylase treatment significantly increased the concentrations of procyanidin B2, quercetin and kaempferol compared to an unfermented enzymatically hydrolyzed control (Zhang et al., 2021).

Glycosyl hydrolases. Fermentation of cereals and legumes also converts flavonoid glycosides to the corresponding aglycones. Cultures of *Lc. casei* or *Lp. plantarum* and *Lm. reuteri* or *Lm. fermentum* displayed glucosidase activity on naringenin-7-O-glucoside and eriodictyol-7-O-glucoside releasing their respective flavanone aglycones in red sorghum sourdough (Svensson et al., 2010). Conversion of isoflavone glycosides

to corresponding aglycones in legume fermentations has been attributed to β -glucosidase activity of *Lactobacillaceae*. Fermentation of soymilk using a wide variety of strains including *Lp. plantarum*, *Lm. fermentum*, *Lc. casei*, *Lc. rhamnosus*, *Lentilactobacillus kefir*, *L. acidophilus* and *L. delbrueckii* significantly increased concentrations of daidzein and genistein with a corresponding decrease of daidzin and genistin (de Queirós et al., 2020; Lodha et al., 2021). Fermentation of whole soybean flour with *Lc. casei* also showed glucosidase activity on glycitin along with malonylglucosides and acetylglucosides of isoflavones (S. Li et al., 2020).

Hydroxycinnamic acids. Strains of *L. johnsonii*, *L. acidophilus* and *Lm. reuteri* increased the content of free hydroxycinnamic acids in whole grain barley and oat groat displaying hydroxycinnamic acid esterase activity (Hole et al., 2012). Glycerol esters of phenolic acids, such as coumaroyl-caffeoylglycerol, were hydrolyzed by strains of *Lactiplantibacillus*, *Lacticaeibacillus* and *Limosilactobacillus* in sorghum sourdough (Svensson et al., 2010). On the other hand, strains of *Lc. rhamnosus* decreased ferulic acid concentration in fermented wheat bran likely via further bioconversion to metabolites (Bertsch et al., 2020).

Co-fermentation using strains displaying complementary activities can further increase free phenolic acid and their metabolite concentrations. Addition of *Lv. hammesii* together with *Lp. plantarum* increased the ferulic acid esterase activity in whole wheat sourdough (Ripari et al., 2019). *Lp. plantarum* produced dihydrocaffeic acid, vinyl guaiacol and ethyl guaiacol via phenolic acid reductase, decarboxylase, and vinyl phenol reductase enzymes respectively, while *Lv. hammesii* only contributed to vinyl guaiacol production due to the absence of enzymes responsible for other two conversions (Ripari et al., 2019). In sorghum fermentations, vinyl phenol adducts of 3-deoxyanthocyanidins and pyrano-3-deoxyanthocyanidins during are formed (Bai et al., 2014). This conversion predominantly attributable to hydroxycinnamic acid decarboxylase activity of lactobacilli (Gaur et al., 2023).

4.3. Vegetables and miscellaneous plants

Glycosyl hydrolases. Fermentation of *Cudrania tricuspidata* leaves using *Lp. plantarum* SDL 1413 deglycosylated flavonol-7-O- β -glucopyranosides and kaempferol-3-O- β -glucopyranoside into their respective aglycones (Y. Lee et al., 2015). β -Glucuronidase and β -glucosidase activities have also been reported by strains of *Lv. brevis* and *Lc. paracasei* during fermentation releasing baicalein and wogonin, and kaempferol from their glycosides in *Scutellaria baicalensis* (Xu and Ji, 2013) and kale (Shimojo et al., 2018) extracts, respectively.

Hydroxycinnamic acids. Hydroxycinnamic acid esterase activity was observed in a wide variety of vegetable and plant fermentations (Table 3). *L. acidophilus* hydrolyzed 4,5-dicaffeoylquinic acid in sweet potato fermentation and displayed ferulic acid esterase activity in sugarcane bagasse (Pattanaik et al., 2022; Shen et al., 2018). Strains of *Lp. plantarum*, *Latilactobacillus sakei*, *Lactobacillus gasseri* and *Limosilactobacillus* displayed chlorogenic acid esterase activity during fermentation of substrates such as kale, sunflower, and broccoli (Filannino et al., 2015; Fritsch et al., 2016; Szutowska et al., 2021). However, a decrease in the released caffeic acid concentrations have also been reported, likely caused by further bioconversion to reduced and/or decarboxylated metabolites (Filannino et al., 2015).

Tannins and hydroxybenzoic acids. A strain specific increase in ellagic acid concentrations was reported after fermentation of African nightshades, which includes several *Solanum* species. This increase was attributed to tannase activity releasing hydroxybenzoic acids from galotannins and ellagitannins (Degrain et al., 2020).

5. Influence of phenolic metabolites on health, food quality and safety

Phenolic compounds have a multi-faceted impact on food quality and safety, and on human health. Fermentation can release bioactive

phenolic compounds from their precursors via esterase and glycosidase activities and significantly alter the phenolic constituents of the food matrix. Flavonoids and phenolic acids have been studied extensively with numerous health benefits reported *in-vitro* and in animal models (Leonard et al., 2021). Phenolic compounds also modulate the gut microbiota and enable the production of various bioactive metabolites during colonic fermentation (Loo et al., 2020). Consumption of plant-based foods has been associated with improved gut health (De Filippis et al., 2016). Epidemiological studies correlated the consumption of a diet with a high content of phenol compounds and dietary fibre with anti-inflammatory, anti-diabetic effects along with reduction in risk factors of cardiovascular diseases and cancer (Cardona et al., 2013; Shahidi and Yeo, 2018; Vitaglione et al., 2015). Recent evidence also supports the hypothesis that health benefits of plant foods that are rich in phenolic compounds and dietary fibre are based on synergism between these two plant components (Zhao et al., 2019; Armet et al., 2022).

Phenolic acids and flavonoids also possess antimicrobial activity (Górnjak et al., 2019; Sánchez-Maldonado et al., 2011), which can contribute to enhanced food safety when used in combination with existing preservatives and safety technologies (Wu and Zhou, 2021). Fermentation can also extend the shelf life of bread with delayed staling caused by the activity of esterases and glycosidases, which may increase the solubility and technological functionality of arabinoxylans.

Phenolic compounds have the potential to alter the digestibility of foods, lowering the glycemic index. Flavonoids and proanthocyanidins are effective in inhibiting digesting enzymes such as α -amylase and α -glucosidase and can also affect regulation of glucose transporters *in-vivo* (Sun and Miao, 2020). Phenolic acids also form complexes with starch reducing its digestibility and altering its rheological properties (M. Li et al., 2020, 2018; Y. Zheng et al., 2020).

Fermentation can increase the palatability of food and animal feed by reducing the content of bitter tasting phenolics and antinutritive compounds. Fermented beverages and porridges made using traditional fermentation of phenolic rich cereals such as sorghum and millet have improved flavor, with biotransformation of phenolic compounds likely playing a role (Gänzle, 2019). Vinyl and ethyl derivatives produced by metabolism of hydroxycinnamic acids are considered as flavor volatiles (Muñoz et al., 2017). Glycosidase activity of *Lactobacillaceae* may contribute to production of aromatic aglycones from odorless precursors (Iorizzo et al., 2016) and convert bitter phenolic compounds to more palatable aglycones such as oleuropein in olives (Gänzle, 2019; Heperkan, 2013). Bitter tasting free phenolics may also provide an opportunity for regulation of health via taste receptors in the gut (Tarragon and Moreno, 2020).

While the technological functionality of phenolic compounds in foods and their nutritional properties are increasingly understood, much less is known about the bacterial metabolites of phenolic compounds. Are technological functionalities, sensory properties, antimicrobial activities and nutritional properties of dihydro-derivatives of hydrocinnamic acids comparable to their substrates? How do stability, color and antioxidant properties of pyrano-anthocyanidins or pyrano-3-deoxyanthocyanidins compare to their well-researched parent compounds? Is the release of phenolic acids from insoluble cell wall polysaccharides relevant for the technological functionality and intestinal fermentation of these polysaccharides? Which specific phenolic compounds impart the bitter taste of plant foods and how is the taste intensity impacted by metabolic conversion during food fermentations? Increasing knowledge on the function of specific enzymes in food-fermenting lactobacilli enables the generation of isogenic strains and the design and execution of experiments that addresses these questions.

6. Concluding remarks

Significant progress has been made over the last years in characterization of genetic determinants responsible for biotransformation of

phenolic compounds. A major finding is the characterization of pathways for metabolism of phenolic acids, and the observation that conversion of hydroxybenzoic acids and hydroxycinnamic acids is mediated by distinct enzymes. Some of the glycosyl hydrolases expressed by lactobacilli appear to be dedicated to hydrolysis of glycosides of plant secondary metabolites but the genetic determinants and substrate specificities for esterases and glycosidases remains work in progress. Currently available data neither identifies those compounds that induce expression of these enzymes, nor provides a comprehensive picture of which of enormous diversity of glycosides or esters of phenolic compounds are metabolized by these diverse esterases and glycosidases. Nomadic and insect-adapted *Lactobacillaceae* display clear association between their ecology and presence of phenolic metabolism genes. The information on the distribution of phenolic metabolism genes provided in this study may enable strain selection and prediction of fermentation metabolites, and may guide further research on open questions.

Declaration of competing interest

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

Data availability

Data will be made available on request.

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