



Antibiotic Resistance Profiles of *Lactobacillus* spp. from Animal and Food Ecosystems

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ABSTRACT

Due to the extensive and frequent careless use of antibiotics in human, veterinary, and agricultural settings, antibiotic resistance (AR) has become one of the biggest risks to worldwide public health. Lactic acid bacteria (LAB), especially *Lactobacillus* species, are crucial for probiotic uses, animal nutrition, and food fermentation. Recent research suggests that *Lactobacillus* strains from animal and food environments may have innate and acquired antibiotic resistance genes (ARGs), despite their long history of safe use. This raises concerns about their safety. With an emphasis on resistance to aminoglycosides, macrolides, tetracyclines, fluoroquinolones, β -lactams, and vancomycin, this review outlines the prevalence, phenotypic characteristics, and genotypic drivers of AR in *Lactobacillus* species isolated from animals and food products. Numerous ARGs in *Lactobacillus* species are linked with mobile genetic elements, indicating the possibility of horizontal gene transfer to other beneficial and pathogenic microorganisms in the food chain and gastrointestinal tract. Acquired resistance poses a serious risk for the spread of ARGs, but intrinsic resistance in *Lactobacillus* (such as to vancomycin and aminoglycosides) is typically regarded as non-transferable and of low safety concern. Because *Lactobacillus* strains are widely used in food and probiotic compositions, strain selection should incorporate thorough safety evaluation, including phenotypic and molecular AR profiling, before commercialization. To prevent the emergence of resistance and protect public health and food safety, it is crucial to continuously monitor AR trends in animal and food-associated *Lactobacillus* spp.

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INTRODUCTION

A rising global concern, antibiotic resistance affects not only the microbiological safety and overall quality of food items but also the health of animals and humans (Floris et al. 2025). The worldwide health situation is being negatively impacted by the antibiotic resistance dilemma, which has escalated dramatically over the last century. Drug resistance has existed from the beginning of the antibiotic period, even throughout the penicillin era (Das et al. 2020), and the World Health Organization currently ranks it as one of the top 10 worldwide public health problems (Kwon and Powderly, 2021; Tian et al. 2025). Basically, antibiotic resistance is a bacterial adaptation. However, due to the overuse and careless application of antibiotics, selective pressure has increased, causing bacterial evolutionary responses to environmental pressures and a rise in resistance rates (Vikesland et al. 2019; Colautti

et al. 2022). The inappropriate use of antibiotics occurs at higher rates in animal agriculture sector (Van Boeckel et al. 2019). Antibiotics have been utilized extensively in fields relating to poultry and livestock production for many years. They are frequently employed as antimicrobial growth promoters and to prevent or treat bacterial infections (Al-Khalifa et al. 2019).

Antibiotics, whether naturally derived, synthetic or semi-synthetic in origin, work by inhibiting the growth of or eradicating the bacterial populations, thereby having a great role in prevention and resolution of bacterial infections. However, the widespread use of these agents has driven the global rise and spread of multidrug resistant (MDR) microbes. Projections indicate that if the current trajectory of MDR bacterial evolution continues, the mortality rate due to the infections associated with resistant bacteria will surpass that of cancer by 2050 (Abreu et al. 2023).

Antibiotics exert selection pressure on indigenous microflora and target pathogens when they are administered because of their loose pathogen specificity, which causes the evolution of resistant strains. This implies that numerous commensal strains will unavoidably develop resistance to the antibiotic treatment that targets a particular bacterial disease. This mechanism produces resistant commensals, which are important sources of genes that confer resistance to antibiotics (Juricova et al. 2021).

Probiotic supplementation is now seen as an alternate approach to infection prevention and therapy. Antibiotic use may be reduced by using probiotic products as a preventative measure. Gut microbiota is not adversely affected by probiotics (HM and Kotb 2021). A probiotic is defined by the World Health Organization (WHO) and the Food and Agriculture Organization of UN (FAO) as "live microorganisms that, when taken in sufficient quantities, exert beneficial effects on the host's health." Probiotics are of great importance because of their two main advantages: boosting the immunity and enhancing the activity of gastrointestinal tract (Zolfaghari et al. 2025).

Lactic acid bacteria (LAB) are often used as probiotic microorganisms and can be found in fermented food items in the GIT of animals and humans (Mandal et al. 2021). Lactic acid bacteria (LAB) is one of the types of bacteria that produce lactic acid as a metabolic product. Leading genera of LAB include *Lactobacillus*, *Streptococcus*, *Propionibacterium*, *Pediococcus*, *Bifidobacterium*, *Lactococcus* and *Leuconostoc*. They may have certain health benefits, and due to these potential health benefits, some periodically refer to them as probiotics and are generally considered harmless (Adeniyi et al. 2024). *Lactobacillus* is the most common and largest genus of LAB, and is extensively used in fermented foods, i.e, dairy and meat products. Various *Lactobacillus* strains are used to assist animals and humans digest food and absorb nutrients at an increased rate (Zommiti et al. 2020; Ojha et al. 2021). Over 300 *Lactobacillus* species (25 genera) are found in human, animal, and plant microbiomes and are useful in agriculture, food systems, and medicine (Mejía-Caballero and Marco, 2025).

Because of their extensive history of safe and technical application, it is likely that *Lactobacillus* strains are the most frequently used as probiotics and starter cultures, both in agriculture and industry (Devirgiliis et al. 2013; Xu et al. 2024). Although lactobacilli are of great economic importance, the issue of lactobacilli safety has not been of much concern. It been reported that lactobacilli may also cause bacteremia, endocarditis, and other opportunistic infections (Rossi et al. 2022). The second big concern is that certain *Lactobacillus* species have acquired resistance to key human and veterinary antibiotics (Devirgiliis et al. 2011, Stefańska et al. 2021). However, they are not pathogenic; therefore, they can potentially act as reservoirs of antibiotic resistance genes (ARGs) that can then be transferred to other gastrointestinal bacterial species (Campedelli et al. 2019). *Lactobacillus* species are said to be naturally (by nature) resistant to various classes of antibiotics, such as glycopeptides, folate synthesis inhibitors, aminoglycosides, nucleic acid synthesis inhibitors, among others (Kerek et al. 2024).

Acquired resistance in lactobacilli can pose a risk to food and nutritional supplements containing probiotic strains

(Zavišić et al. 2023). It is believed that the main route through which antibiotic resistant (AR) bacteria of the environment and animals enter the human digestive system is the food chain (Rossi et al. 2014, Thumu and Halami, 2019). It has been demonstrated that lactobacilli have the ability to transfer its resistance to other bacterial species in both in vivo and in vitro studies (Nawaz et al. 2011; Anisimova et al. 2022). In order to ensure that the effects are positive, it seems important to implement AR testing into the safety assessment of any probiotic and food product prior to its launch onto the market (Aggarwal et al. 2022; Zavišić et al. 2023). In order to assess the propagation of resistant strains and resistance determinants in different ecosystems, antibiotic resistance should be monitored (Dec et al. 2020). Thus, this paper performed a critical literature review on prevalence and trends of antibiotic resistance in *Lactobacillus* strains present in food and veterinary ecosystems, the safety of these strains as probiotics, and the potential role of such strains in the transmission of antibiotic resistance in diverse ecosystems.

Genus *Lactobacillus* and its Significance

One of the first to be classified as a bacterial group is lactobacilli, their taxonomy has been redefined several times since the original description of the genus *Lactobacillus* by Beijerinck in 1901 (Zheng et al. 2020). They are non-sporing, non-motile, catalase-negative and Gram-positive rod-shaped bacteria, although coccobacillary forms do exist. They live in a high-nutrient environment that contains animals, people, food, plants, soil, and feed (Duar et al. 2017, Salvetti et al. 2018, Seneviratne et al. 2023), and are usually categorized into three groups based on their metabolic activity (Coelho et al. 2022).

Obligately Homofermentative

These lactobacilli yield lactic acid as a metabolic product as a result of carbohydrate fermentation (e.g. *L. amylovarus* and *L. johnsonii*).

Facultatively Heterofermentative

These lactobacilli, with specific substrates and conditions, ferment carbohydrates and release lactic acid, carbon dioxide, and acetic acid/ethanol (e.g. *L. rhamnosus*, *L. casei*, *L. plantarum*).

Obligately Heterofermentative

This group comprises the *Lactobacillus* spp. that consistently ferment carbohydrates and yield lactic acid, acetic acid/ethanol, and carbon dioxide (e.g. *L. fermentum*, *L. ruteri*) (Dempsey and Corr, 2022; Aggarwal et al. 2024). Lactobacilli play significant roles in food, industry, and health (humans and veterinary). They are essential in the production of fermented food, enhancing food texture and preservation. Industrially, they are used to produce lactic acid through carbohydrate fermentation, serving as a precursor for bioplastics. In the health sector, many strains of lactobacilli are marketed as probiotics, providing benefits in addition to basic nutrition. Furthermore, emerging research is focused on exploring their role as therapeutics and as delivery vehicles for vaccines (Sun et al. 2015; Zheng et al. 2015; Stefanovic et al. 2017). Lactobacilli in various food and animal sources and associated benefits have been summarized in Table 1.

Role of *Lactobacillus* in Enhancing Gut Health

Lactobacilli occur indigenously in the gut microbiota of animals and humans (Al-Yami et al. 2022; Averina et al. 2021), where they exert beneficial effects on the host's health (Ilinskaya et al. 2017). They are acid tolerant and have the ability to hinder the growth of diverse pathogenic bacteria and fungi, primarily through lactic acid production. Probiotic lactobacilli adopt various mechanisms to colonize intestinal epithelium, thereby sustaining the integrity of the gut barrier, enhancing mucosal defense, and regulating host immunity. The recovery of lactobacilli from excreta or feces reflects their existence and distribution in the GIT (Rastogi and Singh, 2022; Ludfiani et al. 2021; Rosique et al. 2019). Numerous *Lactobacillus* spp. are widely utilized to support and enhance the activity of the GIT and help with the nutrient absorption in livestock and humans (Zommiti et al. 2020).

Role of *Lactobacillus* in Food Production

Lactobacillus strains, due to their fermentative character and related nutritional and health-promoting capabilities, are broadly utilized in the manufacturing of foods (Yao et al. 2025; Adesulu-Dahunsi et al. 2022). Many studies have emphasized their importance in guaranteeing the safety and

quality of fermented food (Chaves-López et al. 2020; Goel et al. 2020). Lactobacilli are often used to ferment food, and they are used as starter cultures to produce fermented vegetables, dairy products, and meat (Aryana and Olson, 2017). In addition to the technological aspect, these bacteria are highly beneficial in the preservation of food by prolonging their shelf life by synthesizing organic acids and antimicrobial metabolites. In the presence of such compounds, pathogens and spoilage causing organisms can't survive, and hence, they maintain the stability and safety of fermented foods (Adesulu-Dahunsi et al. 2022).

Antibiotic Resistance in *Lactobacillus* species

Antibiotic resistance (AR) is the capability of bacteria and other microbes to tolerate the effects of antibiotics that could reduce their growth or eliminate them. Several mechanisms account for the development of antibiotic resistance, including the level of resistance exhibited by a bacterial strain and its ability to persist through various resistance mechanisms (Muteeb et al. 2023). The World Health Organization has identified antibiotic resistance as a major worldwide threat to both food safety and public health (Wang et al, 2021). AR in probiotic lactobacilli is regarded as an important feature for their potential

Table 1: Lactobacilli isolated from diverse sources and their benefits.

Source	Lactobacillus strains.	Positive Effects	Reference
GIT of Animals			
Turkeys	<i>L. ruteri</i> , <i>L. johnsonii</i> , <i>L. frumenti</i>	Expressed probiotic properties, antimicrobial potential	(Altarugio et al. 2018)
Calves	<i>L. fermentum</i> , <i>L. farciminis</i>	Resistance to gastrointestinal conditions, antibiotic susceptibility, antimicrobial activity	(Sandes et al. 2017)
Chicken	<i>L. farciminis</i> , <i>L. salivarius</i> , <i>L. fermentum</i> , <i>L. ingluviei</i> , <i>L. plantarum</i> , <i>L. acidophilus</i>	strong antibacterial activity, Robust Probiotic potential	(Thuy and Trai, 2024; Sirisopapong et al. 2023; Sorescu et al. 2021; Khan et al. 2019)
Food Sources			
Yogurt	<i>L. acidophilus</i> , <i>L. delbrueckii</i> subsp. <i>bulgaricus</i> , <i>L. casei</i> , <i>L. paracasei</i> ,	Enhancing gut health, modulating the immune health, and helping with conditions like diabetes, cardiovascular diseases, and osteoporosis	(Ibrahim et al. 2023; Refaat et al. 2025)
Whey	<i>L. plantarum</i> and <i>L. fermentum</i>	Cholesterol-lowering activity, antibacterial activity	(Rzepakowska et al. 2017; Zielińska and Kolożyn-Krajewska, 2018)
Cheese	<i>L. plantarum</i> , <i>L. brevis</i> , <i>L. delbrueckii</i> subsp. <i>lactis</i> , <i>L. rhamnosus</i>	Reducing aflatoxin M1 in milk, Enhance gastrointestinal health, boost immunity, lower cholesterol, reducing lactose intolerance, and improving oral health by diminishing dental caries and yeast infections	(Hammam and Ahmed, 2019; Erfanpoor et al. 2024)
Dairy Beverages	<i>L. paracasei</i> , <i>L. acidophilus</i> , <i>L. plantarum</i> , <i>L. rhamnosus</i>	Promote gut health, Immunity enhancement, Antioxidant activity	(Turkmen et al. 2019; Liu et al. 2024)
Kefir	<i>L. kefiranofaciens</i> , <i>L. delbrueckii</i> subsp. <i>lactis</i> , <i>L. delbrueckii</i> ssp. <i>bulgaricus</i>	Lowering cholesterol levels, protecting against diabetes, possessing antimicrobial and anticarcinogenic properties	(Georgalaki et al. 2021; Egea et al. 2022; Refaat et al. 2025)
Sauerkraut	<i>L. plantarum</i> , <i>L. brevis</i> , <i>L. paracasei</i> ,	Antioxidant, bacteriocin production antimicrobial, strong resistance to gastrointestinal conditions	(Chaudhary and Saharan, 2019; Yang et al. 2020; Fadare et al. 2023)
Kimchi	<i>L. fermentum</i> , <i>L. curvatus</i> , <i>L. reuteri</i> , <i>L. rhamnosus</i> , <i>L. paracasei</i> , <i>L. sakei</i> , <i>L. salivarius</i> ,	Acid-bile resistance, lowering cholesterol, modulating inflammatory process, antibacterial activity	(Lee et al. 2022; Seo et al. 2021)
Fruit vinegars	<i>L. paracasei</i> , <i>L. plantarum</i> , <i>L. brevis</i> ,	Antimicrobial activity, reducing oxidative stress, blood-glucose lowering activity, reducing obesity, anti-tumor activity, reducing hypertension, reducing the possibility of cardiovascular diseases	(Sengun et al. 2022)
Fermented meat products	<i>L. plantarum</i> , <i>L. brevis</i>	Resistance to gastrointestinal conditions, antimicrobial activity	(Rzepakowska et al. 2017, Zielińska and Kolożyn-Krajewska, 2018; Sivamaruthi et al. 2022)

application alongside antibiotic therapy. However, the consumption of bacteria carrying acquired resistance raises concerns due to the possibility of spreading the resistance determinants within the gut microbiota, more broadly, into the environment (Anisimova and Yarullina, 2019; Anisimova et al. 2022).

Mechanisms of Antibiotic Resistance in Lactobacilli

To become resistant to antibiotics, *Lactobacillus* employs diverse and sophisticated mechanisms. By changing their receptors without changing the antibiotic component (passive effect) or by modifying the antibiotic agent with enzymes (active effect), they can avoid the effects of antibiotics (Álvarez-Cisneros and Ponce-Alquicira, 2018). Transferable antibiotic resistance genes are present in the *Lactobacillus* group, which acts as a carrier of these genes and passes them on to non-resistant individuals. These populations are forced to create defense mechanisms against antibiotics when they are exposed to them (Sharma et al. 2014; Ojha et al. 2021).

The major mechanisms by which lactobacilli develop resistance to antibiotics are:

- 1) Enzymatic alteration of antibiotics, which causes structural modification in the antibiotic compound and prevents its interaction with the target.
- 2) Enzymatic degradation of antibiotics, occurring at either intracellular or extracellular level, thus neutralizing the antibiotic action.
- 3) Activation of efflux pumps, which pump antibiotics actively out of the cell, thereby reducing the amount of drug inside the cell.
- 4) Modification in permeability of the cell wall, resulting in decreased intracellular concentration of antibiotic. Among these mechanisms, multidrug resistant efflux pumps are considered the predominant mechanism causing resistance in lactobacilli (Fraqueza, 2015; Von Wintersdorf et al. 2016).

Intrinsic vs. Acquired Resistance

Lactobacilli can exhibit either intrinsic (primary) resistance or acquired (secondary) resistance to antibiotics (Zheng et al. 2024). Intrinsic resistance is a genetically encoded trait inherent to a bacterial species. It reflects the innate capability of bacteria to resist certain antibiotics due to innate structural

or functional features, such as reduced cell membrane permeability, active efflux pumps, or lack of specific drug targets (Poulton and Rock, 2022). Generally, it is not considered a safety concern. The majority of *Lactobacillus* strains are naturally resistant to the aminoglycoside group of antibiotics (kanamycin, neomycin, streptomycin, and gentamicin), trimethoprim, bacitracin, ciprofloxacin, cefoxitin, nitrofurantoin, vancomycin, and metronidazole (Abriouel et al. 2015; Álvarez-Cisneros and Ponce-Alquicira, 2018; Duche et al. 2023). In contrast, they show sensitivity to beta-lactams, tetracycline, linezolid, chloramphenicol, and erythromycin. However, many studies have reported resistance in *Lactobacillus* strains against these antibiotics, which is most likely acquired (Abriouel et al. 2015; Anisimova and Yarullina, 2019).

Acquired resistance is defined by the ability of bacteria to resist the antibiotics to which they were sensitive previously. This occurs typically through two main processes: horizontal gene transfer (HGT) and genetic mutations within chromosomal DNA (Kumawat et al. 2023). Among the factors contributing to the resistance spread, mobile genetic elements facilitating the horizontal transfer of resistance genes pose a major risk (Dušková et al. 2021, Zavišić et al. 2023). Analytical assessment of antibiotic resistance is generally carried out by employing phenotypic methods such as disk diffusion, E-test, and dilution assays (Colautti et al. 2022) as described in Table 2. However, these techniques are incapable of differentiating between intrinsic and acquired resistance, making them helpful only as preliminary tests, and must be complemented with molecular (genotypic) methods for precise characterization of antibiotic resistance. The focus of recent research is to study antibiotic sensitivity profiles and resistance genes (ARGs) in lactobacilli. To date, many antibiotic resistance genes, both intrinsic and acquired, in *Lactobacillus* spp. have been reported (Anisimova and Yarullina, 2019; Anisimova et al. 2022). Primers utilized, in various studies, for the detection of ARGs in *Lactobacillus* strains have been described in Table 3.

Horizontal Transfer of ARGs

Three mechanisms can cause horizontal transfer of resistance genes: *transformation*, which involves obtaining foreign genetic material from the extracellular environment (Duche et al, 2023); *transduction*, which involves

Table 2: Phenotypic characterization of antibiotic resistance in lactobacilli obtained from various sources.

Antibiotic	Mode of Activity	Source	Phenotypic Method for AR Assessment	Reference
Bacitracin, cephalosporins, methicillin, vancomycin, ampicillin, polymyxin, penicillin	Hinder synthesis of cell wall	Traditional fermented foods, Yogurt, Fermented beverage, nutritional supplements and probiotic formulations	Minimum Inhibitory Concentration (MIC) Assay, Disk diffusion technique	(Poornachandra Rao et al. 2015; Campedelli et al. 2019; Sornsenee et al. 2021; Anisimova et al. 2022; Duche et al. 2023)
Streptomycin, gentamycin, chloramphenicol, tetracycline, neomycin, erythromycin, clindamycin, aminoglycosides, chlortetracycline, kanamycin	Suppress biosynthesis of proteins	Milk and dairy items, yogurt, starter cultures, poultry gut and feces	MIC, E-test, disk diffusion	(Zhou et al. 2005; Huys et al. 2008; Poornachandra Rao et al. 2015; Saleem et al. 2018; Campedelli et al. 2019; Wang et al. 2019; Dec et al. 2020; Shafiei et al. 2021)
Norfloxacin, ciprofloxacin, enrofloxacin nalidixic acid	Block replication of DNA	Fruits, dairy items, fermented foods, feces of piglets, starter cultures	MIC, E-test, disk diffusion	(Zhou et al. 2005; Hummel et al. 2007; Karapetkov et al. 2011; Poornachandra Rao et al. 2015; Zou et al. 2017; Campedelli et al. 2019; Duche et al. 2023)
Sulfonamides/trimethoprim	Inhibit folate synthesis	Dairy items, fruits	MIC	(Muñoz et al. 2014; Karapetkov et al. 2011)

Table 3: Primers employed in various studies to detect ARGs.

Antibiotic Group	Target Gene	Primer Sequence (5'→3')	Amplicon Size (bp)	Reference
Aminoglycosides	<i>aac(6')-Ie-aph(2'')-Ia</i>	CAGAGCCTTGGGAAGATGAAG	348	(Dang et al. 2023; Duche et al. 2023, Vakulenko and Mobashery, 2003)
	<i>ant(6)-Ia</i>	CCTCGTGTAAATTCATGTTCTGGC	563	Duche et al. 2023, Kobayashi et al. 2001)
	<i>aad6</i>	CGGGAGAATGGGAGACTTTG CTGTGGCTCCACAATCTGAT	844	(Jaimee and Halami, 2016; Donabedian et al. 2003)
		CTTTAGCAGAACAGGA TG CCGGCCTCTCTTCTAT ATC	292	(Wang et al. 2018; Rojo-Bezares et al. 2006)
	<i>aph(3')IIIa</i>	GCCGATGTGGATTGCGAAAA GCTTGATCCCCAGTAAGTCA	1060	Obioha et al. 2023, Dec et al. 2018; Van Duijkeren et al. 2014)
	<i>aadE</i>	ATGGAATTATTTCCACCTGA TCAAAAACCCCTATTAAGCC	420	(Wang et al. 2018; Sutcliffe et al. 1996)
Macrolides & Lincosamides	<i>ere(A)</i>	AACACCCTGAACCCAAAGGGACG CTTCACATCCGGATTCGCTCGA	590	(Dec et al. 2018; Malhotra-Kumar et al. 2005)
	<i>erm(A)</i>	CCCAGAAAAATACGCAAAAATTTTCAT CCCTGTTTACCCATTTATAAACG	745	(Duche et al. 2023; Dec et al. 2018)
	<i>erm(B)</i>	TGGTATTCCAAATGCGTAAATG CTGTGGTATGGCGGGTAAGT	323	(Duche et al. 2023; Kastner et al. 2006)
	<i>Inu(A)</i>	GGTGGCTGGGGGTAGATGTATTA ACTGGGCTTCTTTGAAATACATGGT ATTTTTCGATC	515	(Duche et al. 2023; Dec et al. 2018)
Tetracyclines	<i>tet(O)</i>	AACTTAGGCATTCTGGCTCAC TCCCACTGTTCCATATCGTCA	660	(Shao et al. 2015; Ouoba et al. 2008)
	<i>tet(S)</i>	TGGAACGCCAGAGAGGTATT ACATAGACAAGCCGTTGACC	576	(Dang et al. 2023; Saleem et al. 2018; Nawaz et al. 2011)
	<i>tet(M)</i>	GTTAAATAGTGTCTTGGAG CTAAGATATGGCTCTAACAA	697	(Duche et al. 2023; Shao et al. 2015; Aarestrup et al. 2000)
	<i>tet(K)</i>	TTAGGTGAAGGGTTAGGTCC GCAAATCATTCCAGAAGCA	229	(Dec et al. 2018; Malhotra-Kumar et al. 2005)
	<i>tet(L)</i>	TGGTGGAAATGATAGCCCAT CAGGAATGACAGCACGCTAA	168	(Dang et al. 2023; Duche et al. 2023; Kastner et al. 2006)
	<i>tet(W)</i>	GAGAGCCTGCTATATGCCAGC GGGCGTATCCACAATGTTAAC	286	(Duche et al. 2023; Shao et al. 2015; Hummel et al. 2007)
Fluoroquinolones	<i>gyrA</i>	CAMCGKCGKATTCTTTACGGAATG TTRTTGATATRCGBAGCATTTTC	286	
	<i>parC</i>	TATTCYAAATAYATCATTTCARGA GCYTCNGTATAACGCATMGCCG	372	(Rokon-Uz-Zaman et al. 2023; Le et al. 2015)
Beta lactams	<i>blaTEM</i>	GGTCGCCGCATACACTATTCTC TTTATCCGCCTCCATCCAGTC	588	
	<i>blaCTX-M-1</i>	GAATTAGAGCGGCAGTCGGG CACAACCCAGGAAGCAGGC	107	
	<i>blaCTX-M-2</i>	GATGGCGACGCTACCCC CAAGCCGACCTCCCGAAC	454	(Dang et al. 2023; Shao et al. 2015; Chang et al. 2009)
Glycopeptides	<i>VanX</i>	TCGCGGTAGTCCCACCATTTCGTT AAATCATCGTTGACCTGCGTTAT		

incorporating fragments of the bacterial DNA into the bacteriophage genome during replication, which then infects another bacterial cell, resulting in the transfer of genetic material (Lerner et al. 2017); or *conjugation*, which involves DNA transfer induced by cell-to-cell contact (Duche et al. 2023; Morawska et al. 2023). The difficulty of precisely detecting and tracking these DNA exchanges is a significant obstacle to HGT. Plasmid-mediated transfer is the most common HGT mechanism, allowing resistance genes to be exchanged between several taxonomic groups (Kerek et al. 2025).

Antibiotic Resistance in Animal-Derived *Lactobacillus* spp. Aminoglycoside Resistance

Because lactobacilli lack cytochrome dependent electron transport (Dušková et al. 2021; Gueimonde et al. 2013), which promotes drug uptake and reduced membrane permeability (Duche et al. 2023), they are inherently resistant to aminoglycoside antibiotics. *Lactobacillus* species isolated from agricultural settings frequently include aminoglycoside resistance genes, which aid in the

proliferation of harmful bacteria in the gastrointestinal microbiota through horizontal gene transfer (HGT) and enhanced tolerance through structural alterations (Jaimee and Halami, 2016). Since gentamicin is a key medication of choice for treating infections in both humans and animals, aminoglycosides, in particular kanamycin and gentamicin resistance in lactobacilli, should be assessed carefully (Das et al. 2020).

Phenotypic Resistance

High-level resistance to aminoglycosides has been frequently reported in animal-derived *Lactobacillus* isolates. *Lactobacillus* strains obtained from domestic geese displayed resistance to neomycin (27%), and 50% strains were resistant to fluoroquinolones like flumequine and enrofloxacin, with over 44% resistant to protein synthesis inhibitors including aminoglycosides (Dec et al. 2015). Dec et al. (2018), in a study, revealed that 10% of lactobacilli from turkeys were resistant to gentamicin, while 31% showed streptomycin resistance. In poultry-origin lactobacilli, particularly from the broiler gut,

resistance to gentamicin and streptomycin was noted, especially in commercial poultry isolates (Saleem et al. 2018). Rajoka et al. (2018) also documented 100% resistance to streptomycin and gentamicin in the tested *Lactobacillus* strains from poultry intestines.

Genotypic Resistance

Genes resistant to aminoglycosides have frequently been documented. In a study by Jaimee and Halami, (2016), *Lactobacillus* strains from meat and farm animal sources were shown to have *aac(6)'Ie-aph(2)'Ia* and *aph(3)'IIIa* genes. Similarly, *ant(6)-Ia*, and *aad6* were identified in chicken-derived *Lactobacillus* strains (Dec et al. 2017). In addition, Xu et al. (2024) reported the existence of elfamycin resistance genes in pig-derived *Lactobacillus* species. Some of these resistant genes are associated with plasmid and could serve as a reservoir of antibiotic resistance dissemination among other gut pathogens, with the potential to transfer to humans via the food chain. So, antibiotic resistance patterns in these bacteria and relative transferability to other bacteria should be assessed properly before their use as probiotics.

Macrolide and Lincosamide Resistance

Although the majority of lactobacilli are normally sensitive, some strains exhibit resistance to macrolides and lincosamide, suggesting that this resistance is acquired instead of intrinsic (Reefat et al. 2025).

Phenotypic Resistance

Resistance to erythromycin and lincomycin has been widely observed and reported in lactobacilli associated with the GIT. For instance, *Lactobacillus* strains recovered from the gut of chickens displayed erythromycin resistance rates as high as 87% in commercial birds (Saleem et al. 2018). Moreover, Dec et al. (2015) found 15% of goose-derived lactobacilli resistant to lincomycin, while, Dec et al. (2018) observed that 45% of the lactobacilli obtained from feces of turkeys were resistant to erythromycin. Sirisopapong et al. (2023) observed that all poultry-derived *Lactobacillus* strains were resistant to erythromycin.

Genotypic Resistance

Erythromycin resistance correlates with the genes *erm(B)*, *erm(C)*, *erm(T)* and *erm(A)*. The *erm(B)* gene is the most common and frequently reported gene in the genus *Lactobacillus*, and it encodes ribosomal RNA methylase that binds to the 23 S subunit (Gad et al. 2014; Sharma et al. 2016; Campedelli et al 2019). Preethi et al. (2017) confirmed the existence of *erm(B)* in poultry isolates in addition to *msr(A/B)* and *msr(C)*. Dec et al. (2017) found *erm(B)* in 39% of tested isolates. They also observed the lincosamide resistance gene *lnu(A)*. These genes are commonly associated with mobile genetic components such as the *Tn916* transposon family. Their mobility raises concerns about horizontal spread to other gut microorganisms and consequent dispersion into the food chain. Moravkova et al. (2022) also observed *erm(B)* genes in *Lactobacillus* strains recovered from pigs.

Tetracycline Resistance

Tetracyclines are extensively used antibiotics in animal rearing due to their broad-spectrum activity, low cost of

production and absence of any major side effects (Jamal et al. 2017; Ma et al. 2021). Tetracycline resistance is among the best studied characteristics of lactobacilli; 11 resistance genes have been discovered, such as *tet(O)*, *tet(W)*, *tet(Q)*, *tet(M)*, *tet(S)*, *tet(36)*, *tet(K)*, *tet(L)*, *tet(O/W/32/O/W/O)* and *tetZ* (Anisimova and Yarullina, 2018; Anisimova and Yarullina, 2019). Most of these genes, especially *tet(K)* and *tet(L)*, are coded on plasmids, but some are chromosomally-coded and plasmid-coded as in the case of *tet(M)*, *tet(O)* and *tet(Q)*. The resistance mechanism is either via the ribosome protection or efflux pumps (Das et al. 2020).

Phenotypic Resistance

Resistance to tetracycline group of antibiotics is highly prevalent in animal-derived *Lactobacillus* isolates. Dec et al. (2017) observed tetracycline resistance in 74% of *Lactobacillus* strains, while Preethi et al. (2017) witnessed elevated levels of resistance in isolates from conventional poultry. Saleem et al. (2018) also reported moderate resistance in poultry-derived lactobacilli (41% in commercial vs. 32% in indigenous isolates). Dec et al. (2018) found that 68% of turkey-origin lactobacilli exhibited resistance. Likewise, resistance among pig fecal *Lactobacillus* isolates has also been reported (Xu et al. 2024). Lactobacilli are generally reported to exhibit sensitivity to tetracyclines, however, reported resistance against these antibiotics necessitates thorough investigation and assessment.

Genotypic Resistance

Lactobacilli isolated from animals are often reported to harbor tetracycline resistance genes. Dec et al. (2017) tested *Lactobacillus* species obtained from chicken and found that 45%, 26%, and 24% of isolates carried the genes *tet(W)*, *tet(M)*, and *tet(L)*, respectively. While *tet(K)* was also detected by Preethi et al. (2017), and all of these were linked with mobile elements such as *Tn916/Tn917*. Dec et al. (2018) found *tet(W)* (37%), *tet(L)* (40%), and *tet(M)* (29%) genes in lactobacilli obtained from turkeys. Saleem et al. (2018) detected and sequenced *tet(M)* genes from poultry-derived lactobacilli and revealed >99% identity with *tet(M)* from *E. coli*, suggesting the possibility of interspecies transfer and dissemination via the food chain. Dec et al. (2020) observed the prevalence of tetracycline-resistant genes in *Lactobacillus* species isolated from pigeons; they found that 79% of the isolates carried *tet(L)*, *tet(M)*, and *tet(W)* genes.

Fluoroquinolone Resistance

A common subclass of quinolone antibiotics, fluoroquinolones, like ciprofloxacin, have a fluorine atom associated with the core ring structure, which increases their efficacy against bacterial infections (Reefat et al. 2025). By preventing type II topoisomerases, particularly topoisomerase IV and DNA gyrase, from introducing supercoiling into DNA, quinolones prevent bacteria from replicating their DNA (Collins et al. 2024). This inhibition causes DNA to be accumulated with single and double-strand breaks, which blocks DNA unwinding and replication, thereby hindering bacterial surviving and multiplication (Bush et al. 2020; Lungu et al. 2022).

Phenotypic Resistance

Resistance to fluoroquinolones in animals-originated lactobacilli has often been reported. Dec et al. (2015) observed high resistance (60%) in *Lactobacillus* spp. recovered from geese. Dec et al. (2017) found 48% of the chicken-derived lactobacilli resistant to enrofloxacin. Saleem et al. (2018), also witnessed extremely high levels of resistance (>80%) against ofloxacin, ciprofloxacin, and levofloxacin in *Lactobacillus* isolates obtained from indigenous and commercial poultry. However, Zou et al. (2017) observed elevated levels of enrofloxacin resistance in lactobacilli recovered from post-weaned piglets.

Genotypic Resistance

Fluoroquinolone resistance has been found to occur because of the mutations in the quinolone resistance determining regions (QRDR) of the *parC* or *gyrA* gene (Das et al. 2020). Although quinolone-resistant genes are mostly prevalent in food-originated *Lactobacillus* strains (Guo et al. 2017), some studies also report their existence in animal isolates. Dec et al. (2020) observed and sequenced the *gyrA* gene in lactobacilli that expressed high phenotypic resistance to enrofloxacin.

Beta-lactam Resistance

Because of their structural resemblance to the substrate D-alanyl-alanine, β -lactam antibiotics like ampicillin target PBPs by blocking peptidoglycan cross-linking (Kim et al. 2023). While most lactobacilli are naturally vulnerable to these antibiotics (Saini and Tomar, 2017; Anisimova and Yarullina, 2019), various strains of *Lactobacillus* have been shown to be resistant in several investigations.

Phenotypic Resistance

Resistance to β -lactam antibiotics like ampicillin and amoxicillin in lactobacilli obtained from animals has often been reported. Dec et al. (2018) found 47% turkey-derived lactobacilli resistant to ampicillin. Rajoka et al. (2018) reported 100% resistance to penicillin. Saleem et al. (2018) noted higher ampicillin resistance in indigenous poultry (49%) compared to commercial poultry (43%). Tsega et al. (2023) found 90% chicken-derived lactobacilli resistant to ampicillin. These findings are of great concern for both animals and public health, as beta-lactam antibiotics serve as an important treatment option in animals and humans.

Genotypic Resistance

Resistance genes for β -lactam antibiotics have not been reported commonly in animal-derived lactobacilli. Aquilanti et al. (2007) observed *blaZ* gene in animal-derived lactobacilli. Aristimuño Ficooseco et al. (2018) also detected *bla* genes in cattle-derived lactobacilli. Moreover, *blaCTX-M-2*, *blaCTX-M-1*, and *blaTEM* were identified in some poultry probiotic products-derived *Lactobacillus* strains. These genes were shown to have potential for horizontal transfer to other gut bacteria in co-culture experiment (Rokon-Uz-Zaman et al. 2023).

Antibiotic Resistance in Food-derived *Lactobacillus* spp.

Aminoglycoside Resistance

Phenotypic Resistance

Lactobacilli from fermented food items, particularly dairy and meat, have shown significant resistance to

aminoglycosides. Wang et al. (2018) found high resistance to streptomycin and kanamycin in *Lactobacillus* spp. from Chinese cured beef. Erginkaya et al. (2018) also observed gentamicin resistance in *Lactobacillus* spp. isolated from traditional Turkish dairy products. In a study of yogurt and cheese products, Wang et al. (2019) observed high resistance against neomycin, gentamicin, and streptomycin in *Lactobacillus* isolates from cheese and yogurt products.

Genotypic Resistance

Genes conferring resistance to the aminoglycoside group of antibiotics, such as *aph(3')IIIa*, *aad6*, and *aac(6)Ie-aph(2'')Ia*, in food-originated *Lactobacillus* strains have been reported in many studies (Shao et al. 2015; Jaimee and Halami, 2016; Ledina et al. 2018) and are often linked with MGEs, suggesting horizontal gene transfer potential. Wang et al. (2019) also observed the genes *aph* and *aadA2* in lactobacilli recovered from yogurt and cheese. Dušková et al. (2021) found the streptomycin resistance gene *aadE*. Moghimi et al. (2023) found the *aacA-D* gene in majority of the *L. bulgaricus* strains recovered from yogurt. These findings highlight the potential risk of horizontal gene transferability, necessitating the removal of such strains from the food industry.

Beta-lactam Resistance

Phenotypic Resistance

Lactobacilli are naturally sensitive to beta-lactam antibiotics; however, resistance in food-derived lactobacilli has been reported in several studies. Sharma et al. (2016) reported resistance against penicillin, ampicillin, amoxycylav, sulbactam, methicillin, oxacillin, cefotaxime, and cloxacillin. Dušková et al. (2021) also observed ampicillin resistance in food-originated lactobacilli. Duche et al. (2023) also observed strong resistance against beta-lactam antibiotics in lactobacilli recovered from fermented foods.

Genotypic Resistance

Anisimova and Yarullina, (2019) reported widespread existence of the *blaTEM* gene in *Lactobacillus* strains obtained from fermented plant source; however, they also detected *blaSHV* and *blaOXA-1* genes. Zarzecka et al. (2022) reported the presence of the *blaOXA* gene in *Lactobacillus* spp. obtained from food sources. Anisimova et al. (2022) also observed the widespread existence of the *blaTEM* gene in *Lactobacillus* spp. obtained from probiotic preparations. These genes are strongly linked with mobile genetic elements, holding the potential for horizontal transfer.

Fluoroquinolones Resistance

Phenotypic Resistance

Widespread resistance to ciprofloxacin and norfloxacin has been witnessed in food-originated lactobacilli. Anisimova et al. (2022) observed quinolone resistance in all the *Lactobacillus* strains obtained from nutritional supplements and probiotic products. Erginkaya et al. (2018) observed moderate to high resistance levels in *Lactobacillus* spp. derived from dairy foods. Seyirt et al. (2024) also found high resistance against ciprofloxacin, enrofloxacin, and norfloxacin in *Lactobacillus* isolates from dairy probiotic products.

Genotypic Resistance

Guo et al. (2017) detected *gyr(A)* in 30% of fermented milk-derived *Lactobacillus* isolates. Rokon-Uz-Zaman et al. (2023) observed plasmid-encoded quinolone resistance gene *qnrS* in isolates from poultry probiotic products. However, widespread existence of *parC* gene in probiotic products and food-origin *Lactobacillus* strains has also been reported (Anisimova and Yarullina, 2019; Anisimova et al. 2022; Duche et al. 2023)

Macrolide and Lincosamide Resistance

Phenotypic Resistance

Lactobacilli present in fermented dairy and meat products commonly exhibit erythromycin and lincomycin resistance. Erginkaya et al. (2018) documented erythromycin resistance in 11% of *Lactobacillus* spp. isolated from Turkish dairy items. Wang et al. (2018) documented high resistance against erythromycin in beef derived lactobacilli. Seyirt et al. (2024) noticed that 28% of lactobacilli obtained from dairy products demonstrated resistance to erythromycin. The resistance to erythromycin in lactobacilli seems to have declined over time, and recent research reports that resistance occurs in particular locations (Vahabzadeh and Özpınar, 2018).

Genotypic Resistance

Macrolide resistance genes are very common across food ecosystems. Wang et al. (2018) identified the *ere(A)* gene in lactobacilli of beef. Functional plasmids carrying *erm(B)* genes were detected in cheese-derived lactobacilli (Flórez et al. 2021). *Inu(A)*, *msr(C)* and *erm(B)* genes were found in *Lactobacillus* strains having the potential to be used as probiotic silage inoculants and feed supplements by (Stefańska et al. 2021).

Tetracycline Resistance

Phenotypic Resistance

Tetracycline resistance has widespread existence in lactobacilli of food origin. Dec et al. (2018) found tetracycline resistance in 68% of turkey isolates. Varying levels of tetracycline resistance have also been observed in isolates from dairy and cured meat (Erginkaya et al. 2018; Wang et al. 2018). Stefańska et al. (2021) reported high resistance against tetracycline in *Lactobacillus* strains having the potential to be used as feed supplements. Amelia et al. (2024) also observed strong tetracycline resistance in *Lactobacillus fermentum* strains recovered from *dadiyah Lintau*.

Genotypic Resistance

Among genes conferring resistance to tetracycline, the *tet(M)* gene has been documented as the most prevalent gene in lactobacilli of food origin (Guo et al. 2017; Ledina et al. 2018; Wang et al. 2018; Zarzecka et al. 2022). Rozman et al. (2020) detected the *tet(W)* gene in lactobacilli derived from starter cultures. Rodríguez-Sánchez et al. (2021) observed *tet(O)*, *tet(M)*, *tet(L)*, and *tet(S)* genes in fermented food-associated *Lactobacillus* strains. These genes often accompany the mobile genetic elements, increasing the risk of transferability.

Vancomycin Resistance

Vancomycin resistance in lactobacilli is because of the D-alanyl D-alanine ligase-related enzymes (Campedelli et al.

2019; Selim et al. 2022). The drug interacts with the D-alanine terminus of peptidoglycan precursors, thereby inhibiting their polymerization and cell wall synthesis in susceptible bacteria. However, in the resistant bacteria like *Lactobacillus*, D-alanine is substituted with D-lactate or D-serine, which inhibits vancomycin binding and supports the formation of cell walls (Das et al. 2020).

Phenotypic Resistance

Vancomycin resistance, apparently intrinsic, has been reported widely in food-derived lactobacilli. Guo et al. (2017) and Rodríguez-Sánchez et al. (2021) reported 100% vancomycin resistance in *Lactobacillus* spp. recovered from fermented dairy foods. Erginkaya et al. (2018) found 58% of dairy product-derived *Lactobacillus* spp. resistant to vancomycin. Anisimova et al. (2022) also observed high resistance against vancomycin in *Lactobacillus* strains obtained from probiotic products and nutritional supplements.

Genotypic Resistance

Vancomycin resistance genes *van(X)* and *van(E)* have been detected in several isolates from fermented food (Guo et al. 2017; Anisimova et al. 2022; Dang et al. 2023). However, *van(A)*, and *van(B)* genes (often linked with MGEs) have also been detected in lactobacilli recovered from fermented foods (Rodríguez-Sánchez et al. 2021).

Conclusion and Future Outlook

Today, there is a great significance of LAB, particularly *Lactobacillus* spp, and the health advantages that go along with them because of their increasing usage as probiotics in food industry and livestock rearing. It is impossible to ignore the issue of AR in lactobacilli, though. Acquired resistance offers a more complicated situation, even if lactobacilli's intrinsic resistance may increase their survival in hostile antimicrobial settings. Acquired resistance can lead to the spread of AR and related health issues, as well as provide the risk of transferring resistance genes to other pathogenic and beneficial gut bacteria. As lactobacilli are introduced to an already wide range of food products and nutritional supplements, it is even more significantly increased as probiotic markets expand.

The potential threat of horizontal transmission within the gut microbiota and along the food chain is emphasized by the common occurrence of resistance genes to clinically relevant antibiotics in isolates obtained of food and animals, e.g, tetracyclines, macrolides, aminoglycosides, b-lactams as well as fluoroquinolones. This underscores the importance of implementing stringent legislations on the application of antibiotics in animal and food production systems, and the fact that all probiotic candidate strains should pass through stringent AR screening. The strains containing resistance genes, particularly those associated with mobile genetic elements, should be further examined and tested to determine their susceptibility to antibiotics, according to the instructions issued by EFSA. The identification and prediction of ARGs has been made convenient by recent advances in metagenomics, bioinformatics, and artificial intelligence. The adoption of these technologies will help companies to improve their formulation, reducing resistance concerns and understanding better the impact of implementing novel probiotics, leading to safer products to the consumer.

In short, a well-coordinated approach is required. This includes stringent safety standards by manufacturers, increased regulatory surveillance and inventive technological applications. Researchers, regulatory bodies, stakeholders, and medical professionals need to collaborate efficiently to ensure exchange of data, standardized safety requirements and on-going risk evaluation. Together, such synchronized activities will maintain the benefits of using *Lactobacillus* as probiotics in livestock and food production systems and reduce the associated risks, ensuring that the practice can continue to be effective and safe in promoting consumer health.

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