Host-adapted lactobacilli in food fermentations:

Impact of metabolic traits of host-adapted lactobacilli on food quality and human health

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Host adapted lactobacilli and food quality

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Abstract

Back-slopping of fermentation cultures in food fermentations can ensure stability of fermentation microbiota at the species or even at the strain level over extended periods of time. In contrast to the fermentation organisms in spontaneous food fermentations, which are derived from plant-associated or environmental micro-organisms, dominant micro-organisms in back-slopped fermentations are often recruited from lactic acid bacteria that are associated with insect or vertebrate hosts. Lifestyle-associated metabolic traits that relate to the ecological fitness of lactic acid bacteria in the host environment include biofilm formation through production of exopolysaccharides, urease-, glutaminase- and glutamate decarboxylase mediated acid resistance, and polysaccharide hydrolysis through extracellular glycosyl hydrolases. This review will discuss the ecological fitness of these organisms in food fermentations, and relate their specific metabolic properties to the safety, quality, and nutritional properties of food.

Keywords: *Lactobacillus*, food fermentations, acid resistance, exopolysaccharides, reuterin, *Lactobacillus delbrueckii*, *Lactobacillus reuteri*, *Lactobacillus salivarius*.

1. Introduction

A substantial proportion of the human diet consists of fermented foods, where the metabolic activity of fermentation micro-organisms determines and maintains the safety and quality of the products. Historically, non-alcoholic food fermentations aimed to improve the digestibility, nutritional value and / or the storage life of products [1]; their unique sensory properties maintained their popularity even when alternative processing methods become available. Fermented foods are not only a source of nutrients but also a major source of dietary micro-organisms if the fermentation organisms are not killed by a cooking or pasteurization step after the fermentation [2].

The microbiota of traditional food fermentations is controlled by the selection of raw materials, the product formula and the fermentation processes, and by back-slopping or the use of starter cultures. Back-slopping, the practice of inoculating a fermentation with a previous batch, profoundly alters the composition of fermentation microbiota when compared to spontaneous fermentations. In spontaneous fermentations, fermentation micro-organisms are selected from those organisms that are associated with the raw material or the processing environment [1,3,4]. In contrast, micro-organisms in back-slopped fermentations are challenged by microbiota of the raw materials in every new batch. Every time the raw material or the processing environment introduces a new strain that is more competitive than resident strains, the latter will be out-competed after a few fermentation cycles; a process that results eventually in stabilization of fermentation microbiota after a sufficient number of fermentation cycles [5]. Once stabilization of fermentation microbiota is achieved, back-slopping maintains undefined, mixed cultures over decades or centuries with remarkable stability at the species or even strain level [5,6].

2. Back-slopping of food fermentations recruits host-adapted fermentation organisms.

The origin of fermentation micro-organisms in back-slopped food fermentations and hence the source of "contamination" or inoculation with desirable fermentation organisms is in many cases enigmatic. For example, the microbial community of surface-ripened cheeses, which includes *Staphylococcus, Brevibacterium,* and *Corynebacterium* species, is independent of the geographic location but resembles human skin microbiota [1,7,8]; experimental evidence for a human origin of cheese rind microbiota, however, is lacking. As outlined below, increasing knowledge on the phylogeny and ecology of food fermenting lactic acid bacteria, particularly lactobacilli, supports the hypothesis that animal or human host-adapted lactic acid bacteria frequently dominate the microbiota of back-slopped food fermentations. *Lactobacillus* species have free-living, nomadic, insect-adapted or vertebrate host-adapted lifestyles [9]. Host-adapted lactobacilli have specialized to ecological niches that are associated with insect or vertebrate hosts. Some *Lactobacillus* species have specialized to very narrow ecological niches, e.g. *Lactobacillus iners*, which occurs only in the human vagina [9], or species in the *Lactobacillus kunkeei* group which occur only in the intestinal tract of social bees [10]. *Lactobacillus reuteri* and *Lactobacillus ruminis* are examples of species that inhabit the intestinal tract of diverse vertebrate hosts; strains of these species diversified into intra-species phylogenetic lineages that adapted to specific hosts [11,12]. Other lactobacilli, for example *Lactobacillus salivarius* and *Lactobacillus gasseri*, appear not to be adapted to specific hosts but occur in multiple host species and in several body sites [13]. The specialization of host-adapted lactobacilli resulted in a higher ecological fitness in their respective hosts at the expense of ecological fitness in other habitats [14]. When conditions in the food fermentations match their niche conditions, host-adapted lactic acid bacteria

outcompete less specialized competitors and dominate in the microbial community of those products. Experimental evidence for the animal origin of food fermenting lactobacilli was provided for sourdough isolates of *L. reuteri*, which retain all metabolic characteristics of rodent-lineage strains including the ability to colonise mice [15]. An overview on host-adapted lactobacilli in food fermentations is shown in Table 1. This communication aims to explore whether host-adapted lactobacilli share "lifestyle-associated" metabolic traits and whether these metabolic traits are relevant for the safety and quality of fermented foods.

2. Species of host-adapted lactobacilli prevalent in fermented foods

Fermentation control by back-slopping is commonly used in dairy fermentations including cheese cultures, yoghurt, kefir and other fermented milk beverages, and in many cereal fermentations including sourdough fermentations, several African fermentations for production of porridges or beverages, and mash fermentations for production of vinegar or liquor in East Asia [1,16]. Owing to their importance in fermentation control, seed cultures that are used in back-slopped fermentations often have a designation that differentiates them from the corresponding fermented food products, e.g. kefir grain, mother of vinegar, and "chef" or "levain" for seed sourdoughs. Host-adapted lactobacilli associated with cereal fermentation include organisms from the vertebrate host adapted *L. reuteri* and *Lactobacillus delbrueckii* groups, and insect associated species of the *Lactobacillus fructivorans* group. In dairy fermentations, species of the *L. delbrueckii* and *L. salivarius* groups are frequently present (Table 1). The metabolic focus of *L. delbrueckii* on lactose was explained by adaptation to dairy environments though reduction of genome size and silencing of silencing of carbohydrate active enzymes other than β-galactosidase [17], however, the presence of *L. delbrueckii* in the intestine of

93 suckling piglets demonstrates adaptation to the intestine of suckling mammals rather than dairy
94 fermentations [18,19]. Host adapted lactic acid bacteria also include the oral streptococci *S. mutans*, a
95 human adapted pathogen [20,21], and *S. salivarius,* a commensal inhabitant of the oral cavity [22]
96 (Table 1). *Streptococcus thermophilus* was identified as core member of human intestinal microbiota
97 [23]; this organism is closely related to oral streptococci but lost virulence-related genes [24].

98 **3. Metabolic properties in host-adapted lactobacilli associated with fermented food.**

99 Host-adapted lactobacilli harbour lifestyle-associated metabolic traits, including acid resistance,
100 biofilm formation, extracellular hydrolysis of polysaccharides, bacteriocin producing and tetracycline
101 resistance. An overview on metabolic properties of host-adapted lactobacilli that relate to their
102 adaptation to the host is provided in Figure 1.

103 Acid resistance system is essential for competitiveness of vertebrate-host adapted organisms as
104 colonization of a new host by oral or intestinal lactobacilli depends on survival during gastric transit
105 [9,25]. Urease is the most powerful bacterial mechanism against stomach acidity and is present in
106 species of the *L. salivarius*, *L. reuteri* and *L. delbrueckii* groups [25,26]. Urease is also expressed in
107 oral *S. thermophilus* and *S. salivarius* [27,28]; urease activity in *S. thermophilus* and *S. salivarius* is
108 differentially regulated in response to the pH and the carbohydrate supply [28,29]. Glutaminase, which
109 consumes intracellular protons by deamidation of glutamine, is almost exclusively present in host-
110 adapted lactobacilli of the *L. reuteri* and *L. delbrueckii* groups [30]. Arginine deiminase (ADI) also
111 contributes to acid resistance in lactobacilli and is expressed by host-adapted, nomadic, and free-living

112 lactobacilli [31]. The genes of the ADI pathway were overexpressed in lactobacilli colonizing stomach
113 of mice [32] but did not enhance ecological fitness [25].

114 Extracellular polysaccharides (EPS) production in lactobacilli is mediated by extracellular
115 fructansucrases or dextransucrases that use sucrose as substrate, or by intracellular
116 glycosyltransferases. Capsular EPS formation by pyogenic streptococci is a virulence factor to evade
117 the host immune system. Expression of capsular EPS promoted invasive disease caused by
118 *Streptococcus pneumoniae,* a colonizer and pathogen of the nasopharynx [33,34]. In *S. pneumoniae*,
119 capsular EPS expression is regulated by Rgg/small hydrophobic peptide quorum-sensing system and
120 has been inversely associated with biofilm formation, whereas other EPS seem to promote biofilm
121 formation [34,35]. The inhibition of biofilm formation by the capsule is attributed to the capsule effect,
122 which blocks the exposure of *S. pneumoniae* surface adhesins that promote attachment to epithelial
123 cells [36]. Regulation of surface polysaccharide expression by quorum-sensing system may enable *S.*
124 *pneumoniae* to adjust interactions with the host and other bacteria in response to environmental
125 conditions [34]. Capsular EPS of commensal bacteria also contribute to their fitness in the host but
126 benefit health. Capsular EPS produced by *Bifidobacterium breve* aids in long-term *in viv*o persistence
127 [37]. *S thermophilus* also produce capsular hetero-EPS (HePS) primarily consisting of glucose,
128 galactose and rhamnose with glucuronic acid, similar to the capsule of S. *pneumoniae* [38]. Genes
129 found in the *eps* cluster of *S. thermophilus* are related to those involved in capsule synthesis in *S.*
130 *pneumoniae* [39] and were reported to increase acid and bile tolerance [40].

131 Homopolysaccharides (HoPS) produced from sucrose contribute to biofilm formation and thus support
132 colonization of host epithelia by lactic acid bacteria [41–43]. Fructansucrases or glucansucrases of *S.*

133 *mutans* produce glucan or fructan, respectively, which form the biofilm matrix that is necessary to
134 colonize the surface of teeth [43,44]. In lactobacilli, glucansucrase and fructansucrase activity is
135 frequently found in the host-adapted *L. delbrueckii* and *L. reuteri* groups, and in the *Lactobacillus mali*
136 group which predominantly has a free living lifestyle [31]. In direct analogy to *S. mutans*, HoPS
137 produced by *L. reuteri* are required for biofilm formation and cell aggregation, and are essential for
138 colonization of the mouse gastrointestinal tract [42,45]. Glucansucrases and fructansucrases also
139 mediate metabolism of sucrose; in *Lactobacillus sanfranciscensis*, levansucrase is the only enzyme
140 with activity on sucrose [46].

141 Only few lactobacilli express extracellular enzymes catalyzing the hydrolysis of polysaccharides [47].
142 Starch, pullulan, and fructans provide carbon source from polysaccharides or biofilms when other
143 fermentable carbohydrate sources are limited. Extracellular amylopullulanase (AmyX) is present only
144 in few *Lactobacillus* species; most of these are classified in the *Lactobacillus amylophilus, L.*
145 *delbrueckii* and *L. salivarius* groups [47]. As resistant starch is a major carbohydrate source in the
146 human and swine intestine, AmyX may contribute to the ecological fitness of lactobacilli in intestinal
147 tract [47,48]. The extracellular fructosidase FruA mediates fructan degradation in *S. mutans* [49]; in
148 lactobacilli, it is found only in few strains of *Lactobacillus crispatus* and *Lactobacillus amylovorus*
149 from sourdough and the swine intestine [18,50].

150 Sucrose phosphorylase (ScrP) phosphorolyses sucrose into fructose and glucose-1-phosphate.
151 Lactobacilli harboring sucrose phosphorylase belong to the vertebrate host-adapted *L. delbrueckii*, *L.*
152 *reuteri* and *L. salivarius* group, and the free living *Lactobacillus buchneri* group. Sucrose metabolism
153 is repressed by glucose in homofermentative lactobacilli; in heterofermentative lactobacilli of the *L.*

154 *reuteri* group, sucrose metabolism is preferred over glucose metabolism [51]. Phosphorolysis in
155 combination with fructose reduction to mannitol increases the energy yield of the phosphoketolase
156 pathway more than twofold [52] and increases the growth rate in cereal substrates [31,53]. Since
157 sucrose is present only in the upper intestine, ScrP increases ecological fitness only of those lactic acid
158 bacteria that inhabit the oral cavity, the crop, or (fore)-stomach epithelia.

159 Tetracycline resistance of lactobacilli is mediated by the ribosomal protection proteins Tet(M), Tet(S),
160 Tet(Q), and Tet(W), and the efflux pumps [Tet(L) and Tet(P)]. Tet(W) is almost exclusively present in
161 intestinal lactobacilli and was likely acquired by horizontal gene transfer [54]. Tet(M) is the most
162 widespread in lactobacilli; this gene is present in the *L. delbrueckii* and *Lactobacillus amylophilus*
163 groups, and in *Lactobacillus equigenerosi*, a species in the *L. reuteri* group [55]. The gene *tet*(M) is
164 also the most widespread antibiotic resistance gene in food-associated lactobacilli, including *L.*
165 *delbrueckii* supsb. *bulgaricus*, *L. salivarius*, and *L. reuteri* [56]. Tet(M) was shown to have ribosome-
166 dependent GTPase activity. The energy from GTP hydrolysis by Tet(M) releases the tetracycline from
167 the ribosome, thereby reduced the binding of tetracycline to the ribosomes. The distribution of *tet*(M)
168 gene is generally associated with conjugative chromosomal transposons, which transfer mobile
169 plasmids to other species and even unlinked genomic DNA [57]. Tet(M) was also found in
170 bifidobacteria, a commensal genus in the gastrointestinal tracts of humans and animals, and transferred
171 between different *Bifidobacterium* species [58,59]. Therefore, acquisition of *tet*(M) by intestinal
172 lactobacilli likely occurred by lateral gene transfer from bifidobacteria or other intestinal organisms.

173 Bacteriocin production by lactobacilli is strain specific and not limited to host-adapted species.
174 Bacteriocin production is often assumed to be a desirable trait of probiotic bacteria but experimental

175 evidence that bacteriocins of intestinal or probiotic lactobacilli modulate intestinal microbiota remains
176 elusive [60,61]. Analysis of the prevalence of bacteriocin-encoding genes in the metagenome of
177 different human body sites, however, revealed that bacteriocin production is particularly frequent in
178 oral and vaginal microbiota, which implies an ecological role of bacteriocin production by lactobacilli
179 in these body sites [62]. Correspondingly, oral streptococci are prolific producers of bacteriocins [63]
180 and also frequently harbor non-ribosomal peptide synthases with putative function in synthesis of
181 antimicrobial compounds [64]. Also, multiple vaginal isolates produce bacteriocins with antimicrobial
182 activity against vaginal pathogens [65,66].

183 Reuterin is a broad-spectrum antimicrobial compound, which is produced as intermediate of glycerol
184 metabolism by strains of *L. reuteri* [67]. Glycerol metabolism in *L. reuteri* is encoded by the gene
185 cluster *pdu-cbi-hem-cob* that contains the *pdu* genes encoding cobalamin-dependent glycerol/diol
186 dehydratase PduCDE which utilizes glycerol or 1,2-propanediol [68]. The gene cluster is also present
187 in intestinal microbes such as *Salmonella* and *Eubacterium hallii*. In the human colon, intestinal
188 microbiota produce 1,2 propanediol from fucose or rhamnose; 1,2-propanediol metabolism generates
189 propionate and propanol [69]. Glycerol is available in cereals and other plant foods; glycerol
190 metabolism by *L. reuteri* enhances its competitiveness in cereal substrates [70]. In *L. reuteri*, glycerol
191 / propanediol metabolism is frequent only in strains of the human adapted lineage II, which colonizes
192 the intestine of herbivores and humans, and in the poultry- adapted linage VI, which colonizes the crop
193 of birds but also persists in humans [68]. The differential regulation of reuterin production in *L. reuteri*
194 strains of different lineages [68] may reflect the availability of glycerol and 1,2 propanediol in the
195 upper and lower intestine, respectively.

196 Species of the *L. fructivorans* group, likely including *L. sanfranciscensis*, are associated with insect
197 hosts and have distinctive metabolic properties when compared to vertebrate-host adapted lactobacilli.
198 They utilize only few carbohydrates and depend on the availability of fructose as electron acceptor
199 [71]. Their small genome size and restricted metabolic potential indicates specialization to very narrow
200 ecological niches.

201 **4. The contribution of metabolic traits in host-adapted lactobacilli to food quality.**

202 The metabolic traits of host-adapted lactobacilli that contribute to the flavour, structure, and quality of
203 fermented food are shown in Table 2. Glutamine and glutamate metabolism enhance bread quality by
204 generating glutamate and γ-aminobutyric acid (GABA), respectively. The glutaminase mediated
205 glutamate accumulation exceeds the taste threshold in bread and ripened cheese and thus contributes
206 to the umami taste [72,73]. Dietary GABA has relaxing properties [74,75]. In baked goods, arginine
207 conversion by sourdough lactic acid bacteria provides ornithine as precursor to the character impact
208 aroma compound of wheat bread crust, 2-acetyl-1-pyrroline [53]. During malolactic fermentation of
209 wine, arginine deamidation by lactic acid bacteria may accumulate citrulline as an intermediate, which
210 is a precursor for the formation of the carcinogen ethyl carbamate [76].

211 In the initial stages of yoghurt fermentations, urease catalyzes hydrolysis of urea into ammonia and
212 CO_2. During co-culture of *S. thermophilus* and *L. delbrueckii* subsp. *bulgaricus*, urease is essential for
213 effective protocooperation and yogurt acidification of two species by providing ammonia nitrogen to
214 support growth and acidification of *S. thermophilus*, and CO_2 for the CO_2-responsive *L. delbrueckii*
215 subsp. *bulgaricus* [77].

EPS formation in cereal fermentations improves bread volume and texture and reduces bread staling; EPS also contributes to the texture of other fermented cereal foods or beverages [78,79]. Production of HePS in dairy fermentations affects the texture and rheology of the products [80]. The interaction of EPS and milk proteins influences protein gel formation and water binding capacity. Free EPS typically lead to ropiness, while capsular EPS increases viscosity without causing ropiness. In set milk products, EPS is located at the pore/protein network interface or located in the aqueous environment of the pores. Stirring redistributes EPS in the protein network; ropy EPS attached to protein maintains high viscosity and the firmness of the protein network after stirring while EPS in pores maintains only the high viscosity [81]. The presence of capsular EPS lead to a higher firmness, viscosity, thickness and creaminess [81]. The interplay of capsular and free EPS seems also relevant to product texture, influencing protein aggregation, pore size and structure recovery of network [82]. Kefiran is a water-soluble HePS, composed by glucose and galactose, exclusively produced by *Lactobacillus kefiranofaciens* during kefir fermentation and contributes to formation of the kefir grain and the gel formation and viscosity of the finished product [81].

EPS formation by probiotic strains also contributes to human health. HoPS isolated from *L. reuteri* inhibited adhesion of enteroxigenic *Escherichia coli* to the swine intestinal mucosa [83]. HePS produced by probiotic strains, lactic acid bacteria and bifidobacteria, may modulate the immune system of the host. Capsular EPS produced by *B. breve* reduces the levels of colonization by intestinal pathogens [37]. EPS-deficient variants of *B. breve* strains elicited a strong immune response that was absent in the wild type strains producing capsular EPS, indicating that capsular EPS mediates immune

236 evasion, especially avoiding B-cell responses [37]. HePS produced by *S. thermophilus* stimulated
237 human gastric epithelial cell regeneration and immunological innate defense mechanisms [84].

238 The ability of degrading polysaccharides is rare in *Lactobacillus* species. Expression of extracellular
239 fructanases by *L. crispatus* or *L. amylovorans* eliminated fructans from cereal during sourdough
240 fermentation. A reduced fructans content of bread improved the tolerance of patients with irritable
241 bowel syndrome (IBS) to rye bread with a high dietary fiber content [50,85].

242 Bacteriocins of lactobacilli find food applications to inhibit or to eliminate pathogens, particularly in
243 ready-to-eat meat or fish products; none of the strains that find commercial application, however, are
244 of intestinal origin [86]. Reuterin is a highly reactive compound, the reactivity limits its application in
245 food. It was demonstrated, however, that reuterin producing *L. reuteri* in combination with addition of
246 glycerol are an effective approach to prevent late blowing defect of cheese [87,88].

247 Food fermentations with probiotic fermentation organisms is increasingly recognized as a tool to
248 deliver beneficial microbes to the human or animal intestinal tract [89,90]. Host-adapted lactobacilli
249 show improved survival after gastro-intestinal transit in swine and in humans [91,92], which may relate
250 to their increased acid resistance, and enhance probiotic activity of host-adapted lactobacilli that are
251 present in food fermentations. For example, several African non-alcoholic cereal beverages including
252 *mawe*, and *mahewu* contain viable fermentation organisms and were proposed as route of delivery for
253 probiotic bacteria [93]. *Koumiss* contains high cell counts of probiotic *Lactobacillus helveticus,* which
254 contributes to anti-inflammatory attributes [94]. *L. kefiranofaciens* in kefir decreased inflammation in
255 a mouse model of obesity [95]. Traditional kefir has also been proved reducing weight gain, improving

plasma and liver lipid profiles in a mouse model of obesity [96]. Fermented foods containing large numbers of live probiotic bacteria are also considered giving similar health benefits as intake of probiotic lactobacilli of the same species [90]. However, the tetracycline resistance of host-adapted lactic acid bacteria may limit their use as a starter or probiotic cultures [54,55,97].

In conclusion, fermentation micro-organisms in back-slopped food fermentations are often recruited from lactic acid bacteria that have evolved to form stable associations with insects or vertebrate hosts. The ecological fitness of host-adapted lactobacilli in host and food environments is dependent on lifestyle-associated metabolic traits. Some of these traits, including exopolysaccharide formation and bacteriocin production, are also present in free-living or nomadic lactic acid bacteria while other metabolic properties, for example, glutaminase- and urase mediated acid resistance, the extracellular fructanase FruA, and antibiotic synthesis by non-ribosomal peptide synthases are virtually exclusive to host-adapted lactobacilli. An improved understanding of the ecological origin of food fermenting lactic acid bacteria will facilitate the selection of starter cultures for food production and may support the simultaneous use of lactic acid bacteria as food-fermenting and probiotic cultures.

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610 Table 1. Host-adapted lactobacilli in food fermentation

	Products	Substrate	Host-adapted lactic acid bacteria	Stage of production	Reference
Cereal fermentations	Ting	Sorghum	*L. reuteri*	Back-slopping	[93,98]
	Kisra	Sorghum	*L. reuteri, L. amylovorus*	Back-slopping	[99]
	Mawe	Maize	*L. reuteri, L. salivarius*	Back-slopping	[100,101]
	type I sourdough	Wheat or rye	*L. sanfranciscensis, L. pontis, L. panis*	Back-slopping	[102,103]
	type II sourdough	Wheat or rye	*L. pontis, L. amylovorus, L. reuteri, L. panis, L. frumenti, L. crispatus, L. acidophilus*	Back-slopping	[102,103]
	vinegar	Barley, wheat, rice or sorghum	*Lactobacillus acetotolerans*	Back-slopped mash fermentation	[104,105]
	Baijiu		*L. acetotolerans, L. panis*	Back-slopped mash fermentation	[106,107]
	Chicha	Cassava	*Lactobacillus acidophilus, Lactobacillus delbrueckii, L. reuteri, Streptococcus salivarius, Streptococcus mutans*	Spontaneous, inoculation with human saliva	[108,109]
Dairy fermentations	Yoghurt	milk	*L. delbrueckii* subsp. *bulgaricus, Streptococcus thermophilus*	Back-slopping or starter cultures matching traditional back-slopped fermentations	[1,16]
	Koumiss	Mare's milk	*L. helveticus, L. delbrueckii* subsp. *bulgaricus, L. salivarius, L. acidophilus, L. kefiranofaciens, Streptococcus thermophilus*		[100,110]
	kefir	Milk and kefir grain	*L. kefiranofaciens, L. delbrueckii* subsp. *bulgaricus, S. thermophilus, L. helveticus*		[95]
	cheese	milk	*L. delbrueckii* subsp. *bulgaricus, L. helveticus, S. thermophilus*		[1,16]

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612 Figure 1. Representative characteristics of host-adapted lactobacilli associated with food fermentation (partially created with biorender.com)
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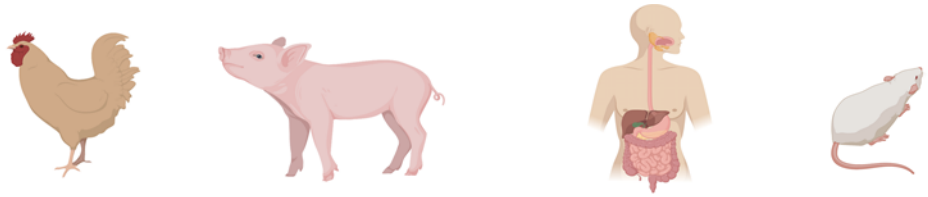

Vertebrate-adapted lactobacilli

Insect-adapted lactobacilli

L. reuteri group

L. delbrueckii group

L. salivarius group

L. fructivorans group

Tetracycline resistance

Small genome size

Formation of glucans and fructans from sucrose

Restricted use of carbohydrates ("sucrose and maltose diet")

Extracellular glucosyl hydrolases, bacteriocin production

Preferred use of fructose as electron acceptor ("Fructophilic")

Acid resistance (glutaminase, glutamate decarboxylase, urease)

Oxygen tolerant

Table 2. Impact of metabolisms in host-adapted lactobacilli on food quality and human health

Metabolic activity / metabolite	Food products	Impact on food quality	References
Glutamine deamidation / Glutamate accumulation	Bread, cheese	Umami taste, salt reduction	[72,73]
Glutamate decarboxylation / GABA accumulation	Bread, cheese, kimchi	Anti-hypertensive properties	[74,75]
Urea metabolism / Acidification	yoghurt	Symbiosis of *L. delbrueckii* and *S. thermophilus* results in stable fermentation culture	[77]
Arginine deamidation to ornithine / formation of 2-acetyl-2-pyrroline, the crust odor compound, from ornithine during baking	Bread	Flavor	[53]
Formation of homopolysaccharides and heteropolysaccharides	Bread; yoghurt	Improved texture and volume of bread; Improved texture and rheology of yoghurt; Prevent adhesion of pathogens; Stimulation of immunological defense mechanisms	[79,81–84]
Degradation of fructans or raffinose (FODMAPs); sugar reduction in wheat products	Bread, other cereal products	Increase the tolerance to rye bread of IBS patients; Increase of sweet taste	[50,85]
Production of bacteriocins or reuterin	Cheese	antimicrobial activity as bio-preservatives / “clean label” products	[1,87,88]
Delivery of dietary microbes	Probiotic	Probiotic activity	[93–96]