International Journal of Food Microbiology 302 (2019) 15–23

Contents lists available at ScienceDirect

International Journal of Food Microbiology

journal homepage: www.elsevier.com/locate/ijfoodmicro

Lifestyles of sourdough lactobacilli – Do they matter for microbial ecology and bread quality?

Michael G. Gänzle[a,b,*], Jinshui Zheng[c]

[a] University of Alberta, Dept. of Agricultural, Food and Nutrional Science, Edmonton, Canada
[b] Hubei University of Technology, College of Bioengineering and Food Science, Wuhan, China
[c] State Key Laboratory of Agricultural Microbiology, Huazhong Agricultural University, Wuhan, China

ARTICLE INFO

Keywords:
Lactobacillus
Sourdough
Microbiota
Evolution
Bread leavening

ABSTRACT

Sourdough is used in production of (steamed) bread as leavening agent (type I sourdoughs) or as baking improver to enhance flavour, texture, and shelf life of bread (type II sourdoughs). The long-term propagation of sourdoughs eliminates dispersal limitation and consistently leads to sourdough microbiota that are composed of host adapted lactobacilli. In contrast, community assembly in spontaneous cereal fermentations is limited by dispersal and nomadic or environmental lactic acid bacteria are the first colonizers of these sourdoughs.

Propagation of sourdoughs for use as sole leavening agent (type I sourdoughs) dictates fermentation conditions that select for rapid growth. Type I wheat- and rye sourdoughs are consistently populated by insect-adapted lactobacilli, particularly *Lactobacillus sanfranciscensis*, which is characterized by a small genome size and a restricted metabolic potential. The diverse fermentation conditions employed in industrial or artisanal Type II sourdough fermentation processes also result in a more diverse microbiota. Nevertheless, type II sourdoughs are typically populated by vertebrate host adapted lactobacilli of the *L. delbrueckii* and *L. reuteri* groups. Metabolic traits of host-adapted lactobacilli that enhance competitiveness in intestinal ecosystems also provide technological functionality in bread making. Examples include formation of exopolysaccharides, arginine-, glutamine- and glutamate based mechanisms of acid resistance, and glycosyl hydrolases that reduce FODMAP levels in sourdough and sourdough bread. In conclusion, consideration of the lifestyle of sourdough lactobacilli facilitates the selection of competitive and functional sourdough starter cultures.

1. Introduction

Sourdough has been traditionally used as leavening agent for bread and steamed bread. CO_2 production in sourdough is mediated by yeasts and heterofermentative lactobacilli, and is coupled to acidification (Brandt et al., 2004). Microbial metabolism in conjunction with the activity of flour enzymes also improves flavour, texture, storage life, and nutritional properties of bread (Gänzle, 2014; Gobbetti et al., 2018). The industrial production of baker's yeast allowed its use as leavening agent after the late 19th century; by the middle of the 20th century, baker's yeast had replaced sourdough as leavening agent in most applications except in some small scale artisanal bakeries, for specialty products, and in rye baking, where acidification is necessary to improve baking properties (Capelle et al., 2013). Recognition of the quality of sourdough bread and the efforts of the baking industry to offer "clean label" products led to a resurgence of sourdough use since the late 20th century. Currently, sourdough or sourdough products are used in most European baked goods with the primary aim to improve bread quality (Brandt, 2007; Pontonio et al., 2017).

Different technological aims of sourdough fermentation – leavening, acidification, or dough improver – necessitate different fermentation conditions. The traditional use of sourdough as sole leavening agent dictates frequent refreshments of the sourdough, or, in microbiological terms, fermentation conditions that maintain sourdough microbiota in the exponential phase of growth. Maintaining sourdough microbiota in a metabolically active state ensures sufficient CO_2 production and leavening power (Brandt et al., 2004). Two examples of fermentation processes to achieve leavening are shown in Fig. 1. Details of the fermentation process, i.e. the number of stages per fermentation cycle, and the conditions with regards to temperature, time, water addition, and level of inoculum, are poorly documented in the scientific literature and vary widely between different bakeries; however, type I fermentation processes generally follow the principle that fermentation microbiota are continuously maintained in a metabolically active state by frequent

---

[*] Corresponding author at: University of Alberta, Dept. of Agricultural, Food and Nutritional Science, 4-10 Ag/For Centre, Edmonton, AB T6G 2P5, Canada.
E-mail address: mgaenzle@ualberta.ca (M.G. Gänzle).

https://doi.org/10.1016/j.ijfoodmicro.2018.08.019
Received 21 June 2018; Received in revised form 9 August 2018; Accepted 18 August 2018
Available online 20 August 2018

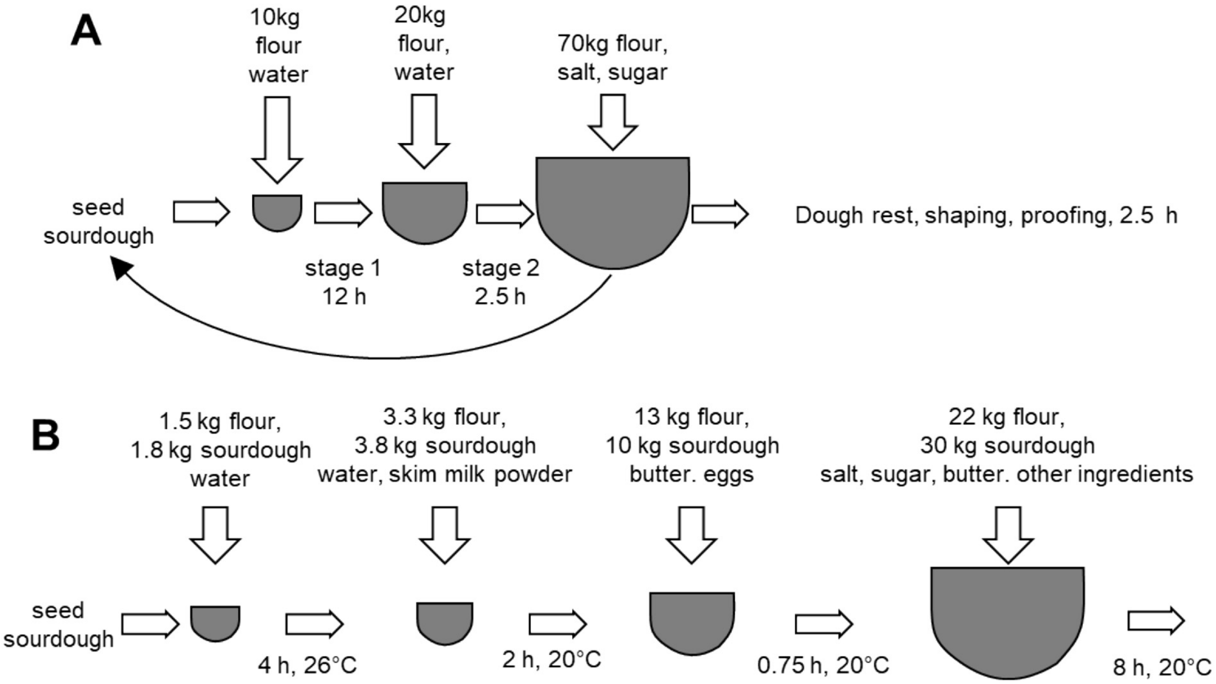

Fig. 1. Two examples of sourdough fermentation processes used to achieve leavening of bread without addition of baker's yeast. **Panel A**, three stage sourdough process (Tang et al., 2017). Tang et al. performed fermentations at 30 °C; in bakery practice, the fermentation stages are performed at 22–28 °C; **Panel B**; sourdough process for production of Colomba (Raimundi et al., 2017). Other type I sourdough fermentation processes follow a different regimen with respect to incubation time and temperature, and inoculum level, however, all sourdoughs that are fermented to achieve leavening of dough without baker's yeast continuously maintain sourdough microbiota in a metabolically active state.

refreshments. This also prevents exposure of sourdough microbiota to low pH (Böcker et al., 1995; Brandt et al., 2004). The use of sourdough as sole leavening agent is generally restricted to artisanal or medium scale bakeries. Industrial sourdough fermentations employ comparable fermentation conditions to support leavening in combination with addition of baker's yeast. Some of the sourdoughs for use as leavening agent have been maintained over long periods of time; documented propagation of sourdoughs exceeds 100 years.

Fermentation of sourdoughs with high levels of acidity requires different fermentation conditions; these sourdoughs are fermented at a high temperature for extended periods of time to achieve high levels of total titrable acidity (Böcker et al., 1995; Müller et al., 2001; Rosenquist and Hansen, 2000; Vera et al., 2012; Viiard et al., 2013 and 2016). Dough acidification is particularly relevant in rye baking to inhibit rye amylases (Brandt, 2007) and it is used predominantly in countries where rye bread is popular. These sourdoughs do not allow leavening without addition of baker's yeast. Comparable to the use of sourdough as leavening agent, sourdoughs that are fermented for dough acidification and improved bread quality are maintained by continuous propagation to achieve a consistent composition and activity of sourdough microbiota (Brandt, 2007; Zheng et al., 2015b).

In addition to those sourdoughs that are maintained by back-slopping, spontaneous sourdough fermentations are also used in bakeries. The most common practice is the use of sponge dough; dough that is fermented for more than 4 h after addition of baker's yeast. Sponge doughs are commonly used in wheat baking and in production of soda crackers (Sugihara, 1978). Spontaneous fermentations of cereals are also used in the production of cereal beverages, porridges, and flat bread; a large diversity of products is traditionally prepared in Africa (Todorov and Holzapfel, 2015).

The assembly of sourdough microbiota in spontaneous fermentations is limited by dispersal, i.e. community assembly depends on contaminants from plant, animal, or environmental sources (Gänzle and Ripari, 2016). In contrast, microbiota of back-slopped sourdoughs are shaped by selection for the most competitive microorganisms (Gänzle and Ripari, 2016). Back-slopping of sourdoughs over long time periods provides opportunity for contaminants from even unlikely sources to establish themselves as stable members of sourdough microbiota. Böcker et al. (1995) proposed that the technological aim of sourdough fermentation – leavening or acidification – determines the fermentation conditions and the composition of sourdough microbiota. The concept, initially based on characterization of only a few German sourdoughs, was further developed in several comprehensive reviews (De Vuyst and Neysens, 2005; De Vuyst et al., 2014; Gobbetti et al., 2016; Vogel et al., 1999) to differentiate between type I sourdoughs, sourdoughs used for leavening; type II sourdoughs, sourdoughs used for acidification; and type 0 sourdoughs, spontaneous sourdoughs. Past reviews focused on microbiological aspects and the impact of fermentation conditions on composition of sourdough microbiota (De Vuyst and Neysens, 2005; De Vuyst et al., 2014; Gobbetti et al., 2016; Vogel et al., 1999) while neglecting the link between technological aim and fermentation microbiota that was initially proposed by Böcker et al. (1995).

The present communication will initially revisit the question which lactic acid bacteria populate sourdoughs. Literature data on sourdough microbiota covers more than 300 sourdoughs with documented composition and use in artisanal or industrial bakeries, allowing to probe relationships between the technological aim of fermentation and the composition of sourdough microbiota. In addition, we address the question where to lactic acid bacteria in sourdoughs come from; i.e. we will explore whether the competitiveness of lactic acid bacteria in sourdoughs relates to their phylogenetic position or their natural habitat. Duar et al. (2017b) proposed that lactobacilli have evolved to specific ecological niches that relate to vertebrate hosts, insects, or plants and the environment. The adaptation of lactobacilli to a specific natural habitat is typically shared by closely related species, i.e. the "lifestyle" is shared by organisms in the same phylogenetic group in the genus *Lactobacillus* (Zheng et al., 2015a). The consideration of the natural habitat of lactic acid bacteria and bifidobacteria has been instrumental in guiding the selection of bacterial strains for use as probiotics to obtain strains that are adapted to intestinal habitats (Walter et al., 2018). The use of this concept for food fermentations will improve our understanding of the factors shaping the composition and activity of sourdough microbiota to guide the selection of competitive organism with beneficial impact on bread quality.

2. Lactic acid bacteria in type I and type II sourdoughs

Literature data were interrogated with respect to the composition of the bacterial microbiota in sourdoughs. Studies were included in the analysis if they met the following criteria, (i) basic information on the fermentation conditions and/or the use of the sourdough was provided, (ii) isolates were obtained on suitable cultivation media, and were characterized at the species level by currently accepted methods, and (iii) information on the composition of microbiota was provided for each sourdough at the species level. The literature search aimed to provide a comprehensive overview on Type I sourdoughs and Type II sourdoughs, and additionally included examples of spontaneous fermentations, laboratory model fermentations started with flour and sterile water, and fermentations of cereals other than wheat or rye. In total, data on the composition of 315 sourdoughs was evaluated. A variable level of detail on fermentation conditions and technological aim of the sourdough fermentation is provided by the different sources; therefore, some of the classifications as type I, type II or spontaneous sourdoughs may be ambiguous.

Literature data for the 227 sourdoughs classified as type I sourdough included mainly samples from Italy, France, Germany, Belgium, the U.S. and Canada; since 2015, data became available for Chinese sourdoughs use for production of steamed bread (Fig. 2 and Table S1 of the online supplementary material). More than 95% of sourdoughs contained heterofermentative lactic acid bacteria alone or in association with homofermentative lactobacilli. *L. sanfranciscensis* was most frequently identified, 178 of the 227 sourdoughs harboured this species. Other frequent representatives include *L. plantarum* and *L. brevis*, species in the *L. alimentarius* group (*L. paralimentarius*, *L. crustorum*, *L. mindensis*, and *L. nantensis*), *Leuconostoc* spp. and *Weissella* spp. Five of the sourdoughs were maintained at the household level; here, the propagation of the sourdoughs was interrupted by refrigerated storage for several days or weeks. All of these sourdoughs harboured a combination of *L. plantarum* and *L. brevis* (Table S1).

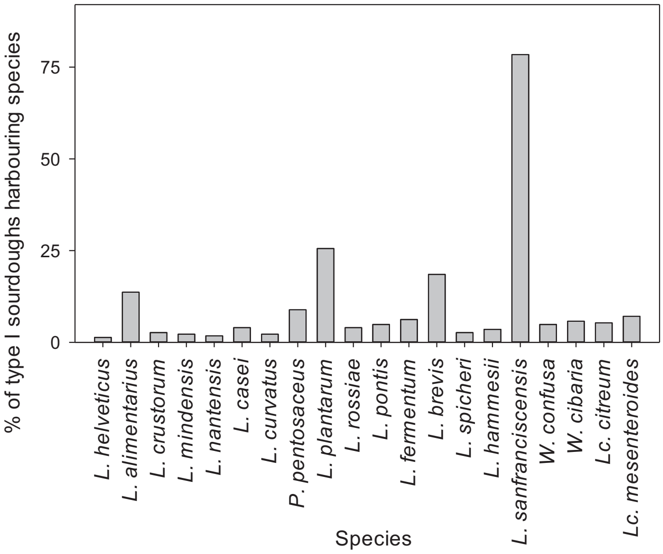

Fig. 2. Occurrence of lactic acid bacteria in wheat and rye sourdoughs used as sole leavening agent. Shown is the percentage of 227 sourdoughs containing the species indicated on the x-axis. Species are shown only if they were identified in 3 or more sourdoughs. Data were compiled from Böcker et al., 1995, Corsetti et al., 2001, Ehrmann et al., 2003, Ferchichi et al., 2007, Foschino et al., 1999, Garofalo et al., 2008 Lattanzi et al., 2013, Lhomme et al., 2015 and 2016, Liu et al., 2016, Kitahara et al., 2005, Kline and Sugihara, 1971, Meroth et al., 2003, Michel et al., 2016, Minervini et al., 2012, Palla et al., 2017, Raimondi et al., 2017, Randazzo et al., 2005, Ripari et al., 2016, Scheirlinck et al., 2007, Spicher, 1987, Yang et al., 2017, Zhang et al., 2015, and unpublished observations for 27 sourdoughs. The composition of all 227 sourdoughs is listed in Table S1 of the online supplementary material.

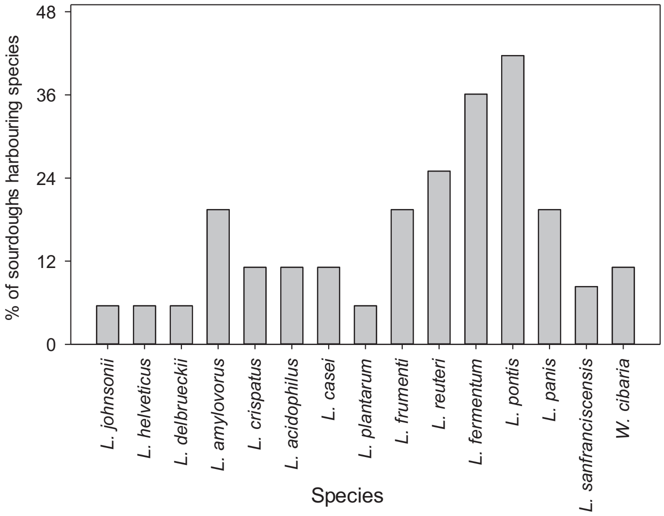

Fig. 3. Occurrence of lactic acid bacteria in wheat and rye sourdoughs used for acidification of wheat and rye sourdoughs, or for production of baking improvers. Shown is the percentage of 32 sourdoughs containing the species indicated on the x-axis. Species are shown only if they were identified in 2 or more sourdoughs. Data were compiled from Böcker et al., 1995, Ferchichi et al., 2007, Meroth et al., 2003, Müller et al., 2001, Rosenquist and Hansen, 2000, Vera et al., 2012, Strohmar and Diekmann, 1992, Viiard et al., 2013 and 2016, and unpublished observations for 17 sourdoughs. The composition of all 32 sourdoughs is listed in Table S2 of the online supplementary material.

Literature data for the 32 sourdoughs classified as type II sourdough included mainly rye sourdoughs from Finland, Estonia, Denmark, and Germany; data for few wheat sourdoughs from the U.S., China, and France are also available (Fig. 3 and Table S2). Type II sourdoughs also contained heterofermentative organisms alone or in association with homofermentative lactobacilli (Table S2). Species of the *L. reuteri* group, particularly *L. pontis*, *L. panis*, *L. frumenti* and *L. reuteri* as well as the *L. delbrueckii* group organisms *L. amylovorus*, *L. crispatus* and *L. acidophilus* were frequently identified in type II sourdoughs (Fig. 3). *L. sanfranciscensis* was identified in 3 Chinese sourdoughs that are used for dough acidification in conjunction with baker's yeast (Fig. 3).

Data on the composition of spontaneous sourdoughs including model sourdoughs prepared in laboratories under aseptic conditions, sourdoughs prepared with cereals other than wheat or rye, and some cereal beverages or porridges is shown in Fig. 4. *L. plantarum* and *L. fermentum* are the most frequently reported organisms; these species are particularly relevant in model sourdoughs that are started and propagated in the laboratory with flour as the only source of microorganisms (Minervini et al., 2015). *L. plantarum* and *L. fermentum* are also the most frequently isolated organisms in spontaneous African cereal fermentations, independent on whether the raw material is tef, maize, sorghum, or millet (Fig. 4, Todorov and Holzapfel, 2015). Spontaneous sourdoughs also often harbour enterococci, lactococci, and pediococci (Fig. 4); these organisms are rapidly displaced by lactobacilli when spontaneous sourdoughs are back-slopped (Van der Meulen et al., 2007; Hamad et al., 1997).

3. Lifestyles of sourdough lactobacilli

Food fermentations including sourdough fermentation thus do not support speciation or even adaptation below the species level (Duar

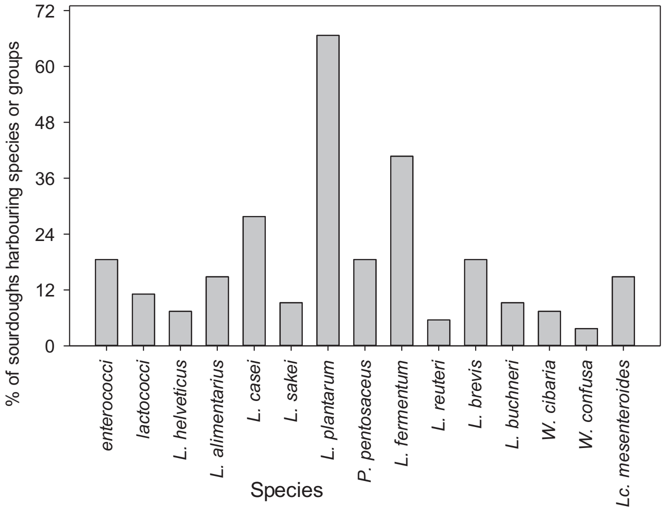

Fig. 4. Occurrence of lactic acid bacteria in spontaneous sourdoughs, model sourdoughs prepared under sterile laboratory conditions, or in cereal fermentations with substrates other than wheat or rye. Shown is the percentage of 54 sourdoughs containing the species indicated on the x-axis. Species are shown only if they were identified in 2 or more sourdoughs. Data were compiled from the reviews of De Vuyst and Neysens, 2005 and De Vuyst et al., 2014 as well as Gassem, 1999, Hamad et al., 1991, Madoroba et al., 2011, Muyanja et al., 2003, Sekwati-Monang and Gänzle, 2011, and unpublished observations for 5 sourdoughs. The composition of all 56 sourdoughs is listed in Table S3 of the online supplementary material.

et al., 2017b; Gänzle and Ripari, 2016; Zheng et al., 2015b). Lactobacilli contaminate sourdough fermentations from their primary habitats in which they form a stable population over long time periods. Large-scale comparative genomic analyses for the genus *Lactobacillus* as well as for several model species allowed identification of the primary habitats for several *Lactobacillus* spp. (Duar et al., 2017b; Martino et al., 2016; Frese et al., 2011; Krumbeck et al., 2016). The adaptation of lactobacilli to specific habitats typically represents an ecological strategy that is generally shared by phylogenetically related species (Duar et al., 2017b; Zheng et al., 2015a).

Several groups of lactobacilli have adapted to insects. Species in the *L. mellifer* and *L. kunkeei* groups and a cluster of species related to *L. apis* were isolated almost exclusively from insects. These species are characterized by a GC of less than 40%, a small genome size of typically less than 2 Mbp, and an extremely restricted carbohydrate fermentation pattern that often includes only maltose and sucrose, and the lack of acid resistance mechanisms (Duar et al., 2017b; Filannino et al., 2016; Zheng et al., 2015a). The identification of the ecological nice for species in the *L. fructivorans* group including *L. sanfranciscensis* is more ambiguous. Many representatives, e.g. *L. lindneri*, *L. sanfranciscensis*, *L. fructivorans* and *L. homohiochii*, were initially isolated from fermented or spoiled food (Zheng et al., 2015a). Comparable to other insect-adapted lactobacilli, *L. fructivorans* group organisms have a small genome size, 1,279,300 to 1,420,000 bp, a low GC content and a very narrow carbohydrate fermentation pattern (Vogel et al., 2011; Zheng et al., 2015a). *L. fructivorans* forms stable associations with fruit flies (Wong et al., 2011) and other species originate from insects (*L. vespulae*; Hoang et al., 2015) or flowers (*L. florum* and *L. ixorae*; Endo et al., 2010; Techo et al., 2016). All isolates of *L. sanfranciscensis* originate from sourdough, however, culture-independent analyses suggested its presence in fruit flies (Groenewald et al., 2006) and grain beetles (Boiocchi et al., 2017). As a small genome size and low GC content indicate adaptation to a narrow ecological niche, *L. sanfranciscensis* and other *L. fructivorans* group organisms likely are adapted to insect hosts.

Species in the *L. delbrueckii* group, the *L. reuteri* group and the *L. salivarius* group are consistently associated with vertebrate hosts; examples include *L. ruminis*, *L. reuteri*, and *L. amylovorus* (Duar et al., 2017a, Frese et al., 2011; Forde et al., 2011; Walter, 2008). Interrogation of the experimental literature and 16S rRNA sequence databases demonstrated that adaptation to vertebrate hosts is a property that is shared across different members of a specific phylogenetic group (Duar et al., 2017b). For example, *L. helveticus* and *L. pontis* occur in cheese and sourdough fermentations but also form stable populations in the intestine of chicken and swine, respectively (Duar et al., 2017b). The *Lactobacillus* species with the smallest genome size, *L. iners*, also exhibits the most restricted ecological niche, the human vagina, confirming that a small genome size relates to a restricted host range (Macklaim et al., 2011). Comparable to insect-adapted lactobacilli, vertebrate host adapted lactobacilli have a relatively small genome size of about 2 Mbp. In contrast to insect associated lactobacilli, they maintain a more extensive toolset for degradation of mono- di, and trisaccharides (Zhao and Gänzle, 2018; Zheng et al., 2015a) or even express extracellular glycosyl hydrolases (Loponen et al., 2016). They generally also maintain multiple amino-acid based mechanisms for acid resistance (Krumbeck et al., 2016; Zheng et al., 2015a). *L. delbrueckii* and *L. fermentum* are exceptions to the general rule that the lifestyle of lactobacilli is shared by closely related species. *L. delbrueckii* adapted to dairy environments; this process included silencing of carbohydrate metabolic genes and the relatively recent acquisition of lactose fermentation (El Kafsi et al., 2014). *L. fermentum* is the only species in the *L. reuteri* group that is not associated with intestinal habitats (Duar et al., 2017b; Walter, 2008).

L. rhamnosus and *L. plantarum* were isolated from a broad range of habitats. For example, *L. plantarum* was identified as member of intestinal microbiota of insects and vertebrate animals but also occurs on plants and in the environment. The origin of strains of *L. plantarum* is unrelated to their phylogenetic position, which indicates that the association of strains with any specific habitat is only temporary (Douillard et al., 2013; Martino et al., 2016). Accordingly, their lifestyle has been termed as "nomadic", implying frequent transition from one habitat to another (Duar et al., 2017b; Martino et al., 2016). *L. plantarum* and *L. rhamnosus* have a relatively large genome size, which provides a broad metabolic potential and enables the organisms to temporarily persist in multiple environments (Martino et al., 2016). In keeping with its broad distribution in insect, animal, and plant microbiota, *L. plantarum* frequently occurs in spontaneous food fermentations including sourdough fermentations (Gänzle, 2015).

A third group of organisms is isolated predominantly from plant or environmental sources. These lactobacilli also typically have a relatively large genome size and a lower optimum and minimum temperature of growth (Duar et al., 2017b). Examples include *L. buchneri*, *L. brevis*, *L. suebicus*, *L. sakei*, and part of the *L. salivarius* group (Duar et al., 2017b).

Current knowledge does not allow identification of the ecological niche of many *Lactobacillus* spp. and related organisms; examples include organisms of the *L. alimentarius* group, pediococci, *Leuconostoc* spp. and *Weissella* spp. Pediococci, *Leuconostoc* spp. and *Weissella* spp. frequently contaminate spontaneous plant fermentations including sourdoughs (Fig. 4), suggesting an environmental or plant-associated origin of these organisms. However, new species descriptions in the *L. alimentarius* group also include insect isolates, and *Weissella* spp., also occur in the intestine of mammals and cold-water fish (Fusco et al., 2015).

Overlapping the frequency of occurrence of lactobacilli in sourdough with their lifestyles provides a consistent association of lifestyle with sourdough microbiota (Fig. 5). Type I sourdough microbiota are dominated by the insect associated *L. sanfranciscensis* (Figs. 2 and 5). It is noteworthy that only one species is frequently found in sourdough; closely related organisms were rarely (*L. fructivorans*, *L. homohiochii*) or never isolated from sourdoughs. Type II sourdough microbiota are dominated by several vertebrate-host adapted species in the *L. delbrueckii* and *L. reuteri* groups (Figs. 3 and 5). In particular, the species *L.*

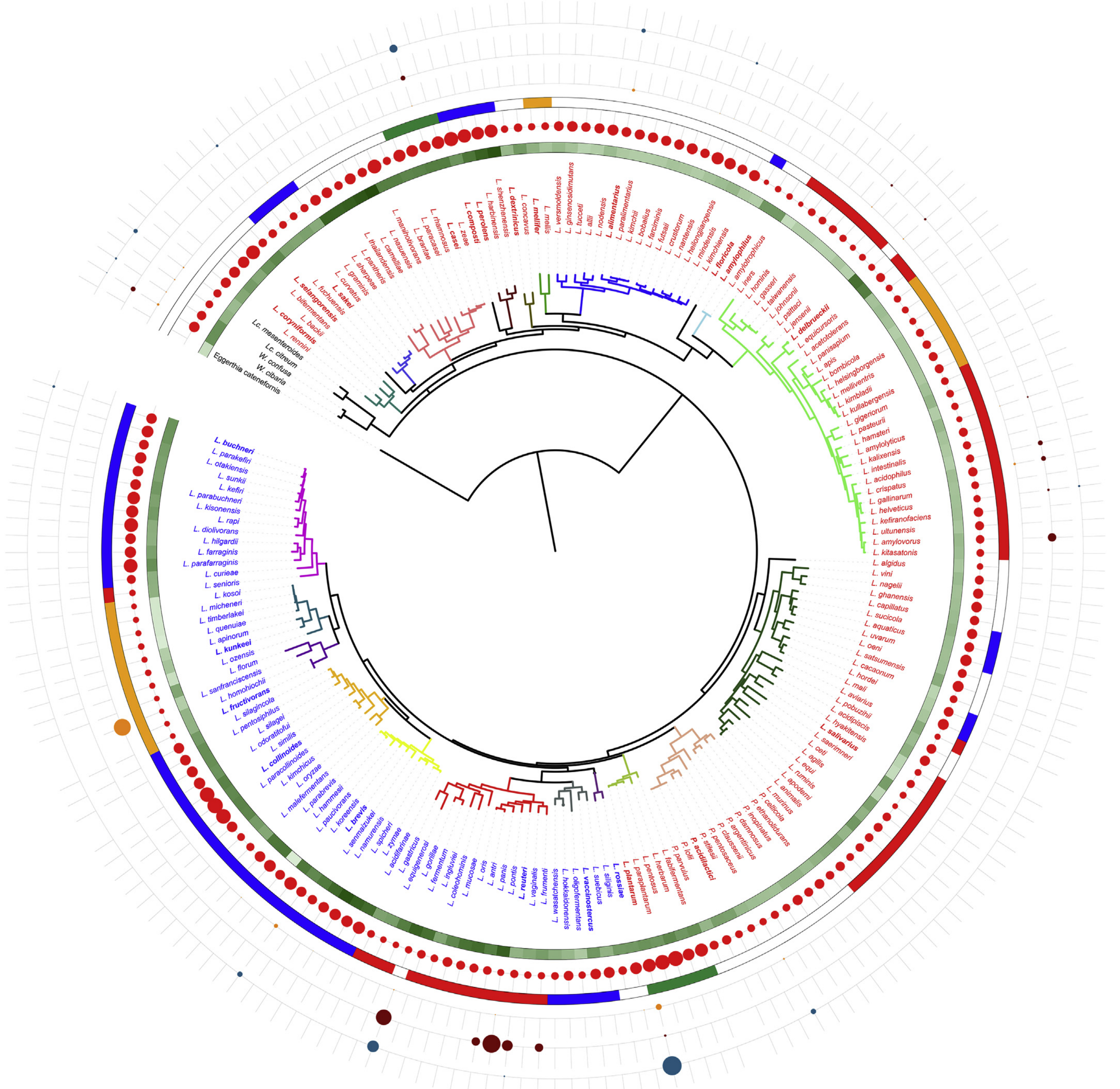

Fig. 5. Phylogenomic analysis of *Lactobacillus*, *Pediococcus*, *Weissella* and *Leuconostoc* species based on the concatenated protein sequences of 99 single-copy core genes. *Eggerthia catenaformis* was used as an outlier for the phylogenetic analysis. The maximum likelihood tree was inferred by PhyML as described (Zheng et al., 2015a) using the 187 species of *Lactobacillus* and *Pediococcus* for which genome sequence data was available on the NCBI database on May 31, 2018, and four *Leuconostoc* and *Weissella* species that occur frequently in sourdough. Members of the same phylogenetic group (Zheng et al., 2015a) are indicated by the same color for branches, and the type strain of each group is printed in bold. The species names of homofermentative species are printed in red; names of heterofermentative species are printed in blue. Outer rings provide information on genomic features, the lifestyle of the species, and their occurrence in sourdoughs as follows: (inside to outside): The color gradient in red represents the GC content of each genome sequence; higher GC contents are indicated by darker shading. The solid circles in brown represent genome sizes; the area of the circle correlates with the genome size. The second ring indicates the natural habitats of the species as vertebrate host-adapted (red), insect-adapted (orange), nomadic (green), environmental (blue) or unassigned (white). The assignment of species to lifestyle was based on Duar et al. (2017b); new species in the *L. kunkeei* and *L. fructivorans* groups were assigned based on the source of isolation; *L. equicursorum* and *L. acetotolerans* were assigned to vertebrate-host adapted lifestyles as intestinal ecosystems represent the only (non-food) origin of the species (Luo et al., 2015; O'Donnell et al., 2013). The orange circles represents the frequency of the occurrence of species in type I sourdoughs; the circle area was calculated with data shown in Fig. 2. The red circles represent the frequency of the occurrence of species in type II sourdoughs; the circle area was calculated with data shown in Fig. 3. The blue circles represent the frequency of the occurrence of species in selected spontaneous sourdoughs and related cereal fermentations; the circle area was calculated with data shown in Fig. 4. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

amylovorus, *L. frumenti* and *L. pontis* are representatives of swine microbiota (Hu et al., 2018; Konstantinov et al., 2006; Leser et al., 2002). *L. reuteri* has specialised to several host-adapted lineages; rodent as well as human lineage strains were identified as stable members of sourdough microbiota (Su et al., 2012). Spontaneous sourdoughs, laboratory sourdoughs, and sourdoughs prepared from cereals other than wheat or rye harbour environmental or nomadic organisms, particularly *L. fermentum*, *L. plantarum* and *L. brevis* (Figs. 4 and 5).

The significant overlap between the natural habitat of lactobacilli and their occurrence in type I sourdoughs, type II sourdoughs, or spontaneous sourdoughs reflects the ecological parameters that shape community assembly in sourdoughs. Environmental or nomadic lactobacilli are most likely to contaminate spontaneous fermentations (Gänzle and Ripari, 2016; Minervini et al., 2015, Figs. 4 and 5). In contrast, if sourdoughs are maintained in bakeries by continuous propagation over several month or years, organisms from intestinal microbiota of insects or vertebrate hosts are likely to contaminate sourdough. In type I and type II sourdoughs, community assembly is thus determined by selection for the most competitive organisms (Gänzle and Ripari, 2016; Lin and Gänzle, 2014). The dominance of a single species, *L. sanfranciscensis*, in type I sourdoughs strongly indicates highly consistent fermentation conditions in bakeries throughout the world, and a very strong selective pressure for the most rapidly growing organisms.

4. Lifestyle-associated metabolic traits impacting bread quality

The fermentation parameters for type I sourdough fermentations select for rapidly growing organisms (Lin and Gänzle, 2014). The genome size of *L. sanfranciscensis* is among the smallest among lactobacilli (Vogel et al., 2011; Zheng et al., 2015a). *L. sanfranciscensis* nevertheless maintains a high rRNA gene density to support rapid growth (Vogel et al., 2011). Growth requirements of *L. sanfranciscensis* with respect to pH, temperature, and NaCl concentrations match conditions in type I sourdough fermentations but *L. sanfranciscensis* does not tolerate low pH or high salt concentrations (Gänzle et al., 1998).

Owing to the small genome size, the metabolism of *L. sanfranciscensis* has little to offer except acid production, gas production and co-factor regeneration. The carbohydrate fermentation pattern of insect adapted lactobacilli is generally very narrow; *L. sanfranciscensis* follow this pattern and growth of some strains is supported only by maltose (Zheng et al., 2015a; Vogel et al., 2011). Strain-specific metabolism of sucrose is supported by extracellular levansucrase activity (Tieking et al., 2005). In sourdough, however, *L. sanfranciscensis* is invariably associated with yeasts; sucrose hydrolysis by yeast invertase (Perlman and Halvorson, 1981) provides glucose and fructose for use by *L. sanfranciscensis*. Heterofermentative hexose metabolism by *L. sanfranciscensis* provides its key contribution to bread quality – acidification to modulate the activity of cereal enzymes (Gänzle, 2014), and CO_2 production to support leavening (Brandt et al., 2004). Cofactor regeneration supports formation of acetate which impacts taste, flavour, and the mould-free shelf life of bread (Hansen and Schieberle, 2005). Of note, beneficial effects of levan production on bread texture are compensated by the associated production of excess acetate (Kaditzky et al., 2008).

Metabolic activities of *L. sanfranciscensis* related to cofactor regeneration include reduction of flavour active aldehydes to alcohols with much lower contribution to bread flavour (Gänzle, 2014; Hansen and Schieberle, 2005), and the reduction of oxidized glutathione (Jänsch et al., 2007). Glutathione and cysteine metabolism also are key elements of the oxidative stress response of *L. sanfranciscensis* (Jänsch et al., 2007; Stetina et al., 2014). The reduction of oxidized glutathione by *L. sanfranciscensis*, however, interferes with disulfide-bond mediated polymerization of gluten proteins (Jänsch et al., 2007). The volume of wheat bread is highly dependent on the quantity and quality of a gluten macropolymer (Wieser, 2007; Reinbold et al., 2008). Comparison of isogenic mutants of *L. sanfranciscensis* differing with respect to glutathione reductase activity indeed demonstrated that reduction of glutathione decreased bread volume when compared to the isogenic glutathione-reducase negative strain (Tang et al., 2017). The glutathione reductase activity of *L. sanfranciscensis* also allows the proteolytic degradation of highly disulfide bonded allergens, e.g. ovotransferrin, that are resistant to proteolysis when the disulfide bond mediated tertiary structure is intact (Loponen et al., 2008).

The potential of *L. sanfranciscensis* to metabolise amino acids or lipids to bioactive metabolites with impact on bread quality is limited. The metabolic flux through the transaminase pathway is low when compared to *L. plantarum* (Vermeulen et al., 2006). Glutaminase, glutamate decarboxylase and arginine deiminase pathway, which mediate acid resistance in lactobacilli (Su et al., 2011; Teixeira et al., 2014), are absent in *L. sanfranciscensis* (Vogel et al., 2011; Zheng et al., 2015a). Accordingly, *L. sanfranciscensis* is rapidly eliminated from sourdough microbiota when fermentation conditions include extended incubation at low pH (Meroth et al., 2003).

Fermentation conditions in type II sourdough impose a second selective pressure, acid stress, as a consequence of prolonged incubation conditions (Lin and Gänzle, 2014; Meroth et al., 2003). Moreover, elevated fermentation temperatures typically select for lactobacilli with an optimum temperature of growth around 37 °C. Vertebrate host adapted lactobacilli, the most abundant representatives of type II sourdough microbiota, are also characterized by a relatively small genome size and a high density of rRNA operons; however, genes coding for acid resistance, adhesion to mucosal surfaces, and biofilm formation are typically required for the vertebrate host adapted lifestyle (Duar et al., 2017b; Frese et al., 2011; Krumbeck et al., 2016). Acid resistance mechanisms of host adapted lactobacilli impact bread quality (Teixeira et al., 2014). Glutaminase activity of sourdough lactobacilli accumulates glutamate, an umami active taste compound (Zhao et al., 2015); further conversion of glutamate generates γ-aminobutyrate, a bioactive compound with relaxing and anti-hypertensive properties (Inoue et al., 2003; Rizzello et al., 2008). Arginine conversion by the arginine deiminase pathway generates ornithine, a precursor compound for formation of the character impact compound of the wheat bread crust odor, 2-acetyl-1-pyrroline (Hansen and Schieberle, 2005; Thiele et al., 2002).

Despite their small genome size, vertebrate host adapted lactobacilli also maintain a relative large spectrum of carbohydrate active enzymes for metabolism of oligosaccharides (Zheng et al., 2015a; Zhao and Gänzle, 2018). The broad carbohydrate fermentation pattern by vertebrate host adapted lactobacilli is used industrially to produce low-FODMAP bread through degradation of raffinose, mannitol, and fructans (Loponen and Gänzle, 2018).

Exopolysaccharide formation by intestinal lactobacilli is essential for formation of biofilms on non-secretory epithelia (Duar et al., 2017b; Frese et al., 2011). Accordingly, the formation of EPS from sucrose is particularly frequent in the host-adapted *L. reuteri* and *L. delbrueckii* groups (Tieking et al., 2003; Zheng et al., 2015a). EPS formation also serves other ecological roles as suggested by the high frequency of glucansucrases in the *L. buchneri* group as well as *Weissella* spp. and *Leuconostoc* spp. The different ecological roles are reflected in the differences of the regulation of gene expression. In *L. reuteri*, reuteransucrase expression is constitutive while dextransucrase expression in *Leuconostoc* spp. is induced by sucrose as well as oxidative stress (Yan et al., 2016). The use of dextran-producing *Weissella* in baking applications is beneficial because *Weissella* spp. often lack mannitol dehydrogenase; dextran formation is thus not associated with production of excess quantities of acetate (Galle and Arendt, 2014; Galle et al., 2012; Katina et al., 2009). Dextransucrase expression in *W. cibaria* 10 M is not induced by sucrose but responds to cold stress (Hu and Gänzle, 2018); however, current data on the regulation of dextransucrase expression in *Weissella* spp. and the ecological role of dextran production are too limited to provide guidance for the optimization of sourdough fermentations.

The reliable occurrence of *L. plantarum* in spontaneous cereal fermentations is linked to the stable association of this species with plants; specific strains of *L. plantarum* were also shown to persist in traditional, back-slopped sourdoughs (Minervini et al., 2015 and 2018). The relatively large genome size and genomic diversity and the corresponding metabolic versatility, however, also enable *L. plantarum* to temporarily colonize insects and vertebrate hosts, allowing probiotic applications (Schwarzer et al., 2016; Siezen and van Hylckama Vlieg, 2011; van den Nieuwboer et al., 2016). With regards to their application in cereal fermentations, strains of *L. plantarum* have an exceptionally broad capacity to metabolise phytochemicals through phenolic acid esterases, decarboxylases, and reductases, and by a diverse array of glycosyl hydrolases (Bai and Gänzle, 2015; Rodríguez et al., 2009; Santamaría et al., 2018). The ability of *L. plantarum* to convert phytochemicals likely relates to its adaptation to plants, and contributes to biochemical conversions in sorghum fermentations as well as in fruit and vegetable fermentations (Filannino et al., 2015; Svensson et al., 2010). The contribution of *L. plantarum* to conversion of phenolic compounds in wheat and rye sourdoughs, or a contribution of these conversions to bread quality remains to be demonstrated.

5. Conclusions and perspectives

Type I sourdoughs are populated by the insect-adapted *L. sanfranciscensis* while type II sourdoughs are populated by vertebrate-host adapted organisms of the *L. delbrueckii* and *L. reuteri* groups. The ecological fitness of lactobacilli in sourdoughs and their impact on bread quality is dependent on niche-specific metabolic traits that accommodate rapid growth and CO_2 production from maltose and sucrose in case of *L. sanfranciscensis*, and amino-acid dependent mechanisms of acid resistance in *L. reuteri* and allied organisms. Remarkably, the stable association of *L. reuteri* group organisms with *L. delbrueckii* group organisms in the intestine of rodents, swine, and poultry is maintained in type II sourdough microbiota (Konstantinov et al., 2006; Leser et al., 2002; Walter, 2008). It is tempting to speculate that the *L. alimentarius* group organisms *L. mindensis*, *L. paralimentarius*, *L. nantensis* and *L. crustorum*, which are often associated with *L. sanfranciscensis* in type I sourdoughs, also share the natural habitat with *L. sanfranciscensis*.

While the composition of sourdough microbiota in traditional sourdoughs is very consistent, literature data also documents that a large diversity of lactobacilli grow in sourdoughs (De Vuyst and Neysens, 2005; De Vuyst et al., 2014; Gobbetti et al., 2016). Alternative choices of fermentation conditions will allow persistence of alternative sourdough microbiota with specific metabolic properties that are not represented by “traditional” sourdough microbiota. For example, co-fermentation of *L. diolivorans* and *L. buchneri* supported propionate formation in sourdoughs (Zhang et al., 2010), and the use of specific grain fractions in sourdough fermentations supports degradation of fructans by lactobacilli with extracellular fructan hydrolases (Loponen et al., 2016; Loponen and Gänzle, 2018). Other proposed applications of sourdough are also dependent on the choice of non-traditional fermentation cultures with specific metabolic properties (Denkova et al., 2014; Gobbetti et al., 2018; Jakob et al., 2012). The use of non-conventional lactic acid bacteria that do not occur in sourdoughs, e.g. *L. buchneri* and *L. diolivorans* (Zhang et al., 2010), propionibacteria or acetic acid bacteria in conjunction with baker's yeast allows adaptation of a traditional food fermentation to the contemporary requirements of industrial food production.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ijfoodmicro.2018.08.019.

References

Bai, Y., Gänzle, M.G., 2015. Conversion of ginsenosides by *Lactobacillus plantarum* studied by liquid chromatography coupled to quadrupole trap mass spectrometry. Food Res. Int. 76, 709–718.

Böcker, G., Stolz, P., Hammes, W.P., 1995. Neue Erkenntnisse zum Ökosystem Sauerteig und zur Physiologie der sauerteigtypischen Stämme *Lactobacillus sanfrancisco* und *Lactobacillus pontis*. Getreide Mehl Brot 49, 370–374.

Boiocchi, F., Porcellato, D., Limonta, L., Picozzi, C., Vigentini, I., Locatelli, D.P., Foschino, R., 2017. Insect frass in stored cereal products as a potential source of *Lactobacillus sanfranciscensis* for sourdough ecosystem. J. Appl. Microbiol. 123, 944–955.

Brandt, M.J., 2007. Sourdough products for convenient use in baking. Food Microbiol. 24, 161–164.

Brandt, J.M., Hammes, W.P., Gänzle, M.G., 2004. Effects of process parameters on growth and metabolism of *Lactobacillus sanfranciscensis* and *Candida humilis* during rye sourdough fermentation. Eur. Food Res. Int. 218, 333–338.

Capelle, S., Guylaine, L., Gänzle, M., Gobbetti, M., 2013. History and social aspects of sourdough. In: Gobbetti, M., Gänzle, M.G. (Eds.), Handbook of Sourdough Biotechnology. Springer, Heidelberg, pp. 1–17.

Corsetti, A., Lavermicocca, P., Morea, M., Baruzzi, F., Tosti, N., Gobbetti, M., 2001. Phenotypic and molecular identification and clustering of lactic acid bacteria and yeasts from wheat (species *Triticum durum* and *Triticum aestivum*) sourdoughs of Southern Italy. Int. J. Food Microbiol. 64, 95–104.

De Vuyst, L., Neysens, P., 2005. The sourdough microflora: biodiversity and metabolic interactions. Trends Food Sci. Technol. 16, 43–56.

De Vuyst, L., Van Kerrebroeck, S., Harth, H., Huys, G., Daniel, H.M., Weckx, S., 2014. Microbial ecology of sourdough fermentations: diverse or uniform? Food Microbiol. 37, 11–29.

Denkova, R., Ilieva, S., Denkova, Z., Georgieva, L., Yordanova, M., Nikolova, D., Evstatieva, Y., 2014. Production of wheat bread without preservatives using sourdough starters. Biotechnol. Biotechnol. Equip. 28, 889–898.

Douillard, F.P., Ribbera, A., Kant, R., Pietilä, T.E., Järvinen, H.M., Messing, M., Randazzo, C.L., Paulin, L., Laine, P., Ritari, J., Caggia, C., Lähteinen, T., Brouns, S.J., Satokari, R., von Ossowski, I., Reunanen, J., Palva, A., de Vos, W.M., 2013. Comparative genomic and functional analysis of 100 *Lactobacillus rhamnosus* strains and their comparison with strain GG. PLoS Genet. 9, e1003683.

Duar, R.M., Frese, S.A., Lin, X.B., Fernando, S.C., Burkey, T.E., Tasseva, G., Peterson, D.A., Blom, J., Wenzel, C.Q., Szymanski, C.M., Walter, J., 2017a. Experimental evaluation of host adaptation of *Lactobacillus reuteri* to different vertebrate species. Appl. Environ. Microbiol. 83, e00132-17.

Duar, R.M., Lin, X.B., Zheng, J., Martino, M.E., Grenier, T., Pérez-Muñoz, M.E., Leulier, F., Gänzle, M., Walter, J., 2017b. Lifestyles in transition: evolution and natural history of the genus *Lactobacillus*. FEMS Microbiol. Rev. 41 (Supp_1), S27–S48.

Ehrmann, M.A., Müller, M.R., Vogel, R.F., 2003. Molecular analysis of sourdough reveals *Lactobacillus mindensis* sp. nov. Int. J. Syst. Evol. Microbiol. 53, 7–13.

El Kafsi, H., Binesse, J., Loux, V., Buratti, J., Boudebbouze, S., Dervyn, R., Kennedy, S., Galleron, N., Quinquis, B., Batto, J.M., Moumen, B., Maguin, E., van de Guchte, M., 2014. *Lactobacillus delbrueckii* ssp. *lactis* and ssp. *bulgaricus*: a chronicle of evolution in action. BMC Genomics 15, 407.

Endo, A., Futagawa-Endo, Y., Sakamoto, M., Kitahara, M., Dicks, L.M., 2010. *Lactobacillus florum* sp. nov., a fructophilic species isolated from flowers. Int. J. Syst. Evol. Microbiol. 60, 2478–2482.

Ferchichi, M., Valcheva, R., Prévost, H., Onno, B., Dousset, X., 2007. Molecular identification of the microbiota of French sourdough using temporal temperature gradient gel electrophoresis. Food Microbiol. 24, 678–686.

Filannino, P., Bai, Y., Di Cagno, R., Gobbetti, M., Gänzle, M.G., 2015. Metabolism of phenolic compounds by *Lactobacillus* spp. during fermentation of cherry juice and broccoli puree. Food Microbiol. 46, 272–279.

Filannino, P., Di Cagno, R., Addante, R., Pontonio, E., Gobbetti, M., 2016. Metabolism of fructophilic lactic acid bacteria isolated from *Apis mellifera* L. bee-gut: a focus on the phenolic acids as external electron acceptors. Appl. Environ. Microbiol. 82, 6899–6911.

Forde, B.M., Neville, B.A., O'Donnell, M.M., Riboulet-Bisson, E., Claesson, M.J., Coghlan, A., Ross, R.P., O'Toole, P.W., 2011. Genome sequences and comparative genomics of two *Lactobacillus ruminis* strains from the bovine and human intestinal tracts. Microb. Cell Factories 10 (Suppl. 1), S13.

Foschino, R., Terraneo, R., Mora, D., Galli, A., 1999. Microbial characterization of sourdoughs for sweet baked products. Ital. J. Food Sci. 11, 19–28.

Frese, S.A., Benson, A.K., Tannock, G.W., Loach, D.M., Kim, J., Zhang, M., Oh, P.L., Heng, N.C., Patil, P.B., Juge, N., Mackenzie, D.A., Pearson, B.M., Lapidus, A., Dalin, E., Tice, H., Goltsman, E., Land, M., Hauser, L., Ivanova, N., Kyrpides, N.C., Walter, J., 2011. The evolution of host specialization in the vertebrate gut symbiont *Lactobacillus reuteri*. PLoS Genet. 7, e1001314.

Fusco, V., Quero, G.M., Cho, G.S., Kabisch, J., Meske, D., Neve, H., Bockelmann, W., Franz, C.M., 2015. The genus *Weissella*: taxonomy, ecology and biotechnological potential. Front. Microbiol. 6, 155.

Galle, S., Arendt, E.K., 2014. Exopolysaccharides from sourdough lactic acid bacteria. Crit. Rev. Food Sci. Nutr. 54, 891–901.

Galle, S., Schwab, C., Dal Bello, F., Coffey, A., Gänzle, M.G., Arendt, E., 2012. Comparison of the impact of dextran and reuteran on the quality of wheat sourdough bread. J. Cereal Sci. 56, 531–537.

Gänzle, M.G., 2014. Enzymatic and bacterial conversions during sourdough fermentation. Food Microbiol. 37, 2–10.

Gänzle, M.G., 2015. Lactic metabolism revisited: metabolism of lactic acid bacteria in food fermentations and food biotechnology. Curr. Opin. Food Sci. 2, 106–117.

Gänzle, M.G., Ripari, V., 2016. Composition and function of sourdough microbiota: from ecological theory to bread quality. Int. J. Food Microbiol. 239, 19–25.

Gänzle, M.G., Ehmann, M., Hammes, W.P., 1998. Modelling of growth of *Lactobacillus sanfranciscensis* and *Candida milleri* in response to process parameters of the sourdough fermentation. Appl. Environ. Microbiol. 64, 2616–2623.

Garofalo, C., Silvestri, G., Aquilanti, L., Clementi, F., 2008. PCR-DGGE analysis of lactic acid bacteria and yeast dynamics during the production processes of three varieties of Panettone. J. Appl. Microbiol. 105, 243–254.

Gassem, M.A., 1999. Study of the micro-organisms associated with the fermented bread (khamir) produced from sorghum in Gizan region, Saudi Arabia. J. Appl. Microbiol. 86, 221–225.

Gobbetti, M., Minervini, F., Pontonio, E., Di Cagno, R., de Angelis, M., 2016. Drivers for the establishment and composition of sourdough lactic acid bacteria. Int. J. Food Microbiol. 239, 3–18.

Gobbetti, M., De Angelis, M., Di Cagno, R., Calasso, M., Archetti, G., Rizzello, C.G., 2018. Novel insights on the functional/nutritional features of the sourdough fermentation. Int. J. Food Microbiol. https://doi.org/10.1016/j.ijfoodmicro.2018.05.018. (Epub ahead of print).

Groenewald, W.H., Van Reenen, C.A., Todorov, S.D., Toit, M.D., Witthuhn, R.C., Holzapfel, W.H., Dicks, L.M.T., 2006. Identification of lactic acid bacteria from vinegar flies based on phenotypic and genotypic characteristics. Am. J. Enol. Vitic. 57, 519–525.

Hamad, S.H., Böcker, G., Vogel, R.F., Hammes, W.P., 1991. Microbiological and chemical analysis of fermented sorghum dough for Kisra production. Appl. Microbiol. Biotechnol. 37, 728–731.

Hamad, S.H., Dieng, M.C., Ehrmann, M.A., Vogel, R.F., 1997. Characterization of the bacterial flora of Sudanese sorghum flour and sorghum sourdough. J. Appl. Microbiol. 83, 764–770.

Hansen, Å., Schieberle, P., 2005. Generation of aroma compounds during sourdough fermentation: applied and fundamental aspects. Trends Food Sci. Technol. 16, 85–94.

Hoang, V.A., Kim, Y.J., Nguyen, N.L., Kim, S.K., Yang, D.C., 2015. *Lactobacillus vespulae* sp. nov., isolated from gut of a queen wasp (*Vespula vulgaris*). Int. J. Syst. Evol. Microbiol. 65, 3326–3332.

Hu, Y., Gänzle, M.G., 2018. Effect of temperature on production of oligosaccharides and dextran by *Weissella cibaria* 10M. Int. J. Food Microbiol. 280, 27–34.

Hu, J., Chen, L., Zheng, W., Shi, M., Liu, L., Xie, C., Wang, X., Niu, Y., Hou, Q., Xu, X., Xu, B., Tang, Y., Zhou, S., Yan, Y., Yang, T., Ma, L., Yan, X., 2018. *Lactobacillus frumenti* facilitates intestinal epithelial barrier function maintenance in early-weaned piglets. Front. Microbiol. 9, 897.

Inoue, K., Shirai, T., Ochiai, H., Kasao, M., Hayakawa, K., Kimura, M., Sansawa, H., 2003. Blood-pressure-lowering effect of a novel fermented milk containing γ-aminobutyric acid (GABA) in mild hypertensives. Eur. J. Clin. Nutr. 57, 490–495.

Jakob, F., Steger, S., Vogel, R.F., 2012. Influence of novel fructans produced by selected acetic acid bacteria on the volume and texture of wheat breads. Eur. Food Res. Technol. 234, 493–499.

Jänsch, A., Korakli, M., Vogel, R.F., Gänzle, M.G., 2007. Glutathione reductase from *Lactobacillus sanfranciscensis* DSM20451T: contribution to oxygen tolerance and thiol-exchange reactions in wheat sourdoughs. Appl. Environ. Microbiol. 73, 4469–4476.

Kaditzky, S., Seitter, M., Hertel, C., Vogel, R.F., 2008. Performance of *Lactobacillus sanfranciscensis* TMW 1.392 and its levansucrase deletion mutant in wheat dough and comparison of their impact on bread quality. Eur. Food Res. Technol. 227, 433–442.

Katina, K., Maina, N.H., Juvonen, R., Flander, L., Johansson, L., Virkki, L., Tenkanen, M., Laitila, A., 2009. *In situ* production and analysis of *Weissella confusa* dextran in wheat sourdough. Food Microbiol. 26, 734–743.

Kitahara, M., Sakata, S., Benno, Y., 2005. Biodiversity of *Lactobacillus sanfranciscensis* strains isolated from five sourdoughs. Lett. Appl. Microbiol. 40, 353–357.

Kline, L., Sugihara, T.F., 1971. Microorganisms of the San Francisco sour dough bread process. II. Isolation and characterization of undescribed bacterial species responsible for the souring activity. Appl. Microbiol. 21, 459–465.

Konstantinov, S.R., Awati, A.A., Williams, B.A., Miller, B.G., Jones, P., Stokes, C.R., Akkermans, A.D., Smidt, H., de Vos, W.M., 2006. Post-natal development of the porcine microbiota composition and activities. Environ. Microbiol. 8, 1191–1199.

Krumbeck, J.A., Marsteller, N.L., Frese, S.A., Peterson, D.A., Ramer-Tait, A.E., Hutkins, R.W., Walter, J., 2016. Characterization of the ecological role of genes mediating acid resistance in *Lactobacillus reuteri* during colonization of the gastrointestinal tract. Environ. Microbiol. 18, 2172–2184.

Lattanzi, A., Minervini, F., Di Cagno, R., Diviccaro, A., Antonielli, L., Cardinali, G., Cappelle, S., De Angelis, M., Gobbetti, M., 2013. The lactic acid bacteria and yeast microbiota of eighteen sourdoughs used for the manufacture of traditional Italian sweet leavened baked goods. Int. J. Food Microbiol. 163, 71–79.

Leser, T.D., Amenuvor, J.Z., Jensen, T.K., Lindecrona, R.H., Boye, M., Møller, K., 2002. Culture-independent analysis of gut bacteria: the pig gastrointestinal tract microbiota revisited. Appl. Environ. Microbiol. 68, 673–690.

Lhomme, E., Lattanzi, A., Dousset, X., Minervini, F., De Angelis, M., Lacaze, G., Onno, B., Gobbetti, M., 2015. Lactic acid bacterium and yeast microbiotas of sixteen French traditional sourdoughs. Int. J. Food Microbiol. 215, 161–170.

Lhomme, E., Urien, C., Legrand, J., Dousset, X., Onno, B., Sicard, D., 2016. Sourdough microbial community dynamics: an analysis during French organic bread-making processes. Food Microbiol. 52, 41–50.

Lin, X.B., Gänzle, M.G., 2014. Effect of lineage-specific metabolic traits of *Lactobacillus reuteri* on sourdough microbial ecology. Appl. Environ. Microbiol. 80, 5782–5789.

Liu, T., Li, Y., Chen, J., Sadiq, F.A., Zhang, G., Li, Y., He, G., 2016. Prevalence and diversity of lactic acid bacteria in Chinese traditional sourdough revealed by culture dependent and pyrosequencing approaches. LWT Food Sci. Technol. 68, 91–97.

Loponen, J., Gänzle, M.G., 2018. Use of sourdough in low-FODMAP baking. Foods 7, 96.

Loponen, J., König, K., Wu, J., Gänzle, M.G., 2008. Breakdown of egg white proteins in wheat sourdoughs: ovotransferrin degradation is dependent on the thiol redox metabolism of *Lactobacillus*. J. Agric. Food Chem. 56, 3357–3362.

Loponen, J., Mikola, M., Sibakov, J., 2016. An Enzyme Exhibiting Fructan Hydrolase Activity Patent WO2017220864A1, 2016.

Luo, Y.H., Yang, C., Wright, A.D., He, J., Chen, D.W., 2015. Responses in ileal and cecal bacteria to low and high amylose/amylopectin ratio diets in growing pigs. Appl. Microbiol. Biotechnol. 99, 10627–10638.

Macklaim, J.M., Gloor, G.B., Anukam, K.C., Cribby, S., Reid, G., 2011. At the crossroads of vaginal health and disease, the genome sequence of *Lactobacillus iners* AB-1. Proc. Natl. Acad. Sci. U. S. A. 108 (Suppl. 1), 4688–4695.

Madoroba, E., Steenkamp, E.T., Theron, J., Scheirlinck, I., Cloete, T.E., Huys, G., 2011. Diversity and dynamics of bacterial populations during spontaneous sorghum fermentations used to produce ting, a South African food. Syst. Appl. Microbiol. 34, 227–234.

Martino, M.E., Bayjanov, J.R., Caffrey, B.E., Wels, M., Joncour, P., Hughes, S., Gillet, B., Kleerebezem, M., van Hijum, S.A., Leulier, F., 2016. Nomadic lifestyle of *Lactobacillus plantarum* revealed by comparative genomics of 54 strains isolated from different habitats. Environ. Microbiol. 18, 4974–4989.

Meroth, C.B., Walter, J., Hertel, C., Brandt, M.J., Hammes, W.P., 2003. Monitoring the bacterial population dynamics in sourdough fermentation processes by using PCR-denaturing gradient gel electrophoresis. Appl. Environ. Microbiol. 69, 475–482.

Michel, E., Monfort, C., Deffrasnes, M., Guezenec, S., Lhomme, E., Barret, M., Sicard, D., Dousset, X., Onno, B., 2016. Characterization of relative abundance of lactic acid bacteria species in French organic sourdough by cultural, qPCR and MiSeq high-throughput sequencing methods. Int. J. Food Microbiol. 239, 35–43.

Minervini, F., Di Cagno, R., Lattanzi, A., De Angelis, M., Antonielli, L., Cardinali, G., Cappelle, S., Gobbetti, M., 2012. Lactic acid bacterium and yeast microbiotas of 19 sourdoughs used for traditional/typical Italian breads: interactions between ingredients and microbial species diversity. Appl. Environ. Microbiol. 78, 251–264.

Minervini, F., Celano, G., Lattanzi, A., Tedone, L., De Mastro, G., Gobbetti, M., De Angelis, M., 2015. Lactic acid bacteria in durum wheat flour are endophytic components of the plant during its entire life cycle. Appl. Environ. Microbiol. 81, 6736–6748.

Minervini, F., Lattanzi, A., Dinardo, F.R., De Angelis, M., Gobbetti, M., 2018. Wheat endophytic lactobacilli drive the microbial and biochemical features of sourdoughs. Food Microbiol. 70, 162–171.

Müller, M.R.A., Wolfrum, G., Stolz, P., Ehrmann, M.A., Vogel, R.F., 2001. Monitoring the growth of *Lactobacillus* species during a rye flour fermentation. Food Microbiol. 18, 217–227.

Muyanja, C.M., Narvhus, J.A., Treimo, J., Langsrud, T., 2003. Isolation, characterisation and identification of lactic acid bacteria from bushera: a Ugandan traditional fermented beverage. Int. J. Food Microbiol. 80, 201–210.

O'Donnell, M.M., Harris, H.M., Jeffery, I.B., Claesson, M.J., Younge, B., O' Toole, P.W., Ross, R.P., 2013. The core faecal bacterial microbiome of Irish thoroughbred racehorses. Lett. Appl. Microbiol. 57, 492–501.

Palla, M., Cristani, C., Giovannetti, M., Agnolucci, M., 2017. Identification and characterization of lactic acid bacteria and yeasts of PDO Tuscan bread sourdough by culture dependent and independent methods. Int. J. Food Microbiol. 250, 19–26.

Perlman, D., Halvorson, H.O., 1981. Distinct repressible mRNAs for cytoplasmic and secreted yeast invertase are encoded by a single gene. Cell 25, 525–536.

Pontonio, E., Di Cagno, R., Mahony, J., Lanera, A., De Angelis, M., van Sinderen, D., Gobbetti, M., 2017. Sourdough authentication: quantitative PCR to detect the lactic acid bacterial microbiota in breads. Sci. Rep. 7, 624.

Raimondi, S., Amaretti, A., Rossi, M., Fall, P.A., Tabanelli, G., Gardini, F., Montanari, C., 2017. Evolution of microbial community and chemical properties of a sourdough during the production of Colomba, an Italian sweet leavened baked product. LWT Food Sci. Technol. 86, 31–39.

Randazzo, C.L., Heilig, H., Restuccia, C., Giudici, P., Caggia, C., 2005. Bacterial population in traditional sourdough evaluated by molecular methods. J. Appl. Microbiol. 99, 251–258.

Reinbold, J., Rychlik, M., Asam, S., Wieser, H., Koehler, P., 2008. Concentrations of total glutathione and cysteine in wheat flour as affected by sulfur deficiency and correlation to quality parameters. J. Agric. Food Chem. 56, 6844–6850.

Ripari, V., Gänzle, M.G, Berardi, E., 2016. Evolution of sourdough microbiota in spontaneous sourdoughs started with different plant materials. Int. J. Food Microbiol. 232, 35–42.

Rizzello, C.G., Cassone, A., Di Cagno, R., Gobbetti, M., 2008. Synthesis of angiotensin I-converting enzyme (ACE)-inhibitory peptides and γ-aminobutyric acid (GABA) during sourdough fermentation by selected lactic acid bacteria. J. Agric. Food Chem. 56, 6936–6943.

Rodríguez, H., Curiel, J.A., Landete, J.M., de las Rivas, B., López de Felipe, F., Gómez-Cordovés, C., Mancheño, J.M., Muñoz, R., 2009. Food phenolics and lactic acid bacteria. Int. J. Food Microbiol. 132, 79–90.

Rosenquist, H., Hansen, Å., 2000. The microbial stability of two bakery sourdoughs made from conventionally and organically grown rye. Food Microbiol. 17, 241–250.

Santamaría, L., Reverón, I., López de Felipe, F., de Las Rivas, B., Muñoz, R., 2018. Unravelling the reduction pathway as an alternative metabolic route to hydroxycinnamate decarboxylation in *Lactobacillus plantarum*. Appl. Environ. Microbiol. 84, e01123-18.

Scheirlinck, I., Van der Meulen, R., Van Schoor, A., Vancanneyt, M., De Vuyst, L., Vandamme, P., Huys, G., 2007. Influence of geographical origin and flour type on diversity of lactic acid bacteria in traditional Belgian sourdoughs. Appl. Environ. Microbiol. 73, 6262–6269.

Schwarzer, M., Makki, K., Storelli, G., Machuca-Gayet, I., Srutkova, D., Hermanova, P., Martino, M.E., Balmand, S., Hudcovic, T., Heddi, A., Rieusset, J., Kozakova, H., Vidal, H., Leulier, F., 2016. *Lactobacillus plantarum* strain maintains growth of infant mice during chronic undernutrition. Science 351, 854–857.

Sekwati-Monang, B., Gänzle, M.G., 2011. Microbiological and chemical characterisation of ting, a sorghum-based sourdough product from Botswana. Int. J. Food Microbiol. 150, 115–121.

Siezen, R.J., van Hylckama Vlieg, J.E., 2011. Genomic diversity and versatility of *Lactobacillus plantarum*, a natural metabolic engineer. Microb. Cell Factories 10 (Suppl. 1), S3.

Spicher, G., 1987. Die Mikrobiologie des Sauerteiges: XXII: Die in Weizensauerteigen vorkommenden Laktobazillen. Z. Lebensm. Unters. Forsch. 300–303.

Stetina, M., Behr, J., Vogel, R.F., 2014. The transcriptional response of *Lactobacillus sanfranciscensis* DSM 20451^T and its *tcyB* mutant lacking a functional cystine transporter to diamide stress. Appl. Environ. Microbiol. 80, 4114–4125.

Strohmar, W., Diekmann, H., 1992. Die Mikroflora eines Langzeit-Sauerteiges. Z. Lebensm. Unters. Forsch. 194, 536–540.

Su, M.S.-W., Schlicht, S., Gänzle, M.G., 2011. Contribution of glutamate decarboxylase in *Lactobacillus reuteri* to acid resistance and persistence in sourdough fermentation. Microb. Cell Factories 10 (Suppl. 1), S8.

Su, M.S.-W., Oh, P.L., Walter, J., Gänzle, M.G., 2012. Intestinal origin of sourdough *Lactobacillus reuteri* isolates as revealed by phylogenetic, genetic, and physiological analysis. Appl. Environ. Microbiol. 78, 6777–6780.

Sugihara, T.F., 1978. Microbiology of the soda cracker process II. Pure culture fermentation studies. J. Food Prot. 41, 980–982.

Svensson, L., Sekwati-Monang, B., Lutz, D.L., Schieber, A., Gänzle, M.G., 2010. Phenolic acids and flavonoids in nonfermented and fermented red sorghum (*Sorghum bicolor* (L.) Moench). J. Agric. Food Chem. 58, 9214–9220.

Tang, K.X., Zhao, J.C., Gänzle, M.G., 2017. Effect of glutathione on the taste and texture of type I sourdough bread. J. Agric. Food Chem. 65, 4321–4328.

Techo, S., Miyashita, M., Shibata, C., Tanaka, N., Wisetkhan, P., Visessanguan, W., Tanasupawat, S., 2016. *Lactobacillus ixorae* sp. nov., isolated from a flower (West-Indian jasmine). Int. J. Syst. Evol. Microbiol. 66, 5500–5505.

Teixeira, J.S., Seeras, A., Sanchez-Maldonado, A.F., Zhang, C., Su, M.S.-W., Gänzle, M.G., 2014. Glutamine, glutamate, and arginine-based acid resistance in *Lactobacillus reuteri*. Food Microbiol. 42, 172–180.

Thiele, C., Gänzle, M.G., Vogel, R.F., 2002. Contribution of sourdough lactobacilli, yeast, and cereal enzymes to the generation of amino acids in dough relevant for bread flavor. Cereal Chem. 79, 45–51.

Tieking, M., Korakli, M., Ehrmann, M.A., Gänzle, M.G., Vogel, R.F., 2003. In situ production of EPS by intestinal and cereal isolates of lactic acid bacteria during sourdough fermentation. Appl. Environ. Microbiol. 69, 945–952.

Tieking, M., Ehrmann, M.A., Vogel, R.F., Gänzle, M.G., 2005. Molecular and functional characterization of a levansucrase from *Lactobacillus sanfranciscensis*. Appl. Microbiol. Biotechnol. 66, 655–663.

Todorov, S.D., Holzapfel, W.H., 2015. Traditional cereal fermented foods as sources of functional microorganisms. In: Holzapfel, W.H. (Ed.), Advances in Fermented Foods and Beverages. Woodhead Publishing, pp. 123–153.

van den Nieuwboer, M., van Hemert, S., Claassen, E., de Vos, W.M., 2016. *Lactobacillus plantarum* WCFS1 and its host interaction: a dozen years after the genome. Microb. Biotechnol. 9, 452–465.

Van der Meulen, R., Scheirlink, L., Van Schoor, A., Huys, G., Vancanneyt, M., Vandamme, P., de Vuyst, L., 2007. Population dynamics and metabolite target analysis of lactic acid bacteria during laboratory fermentations of wheat and spelt sourdoughs. Appl. Environ. Microbiol. 73, 4741–4750.

Vera, A., Ly-Chatain, M.H., Rigobello, V., Demarigny, Y., 2012. Description of a French natural wheat sourdough over 10 consecutive days focussing on the lactobacilli present in the microbiota. Antonie Van Leeuwenhoek 101, 369–377.

Vermeulen, N., Gänzle, M.G., Vogel, R.F., 2006. Influence of peptide supply and co-substrates on phenylalanine metabolism of *Lactobacillus sanfranciscensis* DSM20451T and *Lactobacillus plantarum* TMW1.468. J. Agric. Food Chem. 54, 3832–3839.

Viiard, E., Mihhalevski, A., Rühka, T., Paalme, T., Sarand, I., 2013. Evaluation of the microbial community in industrial rye sourdough upon continuous back-slopping propagation revealed *Lactobacillus helveticus* as the dominant species. J. Appl. Microbiol. 114, 404–442.

Viiard, E., Bessmeltseva, M., Simm, J., Talve, T., Aaspõllu, A., Paalme, T., Sarand, I., 2016. Diversity and stability of lactic acid bacteria in rye sourdoughs of four bakeries with different propagation parameters. PLoS One 11, e0148325.

Vogel, R.F., Knorr, R., Müller, M.R.A., Steudel, U., Gänzle, M.G., Ehrmann, M.A., 1999. Non-dairy lactic fermentations: the cereal world. Antonie Van Leeuwenhoek 76, 403–411.

Vogel, R.F., Pavlovic, M., Ehrmann, M.A., Wiezer, A., Liesegang, H., Offschanka, S., Voget, S., Angelov, A., Böcker, G., Liebl, W., 2011. Genomic analysis reveals *Lactobacillus sanfranciscensis* as stable element in traditional sourdoughs. Microb. Cell Factories 10 (Suppl. 1), S6.

Walter, J., 2008. Ecological role of lactobacilli in the gastrointestinal tract: implications for fundamental and biomedical research. Appl. Environ. Microbiol. 74, 4985–4996.

Walter, J., Maldonado-Gómez, M.X., Martínez, I., 2018. To engraft or not to engraft: an ecological framework for gut microbiome modulation with live microbes. Curr. Opin. Biotechnol. 49, 129–139.

Wieser, H., 2007. Chemistry of gluten proteins. Food Microbiol. 24, 115–1159.

Wong, C.N., Ng, P., Douglas, A.E., 2011. Low-diversity bacterial community in the gut of the fruitfly *Drosophila melanogaster*. Environ. Microbiol. 13 (1889-1800).

Yan, M., Han, J., Xu, X., Liu, L., Gao, C., Zheng, H., Chen, Y., Tao, Y., Zhou, H., Li, Y., Wu, Z., 2016. Gsy, a novel glucansucrase from *Leuconostoc mesenteroides*, mediates the formation of cell aggregates in response to oxidative stress. Sci. Rep. 6, 38122.

Yang, H., Liu, T., Zhang, G., Chen, J., Gu, J., Yuan, L., He, G., 2017. Genotyping of *Lactobacillus sanfranciscensis* isolates from Chinese traditional sourdoughs by multi-locus sequence typing and multiplex RAPD-PCR. Int. J. Food Microbiol. 258, 50–57.

Zhang, C., Brandt, M.J., Schwab, C., Gänzle, M.G., 2010. Propionic acid production by cofermentation of *Lactobacillus buchneri* and *Lactobacillus diolivorans* in sourdough. Food Microbiol. 27, 390–395.

Zhang, G., Sadiq, F.A., Zhu, L., Liu, T., Yang, H., Wang, X., He, G., 2015. Investigation of microbial communities of Chinese sourdoughs using culture-dependent and DGGE approaches. J. Food Sci. 80, M2535–M2542.

Zhao, X., Gänzle, M.G., 2018. Genetic and phenotypic analysis of carbohydrate metabolism and transport in *Lactobacillus reuteri*. Int. J. Food Microbiol. 272, 12–21.

Zhao, C., Kinner, M., Wismer, W., Gänzle, M.G., 2015. Effect of glutamate-accumulation during sourdough fermentation with *L. reuteri* on the taste of bread and sodium-reduced bread. Cereal Chem. 92, 224–230.

Zheng, J., Ruan, L., Sun, M., Gänzle, M.G., 2015a. Genomic analysis of lactobacilli and pediococci demonstrates that phylogeny matches ecology and physiology. Appl. Environ. Microbiol. 81, 7233–7243.

Zheng, J., Zhao, X., Lin, X.B., Gänzle, M.G., 2015b. Comparative genomics of *Lactobacillus reuteri* from sourdough reveals adaptation of an intestinal symbiont to food fermentations. Sci. Rep. 5, 18234.