REVIEW ARTICLE

FOOD FRONTIERS Open Access

Are spontaneously fermented plant-based foods potential sources of transferable antibiotic resistance genes?

Kinga Jasiak | Daniel Amund [ORCID]

School of Life Sciences, Faculty of Health and Life Sciences, Coventry University, Coventry, UK

Correspondence
Daniel Amund, School of Life Sciences, Faculty of Health and Life Sciences, Coventry University, Priory Street, Coventry CV1 5FB, UK.
Email: ac1139@coventry.ac.uk

Abstract

Spontaneously fermented plant-based foods are highly valued for their unique organoleptic characteristics and presumed health benefits. However, because natural (spontaneous) fermentation does not involve the employment of starter cultures, the safety of spontaneously fermented plant-based products is not easily controlled. This review examines the presence of antibiotic resistance determinants in lactic acid bacteria (LAB) from plant-based, naturally fermented foods. Phenotypic resistance to clinically relevant antibiotics has been widely observed in LAB from a variety of food types. The larger proportion of the resistance traits reported in this review can be considered intrinsic to LAB. However, some of the identified traits, especially resistance genes to tetracycline and erythromycin, have the potential for horizontal spread. Further molecular characterization is required to determine the genetic basis of detected resistance traits that have only been assessed using phenotypic methods. The implementation of novel safety measures in the production of spontaneously fermented plant-based foods should be considered in the future.

KEYWORDS
antimicrobial resistance, fermented foods, food safety, lactic acid bacteria, plant-based foods, spontaneous fermentation

1 | INTRODUCTION

Fermented foods can be defined as foods or beverages produced through controlled microbial growth and the conversion of food components through enzymatic action (Marco et al., 2017). The process of fermentation involves the production of various metabolites that can inhibit the growth and survival of unfavorable microorganisms (Ross et al., 2002). Hence, throughout history, it has played a crucial role in the preservation of otherwise quickly perishable foods. Although fundamental, extended shelf life is not the only rationale for fermenting foodstuffs. Fermentation provides other benefits such as desirable

organoleptic characteristics (e.g., taste, aroma, texture) or increased functionality of raw materials (e.g., use of barley for beer making). Recently, increased attention has also been given to the nutritional and health value of fermented products. The suggested mechanisms by which fermented foods might provide health benefits include changes in the nutritional content of the raw product, synthesis of bioactive peptides, modification of gut microbiota, and immune system stimulation (Dimidi et al., 2019; Marco et al., 2021).

Lactic acid fermentation depends on the transformations induced by lactic acid bacteria (LAB), that is, the conversion of carbohydrates into organic acids. The decrease in pH following these reactions inhibits

the growth of most spoilage and pathogenic microorganisms (Bautista-Gallego et al., 2020). Additionally, some LAB produce bacteriocins—antimicrobial peptides that may further inhibit undesirable microbial growth. The key genera classified as LAB include *Lactobacillus, Lactococcus, Enterococcus, Streptococcus, Leuconostoc, Weissella,* and *Pediococcus* (Ross et al., 2002).

The raw materials used for lactic acid fermentation encompass a diverse range of foods such as cereals, fruits, vegetables, milk, meat, and fish. Some of the widely known examples of fermented foods include cheese, yoghurt, kimchi, tempeh, sourdough, and kombucha (Tamang & Kailasapathy, 2010).

Foods can be fermented either by spontaneous (natural) fermentation or with the use of starter cultures (Hutkins, 2006). Natural fermentation relies on the autochthonous (indigenous) microorganisms present in the substrates. Being the oldest way of carrying out fermentation, this method has been utilized in the manufacture of many traditional products. Although some meat and dairy products are spontaneously fermented, spontaneous fermentation is more prevalent in vegetable, fruit, and cereal produce. Several requirements must be met for an uncontrolled fermentation to succeed, for example, suitable environment and presence of desirable microorganisms (Holzapfel, 2014). However, even when adequate conditions are provided, the fermentation outcomes may not meet the safety and quality expectations.

The unpredictability of spontaneously fermented produce has resulted in the widespread use of starter cultures, especially on an industrial scale. Fermentation with starter cultures involves inoculation of raw materials with a defined microbial culture so that it dominates the microflora and creates expected changes (Capozzi et al., 2017). The use of the starter shortens the fermentation period, simultaneously allowing for better control of sensory, safety, and quality aspects (Dolci et al., 2020). Bacterial starters may be used for a variety of foods but are more commonly utilized in the mass production of fermented meat and dairy products such as yoghurts, cheeses, or sausages. To be authorized as a starter culture, bacterial strains must meet certain safety standards, which in the European Union are regulated by the European Food Safety Authority (EFSA). One of the criteria requires that microorganisms intended for food use must lack transferable antibiotic resistance (AR) genes (EFSA, 2012; Laulund et al., 2017).

AR poses one of the greatest global public health challenges and has been extensively researched in pathogenic species. However, limited studies have investigated AR in commensal bacteria (MacLean & San Millan, 2019). Bacteria in food might act as AR reservoirs, a phenomenon related most likely to antibiotic misuse in the food chain (WHO, 2011). Not all resistance traits can be transferred, however. Intrinsic (inherent) resistance, described as resistance typical to all strains of given species or genus, is unlikely to be spread. Conversely, acquired resistance (unless emanating from genomic mutation) presents a risk of being horizontally transferred. Such resistance involves the acquisition of genes located on conjugative or mobilizable plasmids and transposons from the bacterial donor (von Wintersdorff et al., 2016).

Fermented foods, an abundant source of LAB and other microbes, might constitute a vehicle for antimicrobial-resistant bacteria, particularly if the products are consumed without prior heat treatment. In that case, bacteria in possession of AR are likely to be carried over to the gut (Hummel et al., 2007). As a consequence, ingested resistant bacteria add to the pool of AR genes present in the large intestine and therefore increase the likelihood of transfer to pathogenic bacteria. Spontaneously fermented foods present a particular concern because fermentative bacteria are naturally present in the matrix and thus, they are not subject to safety assurance (Capozzi et al., 2017; Laulund et al., 2017). Due to the direct association of antibiotic use with livestock (and consequently fermented animal products), less attention has been given to investigate AR in plant-based fermented products. Many plant-based products are not fermented with a starter culture. Therefore, this review aims to examine the potential of LAB from plant-based spontaneously fermented foods as sources of transferable AR genes (Figure 1).

2 | OVERVIEW OF SPONTANEOUSLY FERMENTED PLANT-BASED FOODS

A wide variety of plant raw material, including fruits, vegetables, and cereals, are spontaneously fermented worldwide. Traditionally, this has been used in their preservation (Ogrodowczyk & Drabinska, 2021; Tamang et al., 2020). Some of the more well-known products include kimchi, sauerkraut, table olives, and pickled vegetables (lacto-fermented pickles). Examples of spontaneously fermented plant-based foods, including the main microorganisms involved, are summarized in Table 1. Recent reviews on the subject have been published by Ashaolu and Reale (2020), Torres et al. (2020), and Voidarou et al. (2021).

There is increasing interest in plant-based fermented foods, as they are sources of potentially probiotic microorganisms, and present nondairy alternatives for the delivery of probiotics (Ogrodowczyk & Drabinska, 2021). Furthermore, such foods produced through spontaneous fermentation by LAB can be consumed without further heat treatment, possibly because of the low pH, making them a source of live microorganisms. However, it is not uncommon for fermented vegetables to be heat processed in order to further increase their shelf life (Rezac et al., 2018).

3 | POTENTIAL OF SPONTANEOUSLY FERMENTED PLANT-BASED FOODS AS SOURCES OF TRANSFERABLE AR GENES

The multiplication of bacteria that occurs during fermentation means that there would be an increase in the abundance of AR genes contained in the fermented foods. If any of the AR genes are mobile, then this increased abundance would raise the chances of horizontal gene transfer (HGT) occurring between the LAB and other bacteria in the gastrointestinal tract (Toth et al., 2020).

A selection of studies published between 2011 and 2020 are summarized in Table 2, showing AR traits in LAB from spontaneously fermented plant-based products. The foods from which LAB were
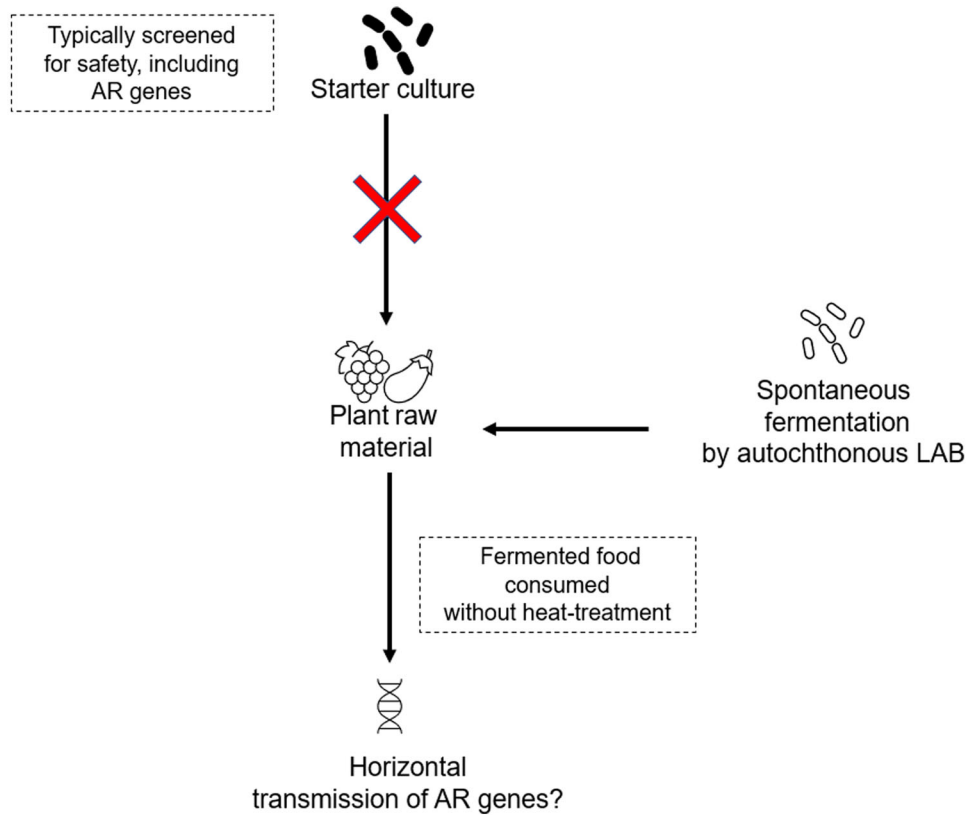
FIGURE 1 Schematic representation of the aim of this review

TABLE 1 Examples of spontaneously fermented plant-based foods

Fermented food type	Region	Main raw materials	Key lactic acid bacteria involved	References
Kimchi	Korea	Chinese cabbage (Napa cabbage), other vegetables, spices	*Lactobacillus* spp., *Leuconostoc* spp., *Weissella* spp., *Lactococcus* spp.	Patra et al. (2016)
Sauerkraut	Europe, United States	Cabbage	*Leuconostoc mesenteroides, Lb. sakei, Lb. brevis, Pediococcus pentosaceus, Lb. plantarum*	Tamang et al. (2016) Zabat et al. (2018)
Table olives	Italy, Spain, Greece	Olives	*Lb. pentosus, Lb. plantarum*	Perpetuini et al. (2020)
Lacto-fermented cucumber pickles	Europe, United States, Canada	Cucumbers	*Lb. plantarum, Lb. brevis, Ln. mesenteroides, Pediococcus acidilactici*	Tamang et al. (2016) Behera et al. (2020)
Boza	Turkey, Bulgaria	Cereals (wheat, maize, millet, rice)	*Lactobacillus* spp., *Pediococcus* spp., *Lactococcus* spp., *Leuconostoc* spp.	Tamang et al. (2016)
Tempoyak	Malaysia, Indonesia	Durian fruit	*Lb. brevis, Lb. fermentum, Ln. mesenteroides, Lb. mali*	Swain et al. (2014) Behera et al. (2020)

isolated include kimchi (Dey et al., 2019; Lee et al., 2011; Lee et al., 2016; Son et al., 2017; Won et al., 2020), sauerkraut (Touret et al., 2018; Yu et al., 2013), table olives (Argyri et al., 2013; Benitez-Cabello et al., 2019; Botta et al., 2014; Casado Munoz et al., 2014; Guantario et al., 2018), boza (Gotcheva et al., 2018; Valledor et al., 2020), tem-

poyak (Chuah et al., 2016; Khalil et al., 2018), fermented juices and nectar (Nawaz et al., 2011; Somashekaraiah et al., 2019; Xu et al., 2018), various fermented fruits and vegetables (Damodharan et al., 2015; Mahasneh et al., 2015; Michalak et al., 2018; Nawaz et al., 2011; Tang et al., 2018; Zielinska et al., 2015), and various "pickles" (Huang et al.,

TABLE 2 Antibiotic resistance traits in lactic acid bacteria from spontaneously fermented plant-based foods

Investigated product	Investigated microorganisms	Phenotypic resistance traits detected	References
Boza (fermented cereal beverage)	*Lactobacillus plantarum*	VAN AMP TET CHL STR GEN RFP CIP	Gotcheva et al. (2018)
	Enterococcus faecium	ERY	Valledor et al. (2020)
Makdoos (fermented aubergines)	*Lb. plantarum, Lb. pentosus, Lb. brevis, Lb. salivarius*	AMP CIP ERY KAN GEN STR TET TMP	Mahasneh et al. (2015)
Pickled cabbage	*Lb. rhamnosus, Lb. plantarum, Lb. johnsonii*	STR VAN TET GEN	Zielinska et al. (2015)
Pickled cucumber	*Lb. plantarum, Lb. casei, Lb. brevis*		
Fermented cornelian cherry	*Lb. plantarum, Lb. casei*	CIP STR AMK GENATM FOX SXT	Tang et al. (2018)
Fermented curly kale	*Weissella hellenica, W. cibaria, Leuconostoc mesenteroides, Lb. curvatus, Lb. plantarum, Lb. brevis, Lb. paraplantarum, Pediococcus pentosaceus, P. acidilactici, Lactococcus lactis*	KAN STR NA TMPBC PIR PEN	Michalak et al. (2018)
Fermented fruit and vegetable juices	*W. cibaria, Ln. mesenteroides, Lc. lactis, P. pentosaceus, E. hirae, Lc. garvieae, W. confusa, Lb. plantarum, Streptococcus thermophilus*	AMP PEN NOR STR AMK ERY LVX	Xu et al. (2018)
Fermented radish	*Lb. plantarum, Lb. pentosus, Lb. fermentum*	KAN GEN VAN STR	Damodharan et al. (2015)
Fermented vegetable	*Lb. animalis, Lb. brevis, Lb. parabuchneri, Lb. plantarum, Lb. salivarius, Lb. vaginalis*	ERY TET	Nawaz et al. (2011)
Jiang shui (fermented vegetable drink)	*Lb. plantarum*	TET	
pickle	*Lb. salivarius*	ERY TET PEN	
Gochu-jangajji (Korean green chili pickled pepper	*Lb. plantarum*	GEN KAN STR	Niu et al. (2019)
Jangajji (Korean pickled vegetable)	*Lb. paraplantarum*	KAN STR CIP	Son et al. (2018)
Kimchi	*W. confusa*	SPT	Dey et al. (2019)
	Lb. plantarum, Ln. mesenteroides	SPT VAN	Lee et al. (2016)
	Lb. sakei	AMP GEN KAN STR PMB PEN	Won et al. (2020)
	Lb. sakei, Lb. plantarum	GEN STR CIP	Lee et al. (2011)
	Lb. plantarum	GEN STR KAN CIP	Son et al. (2017)
Mustard pickles	*Lb. plantarum, Lb. pentosus*	PEN CEF CLO NOV VAN PMB RFP TET KAN GEN NEO STR	Huang et al. (2017)
Neera (fermented coconut palm nectar)	*Lb. brevis, E. lactis, E. durans, Ln. lactis, E. faecium*	KAN CLI AMP GEN ERY CHL	Somashekaraiah et al. (2019)
Table olives	*Ln. mesenteroides, Lb. pentosus, Ln. pseudomesenteroides, Lb. plantarum, Lb. paraplantarum, Lb. paracasei* subsp. *paracasei*	KAN TET GEN AMP CHL VAN	Argyri et al. (2013)
	Lb. pentosus, Lb. plantarum	GEN VAN CLI FOT KAN NA STR	Benitez-Cabello et al. (2019)
	Lb. plantarum, Lb. pentosus, Ln. mesenteroides	KAN GEN TET	Botta et al. (2014)
	Lb. pentosus, Ln. pseudomesenteroides	STR VAN TEC TMP SXT CXM CIP TET CLI	Casado Muñoz et al. (2014)
	Lb. pentosus, Lb. coryniformis	AMP ERY	Guantario et al. (2018)
Pickles	*Lactobacillus* spp.	ERY CIP CHL KAN	Pan et al. (2011)

(Continues)

TABLE 2 (Continued)

Investigated product	Investigated microorganisms	Phenotypic resistance traits detected	References
Sauerkraut	*Leuconostoc* spp., *Lactobacillus* spp.	AMP CHL CLI GEN KAN STR TET ERY	Touret et al. (2018)
	Lb. plantarum	KAN GEN VAN STR PMB	Yu et al. (2013)
Tempoyak (fermented durian fruit)	*Fructobacillus durionis, Lb. plantarum*	VAN NA SF SXT TMP CIP BC CEF STR TET KAN AMC CAR CHL AMP	Chuah et al. (2016)
	Lb. plantarum, Lb. crispatus, Lb. reuteri, Lb. fermentum, Lb. pentosus	ERY VAN TET	Khalil et al. (2018)

Abbreviations: AMC, amoxicillin/clavulanic acid; AMK, amikacin; AMP, ampicillin; ATM, aztreonam; BC, bacitracin; CAR, carbenicillin; CEF, cephalothin; CHL, chloramphenicol; CIP, ciprofloxacin; CLI, clindamycin; CLO, cloxacillin; CXM, cefuroxime; ERY, erythromycin; FOT, cefotaxime; FOX, cefoxitin; GEN, gentamicin; KAN, kanamycin; LVX, levofloxacin; NA, nalidixic acid; NEO, neomycin; NOR, norfloxacin; NOV, novobiocin; PEN, penicillin G; PIR, pirlimycin; PMB, polymyxin B; RFP, rifampicin; SF, sulfafurazole; SPT, spectinomycin; STR, streptomycin; SXT, sulfamethoxazole/trimethoprim; TEC, teicoplanin; TET, tetracycline; TMP, trimethoprim; VAN, vancomycin.

2017; Nawaz et al., 2011; Niu et al., 2019; Pan et al., 2011; Son et al., 2018).

Studies were largely based on examining the probiotic potential of LAB isolated from the products, as part of safety evaluation. The choice of antibiotics tested for susceptibility/resistance appears to be an arbitrary selection of clinically important antibiotics. Most of the studies assessed AR/susceptibility traits only phenotypically, through methods such as disk diffusion, agar dilution, broth microdilution, and E-test. However, a few studies additionally assessed the genotypic basis of resistance through polymerase chain reaction (PCR)-based methods (Casado Munoz et al., 2014; Gotcheva et al., 2018; Nawaz et al., 2011; Pan et al., 2011; Valledor et al., 2020).

Based on the studies included in this review, LAB isolated from spontaneously fermented plant-based foods have shown resistance to antibiotics from a wide range of antibiotic classes. These classes include aminoglycosides (amikacin, gentamicin, kanamycin, neomycin, streptomycin), cephalosporins (cephalothin, cefuroxime, cefotaxime, cefoxitin), quinolones (ciprofloxacin, levofloxacin, nalidixic acid, norfloxacin), phenicols (chloramphenicol), macrolides (erythromycin), glycopeptides (vancomycin, teicoplanin), lincosamides (clindamycin, pirlimycin), penicillins (amoxicillin, carbenicillin, cloxacillin, penicillin G), monobactams (aztreonam), aminocoumarins (novobiocin), polymyxins (polymyxin B), polypeptides (bacitracin), sulfonamides (sulfafurazole, sulfamethoxazole), aminocyclitols (spectinomycin), antifolates (trimethoprim), rifamycins (rifampicin), and tetracyclines (tetracycline).

It can be observed that certain AR traits are commonly present in LAB from spontaneously fermented plant-based foods. Whether or not these traits can be transferred to other nonpathogenic or pathogenic bacteria depends on the genetic basis underpinning the AR. Intrinsic resistance is the natural ability of the bacteria to thrive in the presence of antibiotic; it is unrelated to prior antibiotic exposure and does not result from gene acquisition (Fajardo et al., 2008). Such resistance is conveyed by naturally occurring genes located on the chromosome and has minimal transfer potential. However, genes responsible for intrinsic resistance could potentially be spread if flanked by insertion sequences (Das et al., 2020; Razavi et al., 2020).

In LAB, certain resistance traits may be generally classified as inherent to this bacterial group, although differences in tolerance may arise between species (Mathur & Singh, 2005). Antibi-

otics to which LAB appear to be naturally tolerant include bacitracin, cefoxitin, ciprofloxacin, sulphadiazine, teicoplanin, trimethoprim/sulfamethoxazole, kanamycin, streptomycin, and vancomycin among others (Danielsen & Wind, 2003). Likewise, it was demonstrated elsewhere that LAB tend to tolerate aminoglycosides (amikacin, kanamycin, streptomycin, gentamicin), glycopeptides (vancomycin, teicoplanin), and quinolones (nalidixic acid, ciprofloxacin) (Coppola et al., 2005).

Aside from the wide range of intrinsic resistance displayed by LAB, this bacterial group also has the potential to acquire resistance to many relevant antimicrobials. Bacteria can acquire new genes either via mutation of existing genes (usually nontransferable) or by horizontal transmission (Devanga Ragupathi et al., 2019). The primary mechanism of HGT is thought to be conjugation. Conjugative horizontal transmission involves the direct transfer of mobile genomic elements (MGE)—potential carriers of AR genes, from donor to recipient bacterium (Gazzola et al., 2012). Tolerance to antimicrobials that given bacteria are normally susceptible to indicates that the trait might have been acquired via HGT. Such traits are likely to be subsequently transmitted to other bacteria.

Generally, LAB should be sensitive toward cell wall synthesis inhibitors (mostly penicillins including ampicillin and penicillin G) and protein synthesis inhibitors such as tetracyclines, chloramphenicol, erythromycin, and clindamycin (Federici et al., 2014). Specific resistance traits observed in LAB isolated from spontaneously fermented plant-based foods are discussed below.

3.1 | Resistance to aminoglycosides

Resistance to one or more aminoglycoside antibiotic was reported in most of the articles herein reviewed. Tolerance to aminoglycosides in LAB is attributed to limited drug uptake originating from the lack of cytochrome-mediated electron transport and is regarded as nontransferable (Charteris et al., 2001). However, recently Jaimee and Halami (2016) have argued that the high-level resistance to aminoglycosides may be associated with potentially transmissible genes coding for aminoglycoside-modifying enzymes. So far, no studies have demonstrated the transfer of such resistance in nonpathogenic LAB, whereas

in enterococci, a filter-mating experiment resulted in the successful dissemination of streptomycin/gentamicin resistance gene from the donor to the recipient enterococci (Sparo et al., 2012). In the study by Somashekaraiah et al. (2019), *Enterococcus* species isolated from Neera showed phenotypic resistance to aminoglycosides—kanamycin and gentamicin (Table 2). Molecular characterization may be needed to establish the potential transferability of the resistance.

3.2 | Resistance to vancomycin

In LAB, tolerance to glycopeptides such as vancomycin and teicoplanin is regarded as a common inherent trait (especially in *Lactobacillus* spp.), resulting from the alterations in the chemical structure of the peptidoglycan in the cell wall (Das et al., 2020; Juárez-Castelán et al., 2019). Vancomycin inhibits cell wall synthesis (Gotcheva et al., 2018).

However in enterococci, vancomycin resistance is not an intrinsic feature, being mediated by the *van*(A) gene located on a plasmid (DeLisle & Perl, 2003). Furthermore, there is some evidence demonstrating that *van*(A) may be passed from enterococci to other LAB, as in the case of *Lactobacillus acidophilus*, which acquired transposon-mediated *van*(A) in vivo in the mouse gut (Mater et al., 2008). Among the studies in this review, the presence of vancomycin resistance was reported only in lactobacilli. However, the intrinsic nature of the trait cannot be ascertained without genotypic analysis. In the study by Valledor et al. (2020), PCR analysis of the *Enterococcus faecium* strain isolated from boza was unable to detect various *van* genes (A, B, C, D, E, and G), and this corresponded with the vancomycin sensitivity phenotype. On the other hand, Gotcheva et al. (2018) detected *van*(A) in *Lb. plantarum* strains isolated from boza (Table 2).

3.3 | Resistance to quinolones

Casado Muñoz et al. (2014) reported a high percentage of ciprofloxacin resistance in *Lb. pentosus* strains isolated from naturally fermented olives. Molecular screening of the quinolone resistance-determining region disproved the presence of any mutated genes that would be flanked by insertion sequences, integrons, or transposons. Thus, the trait was considered intrinsic. Chromosomally encoded efflux pumps, such as NorA, MepA, and MdeA, were likely responsible for the intrinsic resistance, and the genes were widely detected (Casado Munoz et al., 2014). Similarly, other studies also suggest that quinolone tolerance is inherent to LAB, although the underlying mechanism is not well-understood (Hummel et al., 2007).

3.4 | Resistance to penicillins

It has been established that spontaneous chromosomal mutations may induce tolerance to penicillin antibiotics, resulting from reduced receptor binding (Danielsen & Wind, 2003). However, it may be also conferred by the plasmid-located *bla*(Z) gene as observed in *Lb. plan-*

tarum (Aquilanti et al., 2007). Yet, because *bla*(Z) is seldom detected in LAB, there is a relatively low chance that resistances reported in this review are transmissible (Rizzotti et al., 2005). For instance, in Pan et al. (2011) 1%–4% of strains were ampicillin resistant and further genotypic screening was carried out to determine the characteristics of the resistance. No isolates were found to possess *bla*(Z) genes. This may therefore suggest that a different resistance mechanism was in place. Nevertheless, in other studies where penicillin resistance was observed, genotypic characterization would be required to exclude the possibility of *bla*(Z) presence.

3.5 | Resistance to tetracycline

At least 11 tetracycline resistance determinants coding either for ribosomal protection proteins or efflux pumps were previously identified in LAB (Lahtinen et al., 2009). These are often associated with MGE and thus are likely to be horizontally spread. For instance, the filter mating experiment by Gevers et al. (2003) led to the successful transfer of the *tet*(M) gene from lactobacilli to *E. faecalis* and *Lc. lactis*. Here, several studies reported the presence of tetracycline resistance in examined foods. In Nawaz et al. (2011), genotypic characterization indicated the presence of *tet*(M) and *tet*(S) tetracycline resistance determinants. Moreover, the subsequent filter mating of *tet*(M)-positive lactobacilli resulted in a transfer to *E. faecalis*, once more confirming the potential transferability of tetracycline resistance. However, tolerance to this antibiotic may be also mediated by efflux pump genes, which are nontransmissible due to their chromosomal location. This can be seen in the case of Casado Muñoz et al. (2014), where the high frequency of phenotypic tetracycline resistance in *Lb. pentosus* from olives was attributed to multidrug efflux pumps.

3.6 | Resistance to chloramphenicol

Tolerance to chloramphenicol in LAB might be associated with the plasmid-borne *cat* gene and although there is no empiric evidence on the transfer of *cat* between LAB species, studies suggest that it is feasible. For instance, Lin et al. (1996) described a high similarity of *cat* gene from *Lactobacillus reuteri* to *cat* from *Staphylococcus aureus* located on a plasmid. Therefore, it could be hypothesized that *Lb. reuteri* acquired the gene through horizontal transmission that brings the possibility of further spread from resistant LAB to other bacteria. In this review, some studies have reported chloramphenicol resistance. However, in the study by Pan et al. (2011), although chloramphenicol resistance in LAB from pickles was detected phenotypically, genotypic characterization did not detect the cat_{pIP501} gene, implying the existence of different AR genes in the investigated strains. It has been suggested recently that chloramphenicol resistance in LAB is in fact predominantly located on the chromosome, which would explain the lack of plasmid-encoded cat_{pIP501} in analyzed isolates (Abriouel et al., 2015). Indeed, in earlier reports, the *cat* determinant has been detected on the chromosome in *Lb. pentosus* and *Lb. plantarum* (Hummel et al., 2007). These

chromosomal genes are not homologous to plasmid-encoded *cat* and are therefore considered nontransferable. Thus, it may be concluded that HGT of chloramphenicol resistance in LAB from fermented foods is possible, yet relatively rare (Abriouel et al., 2015).

3.7 | Resistance to erythromycin

Erythromycin resistance in LAB has been associated with the most frequently plasmid-located *erm*(B) gene (Fraqueza, 2015). Among the studies in the review where tolerance to erythromycin was reported, only Nawaz et al. (2011) performed a genotypic analysis that resulted in the identification of the *erm*(B) determinant. Furthermore, the detected gene was later acquired from resistant lactobacilli by *E. faecalis* in filter-mating trials. The transferability of the *erm*(B) gene in LAB is strongly supported by other literature. For instance, the trait was successfully transferred from *Leuconostoc* to *E. faecalis* strains on the surface of Monte Veronese cheese (Flórez et al., 2016). Moreover, it has been demonstrated elsewhere that *erm*(B) from LAB can also be transmitted to nonlactic acid, pathogenic bacteria such as *Listeria* spp., which presents a major threat to potential antibiotic therapy (Toomey et al., 2009).

3.8 | Resistance to clindamycin

Macrolide–lincosamide–streptogramin (MLS) phenotype is a resistance mechanism that confers the resistance to lincosamides (clindamycin), macrolides (erythromycin), and streptogramin (Casado Muñoz et al., 2014). It is mediated by a mutation in *erm* genes resulting from continuous antibiotic exposure, and because *erm* genes are mostly plasmid located, there is a risk of spread (Pana, 2012). On the other hand, multidrug transporters in LAB such as LmrA might also be responsible for the resistance to clindamycin and up to 20 other antibiotics (Poelarends et al., 2002). Because these traits are located on the chromosome, they are classified as nontransmissible. In this review, clindamycin resistance was documented in some studies. Among them, some *Lactobacillus* and *Enterococcus* isolates were both erythromycin and clindamycin resistant, which indicates the possibility of the aforementioned MLS phenotype presence (Pana, 2012).

4 | CONCLUSION

Based on the findings of reviewed studies, spontaneously fermented plant-based foods may act as reservoirs of transferable AR genes and potentially contribute to the problem of AR. However, many studies tend to only carry out phenotypic characterization of AR traits. Molecular analysis is necessary to determine the genetic basis of observed phenotypes and distinguish between intrinsic and acquired/transferable traits. As highlighted, even some seemingly intrinsic traits might be transmissible. Transferability of AR genes from a donor to a recipient also needs to be demonstrated, through filter-

mating experiments (Das et al., 2020). However, in vitro experiments may not adequately replicate the conditions in the gut, which may influence HGT (Polit et al., 2018).

Metagenomic sequencing approaches may be useful in examining the presence of mobile AR genes in spontaneously fermented foods, and have been applied in studies such as Leech et al. (2020), Toth et al. (2020), and Toth et al. (2021). However, these approaches would rely on robust databases that are representative of the wider microbial and genomic diversity that can occur in foods produced by spontaneous fermentation compared to those produced by starter culture (Leech et al., 2020).

Nevertheless, it can be inferred that there is a need to manage AR in spontaneously fermented plant-based foods. A strategy would be the employment of starter cultures in the manufacturing process. However, this could result in the loss of the unique organoleptic properties associated with natural fermentation (Capozzi et al., 2017). Recent advances enable the development of multistrain starters containing microbes native to the spontaneously fermented food. Therefore, a similar flavor could be obtained with these cultures (Maqueda et al., 2011).

Moreover, safety from an AR perspective could also be controlled by subjecting the fermented foods to heat or other treatments that reduce or eliminate microorganisms (Tamang et al., 2020). This would, however, also potentially impact organoleptic properties and certainly affect the live microbial content of these foods and health benefits that may accrue from live microorganisms. Overall, the presence of AR in fermented plant-based foods is a multifaceted problem that requires addressing not only the manufacturing but also broader issues such as antibiotic overuse in humans and livestock.

ORCID
Daniel Amund https://orcid.org/0000-0002-5639-2790

REFERENCES
Abriouel, H., Casado Muñoz, M. D. C., Lerma, L. L., Montoro, B. P., Bockelmann, W., Pichner, R., Kabisch, J., Cho, G., Franz, C. M., Gálvez, A., & Benomar, N. (2015). New insights in antibiotic resistance of *Lactobacillus* species from fermented foods. *Food Research International*, 78, 465–481.

Aquilanti, L., Garofalo, C., Osimani, A., Silvestri, G., Vignaroli, C., & Clementi, F. (2007). Isolation and molecular characterization of antibiotic-resistant lactic acid bacteria from poultry and swine meat products. *Journal of Food Protection*, 70, 557–565.

Argyri, A. A., Zoumpopoulou, G., Karatzas, K. G., Tsakalidou, E., Nychas, G. E., Panagou, E. Z., & Tassou, C. C. (2013). Selection of potential probiotic lactic acid bacteria from fermented olives by in vitro tests. *Food Microbiology*, *33*(2), 282–291.

Ashaolu, T. J., & Reale, A. (2020). A holistic review on Euro-Asian lactic acid bacteria fermented cereals and vegetables. *Microorganisms*, *8*(8), 1176.

Bautista-Gallego, J., Medina, E., Sánchez, B., Benítez-Cabello, A., & Arroyo-López, F. (2020). Role of lactic acid bacteria in fermented vegetables. *Grasas y Aceites*, *71*(2), e358.

Behera, S. S., El Sheikha, A. F., Hammami, R., & Kumar, A. (2020). Traditionally fermented pickles: How the microbial diversity associated with their nutritional and health benefits? *Journal of Functional Foods*, *70*, 103971.

Benítez-Cabello, A., Calero-Delgado, B., Rodríguez-Gómez, F., Garrido-Fernández, A., Jiménez-Díaz, R., & Arroyo-López, F. N. (2019). Biodiversity and multifunctional features of lactic acid bacteria isolated from table olive biofilms. *Frontiers in Microbiology*, *10*, 836.

Botta, C., Langerholc, T., Cencič, A., & Cocolin, L. (2014). *In vitro* selection and characterization of new probiotic candidates from table olive microbiota. *PLoS ONE*, *9*(4), e94457.

Capozzi, V., Fragasso, M., Romaniello, R., Berbegal, C., Russo, P., & Spano, G. (2017). Spontaneous food fermentations and potential risks for human health. *Fermentation*, *3*(4), 49.

Casado Muñoz, M. C., Benomar, N., Lerma, L. L., Gálvez, A., & Abriouel, H. (2014). Antibiotic resistance of *Lactobacillus pentosus* and *Leuconostoc pseudomesenteroides* isolated from naturally-fermented Aloreña table olives throughout fermentation process. *International Journal of Food Microbiology*, *172*, 110–118.

Charteris, W. P., Kelly, P. M., Morelli, L., & Collins, J. K. (2001). Gradient diffusion antibiotic susceptibility testing of potentially probiotic lactobacilli. *Journal of Food Protection*, *64*(12), 2007–2014.

Chuah, L., Shamila-Syuhada, A. K., Liong, M. T., Rosma, A., Thong, K. L., & Rusul, G. (2016). Physio-chemical, microbiological properties of tempoyak and molecular characterisation of lactic acid bacteria isolated from tempoyak. *Food Microbiology*, *58*, 95–104.

Coppola, R., Succi, M., Tremonte, P., Reale, A., Salzano, G., & Sorrentino, E. (2005). Antibiotic susceptibility of *Lactobacillus rhamnosus* strains isolated from Parmigiano Reggiano cheese. *Le Lait*, *85*(3), 193–204.

Damodharan, K., Palaniyandi, S. A., Yang, S. H., & Suh, J. (2015). *In vitro* probiotic characterization of *Lactobacillus* strains from fermented radish and their anti-adherence activity against enteric pathogens. *Canadian Journal of Microbiology*, *61*(11), 837–850.

Danielsen, M., & Wind, A. (2003). Susceptibility of *Lactobacillus* spp. to antimicrobial agents. *International Journal of Food Microbiology*, *82*(1), 1–11.

Das, D. J., Shankar, A., Johnson, J. B., & Thomas, S. (2020). Critical insights into antibiotic resistance transferability in probiotic *Lactobacillus*. *Nutrition*, *69*, 110567.

DeLisle, S., & Perl, T. M. (2003). Vancomycin-resistant enterococci: A road map on how to prevent the emergence and transmission of antimicrobial resistance. *Chest*, *123*(5), 504S–518S.

Devanga Ragupathi, N. K., Muthuirulandi Sethuvel, D. P., Gajendran, R., Anandan, S., Walia, K., & Veeraraghavan, B. (2019). Horizontal transfer of antimicrobial resistance determinants among enteric pathogens through bacterial conjugation. *Current Microbiology*, *76*(6), 666–672.

Dey, D. K., Koo, B. G., Sharma, C., & Kang, S. C. (2019). Characterization of *Weissella confusa* DD_A7 isolated from kimchi. *LWT - Food Science and Technology*, *111*, 663–672.

Dimidi, E., Cox, S. R., Rossi, M., & Whelan, K. (2019). Fermented foods: Definitions and characteristics, impact on the gut microbiota and effects on gastrointestinal health and disease. *Nutrients*, *11*(8), 1806.

Dolci, P., Ferrocino, I., Giordano, M., Pramotton, R., Vernetti-Prot, L., Zenato, S., & Barmaz, A. (2020). Impact of *Lactococcus lactis* as starter culture on microbiota and metabolome profile of an Italian raw milk cheese. *International Dairy Journal*, *110*, 104804.

European Food Safety Authority (EFSA). (2012). Guidance on the assessment of bacterial susceptibility to antimicrobials of human and veterinary importance. *EFSA Journal*, *10*, 2740–2749.

Fajardo, A., Martínez-Martín, N., Mercadillo, M., Galán, J. C., Ghysels, B., Matthijs, S., Cornelis, P., Wiehlmann, L., Tümmler, B., Baquero, F., & Martínez, J. L. (2008). The neglected intrinsic resistome of bacterial pathogens. *PLoS ONE*, *3*(2), e1619.

Federici, S., Ciarrocchi, F., Campana, R., Ciandrini, E., Blasi, G., & Baffone, W. (2014). Identification and functional traits of lactic acid bacteria isolated from Ciauscolo salami produced in Central Italy. *Meat Science*, *98*(4), 575–584.

Flórez, A. B., Campedelli, I., Delgado, S., Alegría, Á., Salvetti, E., Felis, G. E., Mayo, B., & Torriani, S. (2016). Antibiotic susceptibility profiles of dairy *Leuconostoc*, analysis of the genetic basis of atypical resistances and transfer of genes *in vitro* and in a food matrix. *PLoS ONE*, *11*(1), e0145203.

Fraqueza, M. J. (2015). Antibiotic resistance of lactic acid bacteria isolated from dry-fermented sausages. *International Journal of Food Microbiology*, *212*, 76–88.

Gazzola, S., Fontana, C., Bassi, D., & Cocconcelli, P. S. (2012). Assessment of tetracycline and erythromycin resistance transfer during sausage fermentation by culture-dependent and -independent methods. *Food Microbiology*, *30*(2), 348–354.

Gevers, D., Huys, G., & Swings, J. (2003). *In vitro* conjugal transfer of tetracycline resistance from *Lactobacillus* isolates to other Gram-positive bacteria. *FEMS Microbiology Letters*, *225*(1), 125–130.

Gotcheva, V., Petrova, G., Petkova, M., Kuzmanova, Y., & Angelov, A. (2018). Molecular and *in vitro* assessment of some probiotic characteristics of amylolytic *Lactobacillus plantarum* strains from Bulgarian fermented products. *Engineering in Life Sciences*, *18*(11), 820–830.

Guantario, B., Zinno, P., Schifano, E., Roselli, M., Perozzi, G., Palleschi, C., Uccelletti, D., & Devirgiliis, C. (2018). *In vitro* and *in vivo* selection of potentially probiotic lactobacilli from Nocellara Del Belice table olives. *Frontiers in Microbiology*, *9*, 595.

Holzapfel, W. (Ed.). (2014). *Advances in fermented foods and beverages: Improving quality, technologies and health benefits.* Elsevier.

Huang, J. Y., Kao, C. Y., Liu, W. S., & Fang, T. J. (2017). Characterization of high exopolysaccharide-producing *Lactobacillus* strains isolated from mustard pickles for potential probiotic applications. *International Microbiology*, *20*(2), 75–84.

Hummel, A. S., Hertel, C., Holzapfel, W. H., & Franz, C. M. (2007). Antibiotic resistances of starter and probiotic strains of lactic acid bacteria. *Applied and Environmental Microbiology*, *73*(3), 730–739.

Hutkins, R. (2006). *Microbiology and technology of fermented foods.* Blackwell Publishing.

Jaimee, G., & Halami, P. M. (2016). Emerging resistance to aminoglycosides in lactic acid bacteria of food origin – An impending menace. *Applied Microbiology and Biotechnology*, *100*(3), 1137–1151.

Juárez-Castelán, C., García-Cano, I., Escobar-Zepeda, A., Azaola-Espinosa, A., Álvarez-Cisneros, Y., & Ponce-Alquicira, E. (2019). Evaluation of the bacterial diversity of Spanish-type chorizo during the ripening process using high-throughput sequencing and physicochemical characterization. *Meat Science*, *150*, 7–13.

Khalil, E. S., Abd Manap, M., Mustafa, S., Alhelli, A. M., & Shokryazdan, P. (2018). Probiotic properties of exopolysaccharide-producing *Lactobacillus* strains isolated from tempoyak. *Molecules*, *23*(2), 398.

Lahtinen, S. J., Boyle, R. J., Margolles, A., Frías, R., & Gueimonde, M. (2009). Safety assessment of probiotics. In D. Charalampopoulos & R. A. Rastall (Eds.), *Prebiotics and probiotics science and technology* (pp. 1193–1225). Springer-Verlag.

Laulund, S., Wind, A., Derkx, P. M. F., & Zuliani, V. (2017). Regulatory and safety requirements for food cultures. *Microorganisms*, *5*, 28.

Leech, J., Cabrero-Rubio, R., Walsh, A. M., Macori, G., Walsh, C. J., Barton, W., Finnegan, L., Crispie, F., O'Sullivan, O., Claesson, M. J., & Cotter, P. D. (2020). Fermented-food metagenomics reveals substrate-associated

differences in taxonomy and health-associated and antibiotic resistance determinants. *mSystems*, 5(6), e00522-20.

Lee, H., Yoon, H., Ji, Y., Kim, H., Park, H., Lee, J., Shin, H., & Holzapfel, W. (2011). Functional properties of *Lactobacillus* strains isolated from kimchi. *International Journal of Food Microbiology*, 145(1), 155–161.

Lee, K. W., Shim, J. M., Park, S., Heo, H., Kim, H., Ham, K., & Kim, J. H. (2016). Isolation of lactic acid bacteria with probiotic potentials from kimchi, traditional Korean fermented vegetable. *LWT – Food Science and Technology*, 71, 130–137.

Lin, C. F., Fung, Z. F., Wu, C. L., & Chung, T. C. (1996). Molecular characterization of a plasmid-borne (pTC82) chloramphenicol resistance determinant (cat-TC) from *Lactobacillus reuteri* G4. *Plasmid*, 36(2), 116–124.

MacLean, R., & San Millan, A. (2019). The evolution of antibiotic resistance. *Science*, 365(6458), 1082–1083.

Mahasneh, S. A., Mahasneh, A. M., & Hamdan, S. (2015). Probiotic properties of *Lactobacillus* species isolated from local traditional fermented products. *Jordan Journal of Biological Sciences*, 8(2), 81–87.

Maqueda, M., Pérez-Nevado, F., Regodón, J. A., Zamora, E., Álvarez, M. L., Rebollo, J. E., & Ramírez, M. (2011). A low-cost procedure for production of fresh autochthonous wine yeast. *Journal of Industrial Microbiology and Biotechnology*, 38(3), 459–469.

Marco, M. L., Heeney, D., Binda, S., Cifelli, C. J., Cotter, P. D., Foligné, B., Gänzle, M., Kort, R., Pasin, G., Pihlanto, A., Smid, E. J., & Hutkins, R. (2017). Health benefits of fermented foods: Microbiota and beyond. *Current Opinion in Biotechnology*, 44, 94–102.

Marco, M. L., Sanders, M. E., Gänzle, M., Arrieta, M. C., Cotter, P. D., De Vuyst, L., Hill, C., Holzapfel, W., Lebeer, S., Merenstein, D., Reid, G., Wolfe, B. E., & Hutkins, R. (2021). The International Scientific Association for Probiotics and Prebiotics (ISAPP) consensus statement on fermented foods. *Nature Reviews Gastroenterology & Hepatology*, 18(3), 196–208.

Mater, D. D., Langella, P., Corthier, G., & Flores, M. (2008). A probiotic *Lactobacillus* strain can acquire vancomycin resistance during digestive transit in mice. *Journal of Molecular Microbiology and Biotechnology*, 14(1-3), 123–127.

Mathur, S., & Singh, R. (2005). Antibiotic resistance in food lactic acid bacteria – A review. *International Journal of Food Microbiology*, 105(3), 281–295.

Michalak, M., Gustaw, K., Waśko, A., & Polak-Berecka, M. (2018). Composition of lactic acid bacteria during spontaneous curly kale (*Brassica oleracea* var. *sabellica*) fermentation. *Microbiological Research*, 206, 121–130.

Nawaz, M., Wang, J., Zhou, A., Ma, C., Wu, X., Moore, J. E., Cherie Millar, B., & Xu, J. (2011). Characterization and transfer of antibiotic resistance in lactic acid bacteria from fermented food products. *Current Microbiology*, 62(3), 1081–1089.

Niu, K., Kothari, D., Cho, S., Han, S., Song, I., & Kim, S. (2019). Exploring the probiotic and compound feed fermentative applications of *Lactobacillus plantarum* SK1305 isolated from Korean green chili pickled pepper. *Probiotics and Antimicrobial Proteins*, 11(3), 801–812.

Ogrodowczyk, A. M., & Drabinska, N. (2021). Crossroad of tradition and innovation – The application of lactic acid fermentation to increase the nutritional and health-promoting potential of plant-based food products – A review. *Polish Journal of Food and Nutrition Sciences*, 71(2), 107–134.

Pan, L., Hu, X., & Wang, X. (2011). Assessment of antibiotic resistance of lactic acid bacteria in Chinese fermented foods. *Food Control*, 22(8), 1316–1321.

Pana, M. (Ed.). (2012). *Antibiotic resistant bacteria: A continuous challenge in the new millennium*. InTech.

Patra, J. K., Das, G., Paramithiotis, S., & Shin, H. (2016). Kimchi and other widely consumed traditional fermented foods of Korea: A review. *Frontiers in Microbiology*, 7, 1493.

Perpetuini, G., Prete, R., Garcia-Gonzalez, N., Alam, M. K., & Corsetti, A. (2020). Table olives more than a fermented food. *Foods*, 9, 178.

Poelarends, G., Mazurkiewicz, P., & Konings, W. (2002). Multidrug transporters and antibiotic resistance in *Lactococcus lactis*. *Biochimica et Biophysica Acta*, 1555(1-3), 1–7.

Polit, A., Yang, H., & Amund, D. (2018). Investigating the transmissibility of *tet*(W) in bifidobacterial exposed to acid and bile stress. *Bioscience of Microbiota, Food and Health*, 37(2), 39–43.

Razavi, M., Kristiansson, E., Flach, C., & Larsson, D. G. J. (2020). The association between insertion sequences and antibiotic resistance genes. *mSphere*, 5(5), e00418-20.

Rezac, S., Kok, C. R., Hermann, M., & Hutkins, R. (2018). Fermented foods as a dietary source of live organisms. *Frontiers in Microbiology*, 9, 1785.

Rizzotti, L., Simeoni, D., Cocconcelli, P., Gazzola, S., Dellaglio, F., & Torriani, S. (2005). Contribution of enterococci to the spread of antibiotic resistance in the production chain of swine meat commodities. *Journal of Food Protection*, 68(5), 955–965.

Ross, R. P., Morgan, S., & Hill, C. (2002). Preservation and fermentation: Past, present and future. *International Journal of Food Microbiology*, 79(1-2), 3–16.

Somashekaraiah, R., Shruthi, B., Deepthi, B. V., & Sreenivasa, M. Y. (2019). Probiotic properties of lactic acid bacteria isolated from Neera: A naturally fermenting coconut palm nectar. *Frontiers in Microbiology*, 10, 1382.

Son, S., Jeon, H., Jeon, E. B., Lee, N., Park, Y., Kang, D., & Paik, H. (2017). Potential probiotic *Lactobacillus plantarum* Ln4 from kimchi: Evaluation of *β*-galactosidase and antioxidant activities. *LWT – Food Science and Technology*, 85, 181–186.

Son, S., Yang, S., Jeon, H., Yu, H., Lee, N., Park, Y., & Paik, H. (2018). Antioxidant and immunostimulatory effect of potential probiotic *Lactobacillus paraplantarum* SC61 isolated from Korean traditional fermented food, jangajji. *Microbial Pathogenesis*, 125, 486–492.

Sparo, M., Urbizu, L., Solana, M. V., Pourcel, G., Delpech, G., Confalonieri, A., Ceci, M., & Sanchez Bruni, S. F. (2012). High-level resistance to gentamicin: Genetic transfer between *Enterococcus faecalis* isolated from food of animal origin and human microbiota. *Letters in Applied Microbiology*, 54(2), 119–125.

Swain, M. R., Anandharaj, M., Ray, R. C., & Rani, R. P. (2014). Fermented fruits and vegetables of Asia: A potential source of probiotics. *Biotechnology Research International*, 2014, 250424.

Tamang, J. P., Cotter, P. D., Endo, A., Han, N. S., Kort, R., Liu, S. Q., Mayo, B., Westerik, N., & Hutkins, R. (2020). Fermented foods in a global age: East meets West. *Comprehensive Reviews in Food Science and Food Safety*, 19, 184–217.

Tamang, J. P., & Kailasapathy, K. (Eds.). (2010). *Fermented foods and beverages of the world*. CRC Press.

Tamang, J. P., Watanabe, K., & Holzapfel, W. H. (2016). Review: Diversity of microorganisms in global fermented foods and beverages. *Frontiers in Microbiology*, 7, 377.

Tang, H., Qian, B. B., Xia, B., Zhuan, Y. Y., Yao, Y., Gan, R., & Zhang, J. (2018). Screening of lactic acid bacteria isolated from fermented *Cornus officinalis* fruits for probiotic potential. *Journal of Food Safety*, 38, e12565.

Toomey, N., Monaghan, A., Fanning, S., & Bolton, D. J. (2009). Assessment of antimicrobial resistance transfer between lactic acid bacteria and potential foodborne pathogens using *in vitro* methods and mating in a food matrix. *Foodborne Pathogens and Disease*, 6(8), 925–933.

Torres, S., Veron, H., Contreras, L., & Isla, M. I. (2020). An overview of plant-autochthonous microorganisms and fermented vegetable foods. *Food Science and Human Wellness*, 9(2), 112–123.

Toth, A. G., Csabai, I., Judge, M. F., Maroti, G., Becsei, A., Spisak, S., & Solymosi, N. (2021). Mobile antimicrobial resistance genes in probiotics. *Antibiotics*, 10, 1287.

Toth, A. G., Csabai, I., Maroti, G., Jerzsele, A., Dubecz, A., Patai, A. V., Judge, M. F., Nagy, S. A., Makrai, L., Banyai, K., Szita, G., & Solymosi, N. (2020). A glimpse of antimicrobial resistance gene diversity in kefir and yoghurt. *Scientific Reports*, 10, 22458.

Touret, T., Oliveira, M., & Semedo-Lemsaddek, T. (2018). Putative probiotic lactic acid bacteria isolated from sauerkraut fermentations. *PLoS ONE*, 13(9), e0203501.

Valledor, S. J. D., Bucheli, J. E. V., Holzapfel, W. H., & Todorov, S. D. (2020). Exploring beneficial properties of the bacteriocinogenic *Enterococcus*

faecium ST10Bz strain isolated from boza, a Bulgarian cereal-based beverage. *Microorganisms*, 8(10), 1474.

Voidarou, C., Antoniadou, M., Rozos, G., Tzora, A., Skoufos, I., Varzakas, T., Lagiou, A., & Bezirtzoglou, E. (2021). Fermentative foods: Microbiology, biochemistry, potential human health benefits and public health issues. *Foods*, 10, 69.

von Wintersdorff, C. J., Penders, J., van Niekerk, J. M., Mills, N. D., Majumder, S., van Alphen, L. B., Savelkoul, P. H., & Wolffs, P. F. (2016). Dissemination of antimicrobial resistance in microbial ecosystems through horizontal gene transfer. *Frontiers in Microbiology*, 7, 173.

Won, S., Chen, S., Park, K. W., & Yoon, J. (2020). Isolation of lactic acid bacteria from kimchi and screening of *Lactobacillus sakei* ADM14 with anti-adipogenic effect and potential probiotic properties. *LWT - Food Science and Technology*, 126, 109296.

World Health Organization. (2011). Tackling antibiotic resistance from a food safety perspective in Europe. https://apps.who.int/iris/bitstream/handle/10665/326398/9789289014212-eng.pdf

Xu, X., Luo, D., Bao, Y., Liao, X., & Wu, J. (2018). Characterization of diversity and probiotic efficiency of the autochthonous lactic acid bacteria in the fermentation of selected raw fruit and vegetable juices. *Frontiers in Microbiology*, 9, 2539.

Yu, Z., Zhang, X., Li, S., Li, C., Li, D., & Yang, Z. Z. (2013). Evaluation of probiotic properties of *Lactobacillus plantarum* strains isolated from Chinese sauerkraut. *World Journal of Microbiology and Biotechnology*, 29(3), 489–498.

Zabat, M. A., Sano, W. H., Wurster, J. I., Cabral, D. J., & Belenky, P. (2018). Microbial community analysis of sauerkraut fermentation reveals a stable and rapidly established community. *Foods*, 7, 77.

Zielińska, D., Rzepkowska, A., Radawska, A., & Zieliński, K. (2015). *In vitro* screening of selected probiotic properties of *Lactobacillus* strains isolated from traditional fermented cabbage and cucumber. *Current Microbiology*, 70(2), 183–194.