

Vital Surveillances

Comparative Analysis of Antibiotic Resistance and Genomic Characteristics of *Enterococcus faecium* and *Enterococcus lactis* Along the Food Chain — 5 PLADs, China, 2015–2024

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ABSTRACT

Introduction: Foodborne antibiotic-resistant enterococci pose significant risks to One Health and clinical antimicrobial efficacy through food chain transmission. Following the taxonomic reclassification of *Enterococcus faecium* (*E. faecium*), comprehensive long-term surveillance data on antibiotic resistance (ABR) patterns and genomic characteristics of *E. faecium* and *Enterococcus lactis* (*E. lactis*) across food animals, environmental sources, and human populations remain limited.

Methods: A total of 2,233 samples were collected from multiple nodes along the food chain across 5 Chinese provincial-level administrative divisions (PLADs) during 2015–2019 and 2023–2024. *E. faecium* (87 isolates) and *E. lactis* (153 isolates) were identified through whole-genome sequencing and average nucleotide identity analysis. Antimicrobial susceptibility testing, comprehensive genomic content analysis, and pan-genome-wide association studies were performed.

Results: *E. faecium* demonstrated significantly higher resistance rates to 12 antimicrobials compared with *E. lactis* ($P < 0.05$). Conversely, *E. lactis* exhibited a higher resistance rate to erythromycin than *E. faecium* ($P < 0.01$). The multidrug-resistant (MDR) rate of *E. faecium* (43/87, 49.4%) substantially exceeded that of *E. lactis* (16/153, 10.5%) ($P < 0.001$). Genomic analysis revealed that *E. faecium* harbors significantly more antibiotic resistance genes, mobile genetic elements, and plasmid replicons than *E. lactis*. No significant interspecies differences were observed in virulence gene profiles associated with adhesion, immune modulation, biofilm formation, and exotoxin production.

Conclusions: *E. faecium* presents substantially greater ABR risks than *E. lactis* within the Chinese food chain, necessitating enhanced species-specific surveillance programs. Future interventions should prioritize targeted control strategies tailored to each

species to effectively mitigate One Health threats.

Foodborne antibiotic-resistant enterococci represent a critical surveillance priority within the “Human-Animal-Environment” One Health framework (1). *Enterococcus faecium* (*E. faecium*) exhibits a dual nature: it serves as a beneficial probiotic in fermented foods and dietary supplements while simultaneously acting as an opportunistic pathogen capable of causing antibiotic-resistant infections, including endocarditis and sepsis (2). In contrast, *Enterococcus lactis* (*E. lactis*) strains are generally regarded as non-pathogenic probiotic bacteria (3). Historically, phylogenetic analyses classified *E. faecium* into two distinct clades: Clade A, comprising clinical and animal isolates, and Clade B, consisting of strains from healthy humans (4). However, recent genomic studies demonstrated that Clade B isolates share >97% average nucleotide identity (ANI) with *E. lactis*, exceeding the 95% species delineation threshold and prompting their reclassification as *E. lactis* (5). Despite this taxonomic revision, comprehensive long-term surveillance data characterizing the antibiotic resistance (ABR) profiles and genomic features of redefined *E. faecium* and *E. lactis* populations within the Chinese food chain remain limited.

In this study, we collected samples from multiple nodes along the food chain across five provincial-level administrative divisions (PLADs) in China during 2015–2019 and 2023–2024. We conducted a comparative analysis of ABR phenotypes and genomic content between *E. faecium* and *E. lactis* isolates. This investigation aimed to elucidate the distinct ABR risks posed by these two species within the Chinese food chain and provide evidence-based data to support risk assessment and control strategies for foodborne antibiotic-resistant enterococci.

METHODS

Sample Collection and *Enterococcus* Detection and Identification

During 2015–2019, 694 samples were collected from Beijing, Henan, Hubei, and Jilin PLADs. From 2023–2024, 1,539 samples were collected from Beijing, Henan, Hubei, Jilin, and Hebei PLADs (Supplementary Table S1, available at <https://weekly.chinacdc.cn/>). Samples were obtained from multiple sites and sources across the food chain, including food animals, food products, environmental surfaces, and human specimens, to capture the diversity of enterococcal populations. Sample collection, *Enterococcus* detection, and identification procedures followed previously established methods (1).

Whole-genome Sequencing (WGS), Genome Assembly, and ANI Analysis

Whole-genome sequencing of *Enterococcus* isolates was performed using the Illumina HiSeq platform (Illumina Inc., United States). Paired-end libraries (2×150 bp) were prepared with the Nextera DNA Sample Preparation Kit (Illumina Inc., United States) according to the manufacturer's protocol. High-quality paired-end reads were processed using Shovill v1.1.0 (<https://github.com/tseemann/shovill>), and *de novo* genome assemblies were generated with SPAdes (version 3.15.5; Algorithmic Biology Lab, St. Petersburg, Russia), yielding contigs (6). ANI values were calculated for all assembled *Enterococcus* genomes using FastANI (version 1.3.3; Atlanta, USA), with a species delineation threshold of 95% (7).

Antimicrobial Susceptibility Testing (AST)

Antimicrobial susceptibility of *E. faecium* and *E. lactis* isolates was determined by broth microdilution and interpreted according to Clinical & Laboratory Standards Institute (CLSI) interpretive criteria. Minimum inhibitory concentrations (MICs) were determined for 13 antibacterial compounds: ampicillin and penicillin (β-lactams), erythromycin (a macrolide), enrofloxacin and ciprofloxacin (quinolones), daptomycin and vancomycin (glycopeptides), tetracycline and doxycycline (tetracyclines), chloramphenicol (a phenicol), high-level gentamicin (HLGA) and high-level streptomycin (HLSA) (aminoglycosides), and linezolid (an oxazolidinone). An isolate was classified as multidrug-resistant (MDR) if it exhibited resistance to three or more antibacterial compounds from different classes.

Bioinformatics Analysis

Antibacterial resistance genes (ARGs), virulence factor encoding genes (VFs), mobile genetic elements (MGEs), and plasmid replicons were identified using ABRicate (<https://github.com/tseemann/abricate>) against the following databases: the Comprehensive Antimicrobial Resistance Database for ARGs (8), the Virulence Factors Database for VFs (9), the Mobile Orthologous Groups Database for MGEs (10), and PlasmidFinder (11) for plasmid replicons. Detection thresholds of 80% minimum coverage and 80% minimum identity were uniformly applied across all analyses.

To construct the core genome single nucleotide polymorphism (SNP)-based phylogenetic tree, the following bioinformatic pipeline was employed: Snippy v4.6.0 (<https://github.com/tseemann/snippy>) was used for core genome alignment and variant calling. Core genome alignment was reconstructed using Gubbins (version 2.4.1; Hinxton, UK) (12). A maximum likelihood phylogenetic tree was then inferred from non-repetitive core SNPs using FastTree (version 2.1.11; Berkeley, USA) with the GTR+CAT substitution model (13).

Roary (version 3.6.1; Exeter, UK) (14) was used to identify core genes and pan-genes. Pan-genome-wide association study (Pan-GWAS) was performed using Scoary (version 1.6.16; Oslo, Norway) (15). Species-specific genes were defined as those present in more than 80% of isolates from one species but absent in the other species. Clusters of Orthologous Groups (COG) classification of significantly associated genes was performed by mapping to the COG function database using BLAST.

Statistical Analysis

Statistical analyses were conducted using SPSS Statistics for Windows, version 17.0 (SPSS Inc., Chicago, IL, USA). Categorical variables were compared using Pearson's chi-squared test and Fisher's exact test. Correlation analyses between dichotomous categorical variables were performed using the Phi coefficient. Statistical significance was defined as $P < 0.05$.

RESULTS

Prevalence of *E. faecium* and *E. lactis* in Food Chain

As shown in Supplementary Table S2 (available at <https://weekly.chinacdc.cn/>), *E. lactis* exhibited a

significantly higher prevalence rate (6.9%, 153/2,233) in the food chain compared to *E. faecium* (3.9%, 87/2,233) ($P<0.001$). Additionally, *E. lactis* demonstrated significantly higher prevalence rates than *E. faecium* in both food and livestock samples ($P<0.05$). This pattern was particularly pronounced during 2023–2024, when *E. lactis* prevalence significantly exceeded that of *E. faecium* ($P<0.001$). Temporal analysis revealed that neither species exhibited significant changes in prevalence rates when comparing the 2015–2019 period to the 2023–2024 period ($P>0.05$).

ABR and ARGs of *E. faecium* and *E. lactis*

E. faecium isolates demonstrated significantly higher resistance rates to 12 antimicrobials compared with *E. lactis* ($P<0.05$) (Figure 1). In contrast, *E. lactis* exhibited a significantly higher resistance rate to erythromycin than *E. faecium* ($P<0.01$). Specifically, *E. faecium* showed elevated resistance to erythromycin (58/87, 66.7%), tetracycline (51/87, 58.6%), and enrofloxacin (48/87, 55.2%), while displaying minimal resistance to daptomycin (3/87, 3.4%), vancomycin (6/87, 6.9%), and linezolid (6/87, 6.9%). *E. lactis* exhibited the highest resistance rates to erythromycin (127/153, 83.0%), tetracycline (29/153, 19.0%), and ciprofloxacin (18/153, 11.8%), but demonstrated negligible resistance to vancomycin (0%), daptomycin (1/153, 0.7%), and ampicillin (1/153, 0.7%). The MDR rate of *E. faecium* (43/87, 49.4%) significantly

exceeded that of *E. lactis* (16/153, 10.5%) ($P<0.001$). Among MDR *E. faecium* isolates, the largest proportion originated from hospital patients (19/43, 44.2%), whereas among MDR *E. lactis* isolates, the largest proportion was food-derived (7/16, 43.8%). The most common resistance profile in *E. faecium* was ciprofloxacin-enrofloxacin co-resistance (5/87, 5.7%), while *E. lactis* most frequently exhibited tetracycline-erythromycin co-resistance (10/153, 6.5%).

A total of 20 distinct ARG types belonging to 8 functional categories were detected across *E. faecium* and *E. lactis* genomes (Figure 2A). *E. faecium* carried significantly more ARGs than *E. lactis* ($P<0.001$). Furthermore, the *tetM*, *tetL*, *ermB*, and *fexA* genes in *E. faecium* showed significant associations with resistance phenotypes to their corresponding antimicrobials (tetracycline, erythromycin, and chloramphenicol) (Figure 2B). Notably, the macrolide resistance gene *ermT* in *E. faecium* demonstrated a significant association with resistance phenotypes to the two β -lactam antibacterials (ampicillin and penicillin). In *E. lactis*, the tetracycline resistance genes (*tetL* and *tetM*) exhibited significant correlations with resistance to both tetracycline antibacterials tested (doxycycline and tetracycline) (Figure 2C).

Genomic content of *E. faecium* and *E. lactis*

Core genome-based SNP phylogenetic analysis demonstrated distinct separation between *E. faecium*

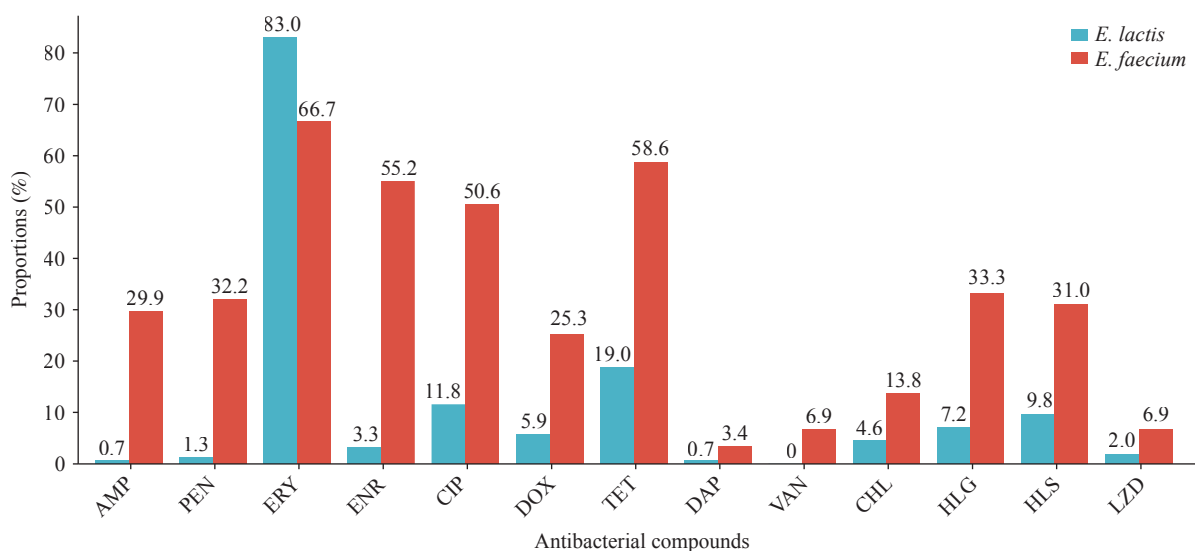


FIGURE 1. Enterococcal resistance profiles against a panel of 13 antibacterial compounds.

Abbreviation: AMP=ampicillin; PEN=penicillin; ERY=erythromycin; ENR=enrofloxacin; CIP=ciprofloxacin; DOX=doxycycline; TET=tetracycline; DAP=daptomycin; VAN=vancomycin; CHL=chloramphenicol; HLG=high-level gentamicin; HLSA=high-level streptomycin; LZD=linezolid; *E. faecium*=*Enterococcus faecium*; *E. lactis*=*Enterococcus lactis*.

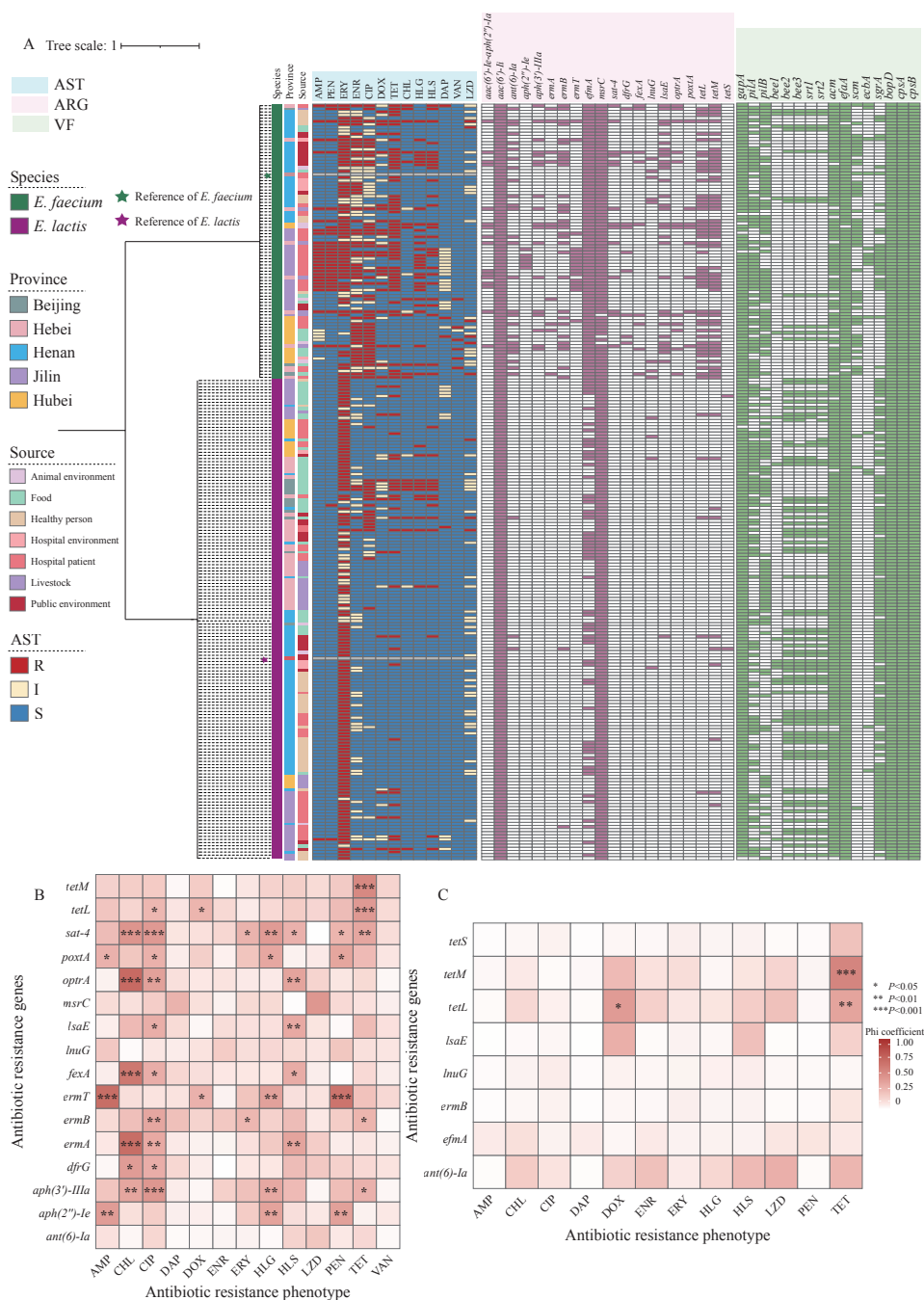


FIGURE 2. Phylogenetic relationships of *E. faecium* and *E. lactis* and correlation analysis between ARGs and ABR phenotypes. (A) Midpoint-rooted maximum likelihood phylogenetic tree constructed from 87 *E. faecium* genomes and 153 *E. lactis* genomes. (B) Correlation heatmap between ARGs and ABR phenotypes in *E. faecium*. (C) Correlation heatmap between ARGs and ABR phenotypes in *E. lactis*.

Note: For (A), reference strains used were SRR24 (accession number: GCA_009734005.2) for *E. faecium* and CX262 (accession number: GCA_019343125.1) for *E. lactis*. Colored bands on the right display genomic information for *Enterococcus* isolates. The first heatmap presents antibacterial susceptibility testing results for *Enterococcus*. The second heatmap illustrates the distribution of antibacterial resistance genes (ARGs) across *Enterococcus* isolates. The third heatmap depicts the distribution of virulence factor encoding genes in *Enterococcus*.

Abbreviation: ABR=antibacterial resistance; AMP=ampicillin; PEN=penicillin; ERY=erythromycin; ENR=enrofloxacin; CIP=ciprofloxacin; DOX=doxycycline; TET=tetracycline; DAP=daptomycin; VAN=vancomycin; CHL=chloramphenicol; HLGA=high-level gentamicin; HLSA=high-level streptomycin; LZD=linezolid; S=susceptible; I=intermediate; R=resistant; AST=antibacterial susceptibility testing; ARG=antibacterial resistance gene; *E. faecium*=*Enterococcus faecium*; *E. lactis*=*Enterococcus lactis*.

and *E. lactis* (Figure 2A). The two species carried comparable numbers of virulence factor genes, with no significant difference observed ($P>0.05$). We identified 25 unique VFs across four functional categories — adhesion, immune modulation, biofilm formation, and exotoxin production — in both *E. faecium* and *E. lactis* genomes. Adhesion genes predominated (18/26, 69.2%), followed by immune modulation factors (*galE*, *cpsA*, *cpsB*, and *cpsD*), biofilm formation genes (*bopD* and *papR*), and a single exotoxin gene (*nheB*). Three VFs — *bopD* (biofilm formation), *cpsA*, and *cpsB* (immune modulation) — were universally present across all isolates. The most prevalent adhesion genes were *efaA* (236/240, 98.3%), *gapA* (234/240, 97.5%), and *acm* (223/240, 92.9%). Notably, the adhesion gene *sgrA* exhibited differential distribution, appearing in 67.7% (20/30) of *E. faecium* isolates from hospital patients versus 83.0% (127/153) of *E. lactis* isolates. Comparative genomic analysis revealed that *E. faecium* harbored significantly higher numbers of ARGs, MGEs, and plasmid replicons compared to *E. lactis* ($P<0.05$) (Figure 3).

Pan-GWAS analysis identified 267 species-specific genes in *E. lactis* and 222 in *E. faecium* (Figure 4A).

COG functional classification demonstrated that species-specific genes from both enterococcal species were significantly enriched in three major categories: metabolism, cellular processes and signaling, and information storage and processing (Figure 4B).

DISCUSSION

The distinct ABR and genomic characteristics of *E. lactis* and *E. faecium* pose different food safety risks. *E. faecium* demonstrated significantly higher resistance to 12 antimicrobials, a substantially elevated MDR rate, and greater abundance of ARGs, MGEs, and plasmid replicons compared to *E. lactis*. These genetic elements increase the potential for ABR transmission throughout the food chain, with specific gene-phenotype correlations providing mechanistic explanations for the observed resistance patterns. The unexpected correlation between *ermT* and β -lactam resistance in *E. faecium* warrants further investigation to elucidate the underlying mechanisms. Although *E. lactis* exhibited overall lower ABR, it showed notably higher erythromycin resistance than *E. faecium*. This elevated resistance is likely attributable to the

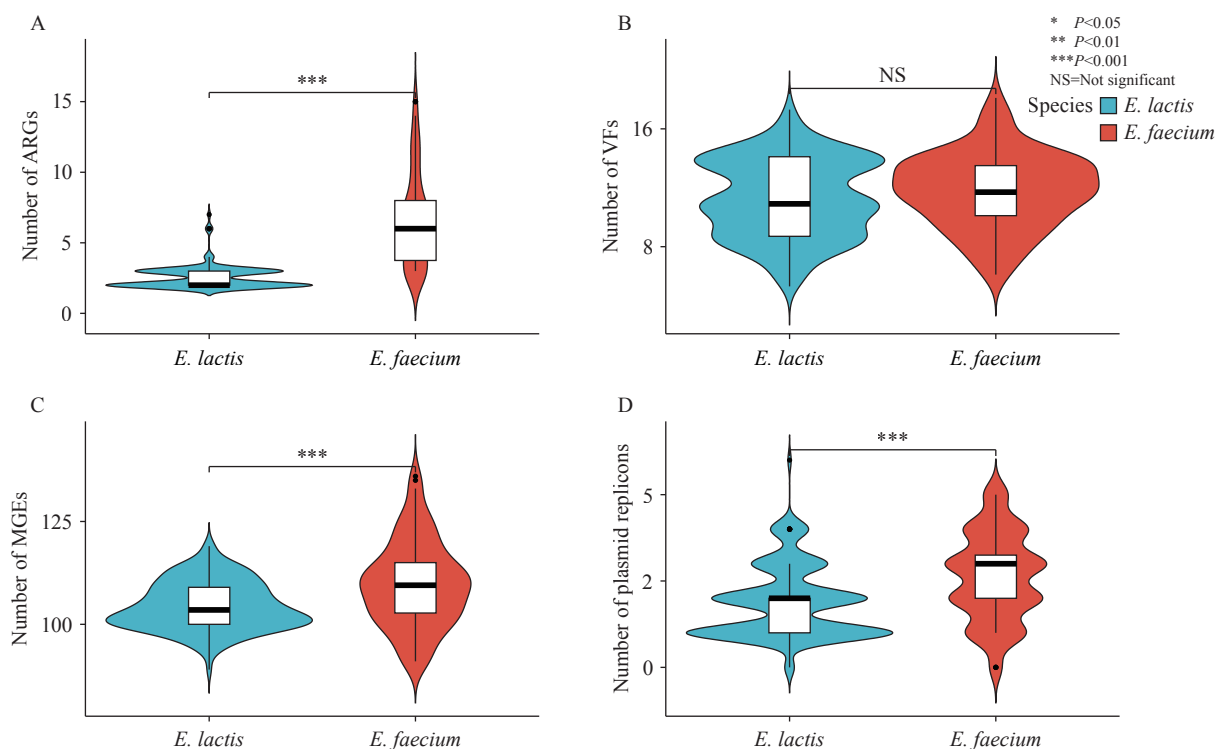


FIGURE 3. Comparative analysis of *E. faecium* and *E. lactis* genomic content. (A) Antibacterial resistance genes, (B) Virulence factor encoding genes, (C) Mobile genetic elements; (D) Plasmid replicons. Abbreviation: ARG=antibacterial resistance gene; VF=virulence factor encoding gene; MGE=mobile genetic element; *E. faecium*=*Enterococcus faecium*; *E. lactis*=*Enterococcus lactis*.

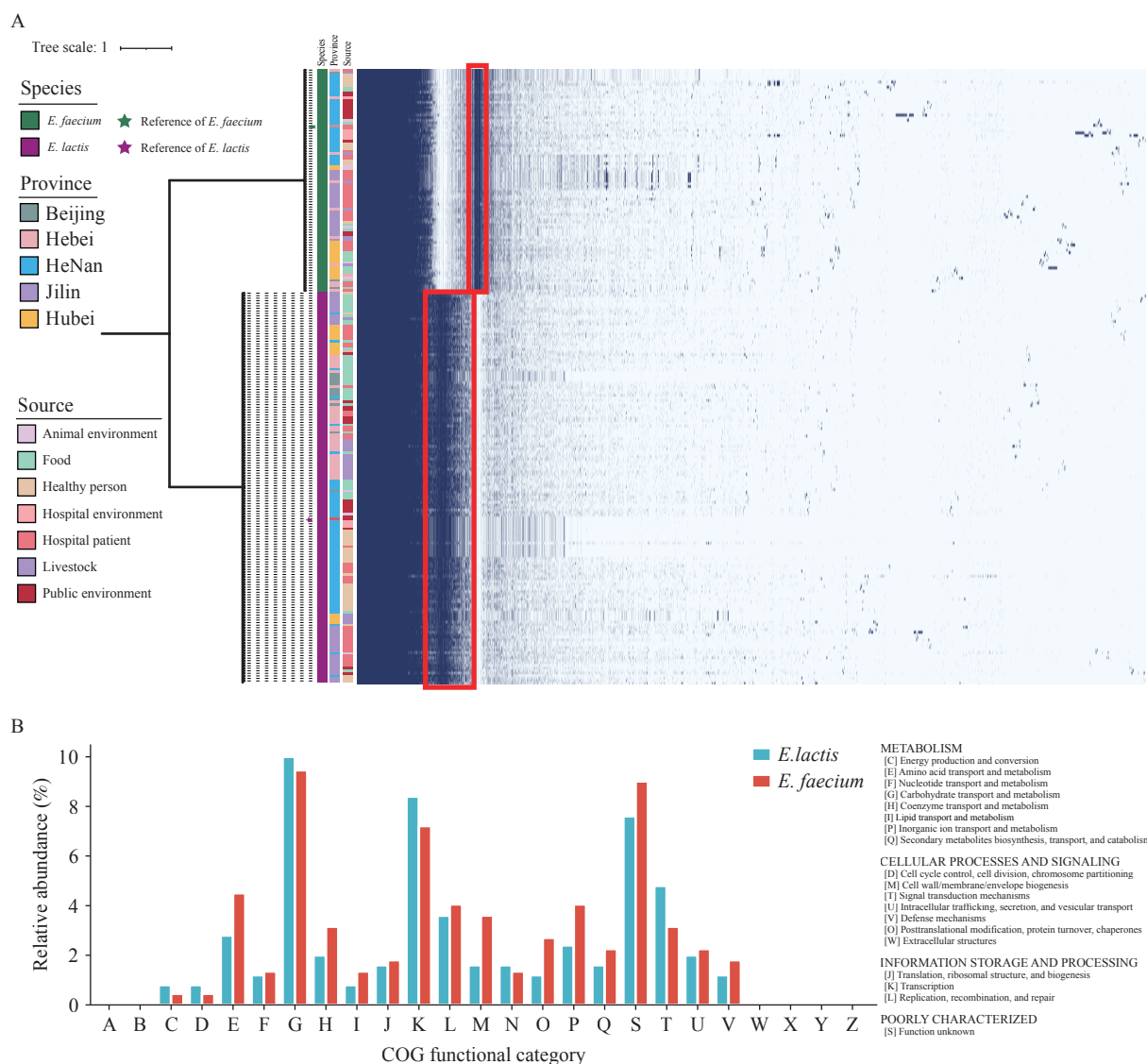


FIGURE 4. Pan-genome-wide association study of *E. faecium* and *E. lactis*. (A) Species-specific differential genes are highlighted in the red box. (B) Relative abundance of differential genes between *E. lactis* and *E. faecium* across distinct Clusters of Orthologous Groups functional categories.

Note: For (A), the colored bands on the right side of the phylogenetic tree represent genomic information for *Enterococcus* isolates. For (B), functional category explanations are provided on the right side of the figure.

Abbreviation: *E. faecium*=*Enterococcus faecium*; *E. lactis*=*Enterococcus lactis*.

macrolide resistance gene *msrC*, which is chromosomally encoded and therefore presents limited risk for horizontal gene transfer to other bacterial species (16).

The widespread distribution of adhesion genes likely contributes substantially to colonization capacity and virulence expression of both *E. faecium* and *E. lactis* within the food chain. Previous research has demonstrated that *sgrA* plays a critical role in bacterial adherence during hospital-associated infections by facilitating biofilm formation in *E. faecium* (17). The high prevalence of *sgrA* among *E. lactis* isolates suggests

that this species may harbor underappreciated clinical virulence potential, warranting enhanced surveillance of its pathogenic characteristics throughout food production and distribution systems.

Pan-GWAS analysis revealed substantial inter-species variation in gene content between *E. faecium* and *E. lactis*, while their functional gene distributions demonstrated remarkable conservation. This pattern suggests that despite divergent evolutionary trajectories involving species-specific gene acquisition and loss events, both species have maintained similar functional capabilities in essential biological processes (3).

Several limitations should be acknowledged. The absence of sampling data from 2020–2022 and the restriction to five PLADs may limit the generalizability of these findings to other time periods and geographic regions. Future surveillance efforts should expand temporal and spatial coverage while implementing species-specific monitoring strategies to comprehensively assess the evolving ABR landscape of enterococci in food production systems.

This research provides valuable insights for addressing antimicrobial resistance risks in the food chain, a central priority within the One Health framework. By characterizing the distinct ABR profiles and genomic features of *E. faecium* and *E. lactis*, this study addresses critical knowledge gaps in species-specific risk assessments of enterococci in Chinese food systems. These findings facilitate the integration of food safety, animal health, and public health perspectives, supporting the development of targeted interventions to prevent ABR transmission across food-animal-human interfaces.

Conflicts of interest: No conflicts of interest.

Ethical statement: Approved by the Ethics Committee of the State Key Laboratory of the China National Centre for Food Safety Risk Assessment (CFSA).

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SUPPLEMENTARY MATERIAL

SUPPLEMENTARY TABLE S1. Geographic prevalence of *Enterococcus faecium* and *Enterococcus lactis* in samples.

PLADs	No. of samples	No. of <i>E. faecium</i> samples	Prevalence of <i>E. faecium</i> (%)	No. of <i>E. lactis</i> samples	Prevalence of <i>E. lactis</i> (%)
Beijing	405	3	0.7	12	3.0
Hebei	404	10	2.5	34	8.4
Henan	425	33	7.8	60	14.1
Hubei	503	16	3.2	15	3.0
Jilin	496	25	5.0	32	6.5
Total	2,233	87	3.9	153	6.9

Abbreviation: PLAD=provincial-level administrative division; *E. faecium*=*Enterococcus faecium*; *E. lactis*=*Enterococcus lactis*.

SUPPLEMENTARY TABLE S2. Distribution and prevalence rates of *Enterococcus faecium* and *Enterococcus lactis* across sampling sources.

Sample category	No. of samples	No. of <i>E. faecium</i> samples	Prevalence of <i>E. faecium</i> (%)	No. of <i>E. lactis</i> samples	Prevalence of <i>E. lactis</i> (%)	χ^2	<i>P</i>
Environment	521	24	4.6	23	4.4	0	<i>P</i>>0.05
Public environment	234	13	5.6	16	6.8	0.2	<i>P</i> >0.05
Hospital environment	119	6	5.0	4	3.4	0.1	<i>P</i> >0.05
Animal environment	168	5	3.0	3	1.8	Fisher's exact test	<i>P</i> >0.05
Food	701	14	2.0	42	6.0		<i>P</i><0.001
Poultry	70	1	1.4	0	0.0	Fisher's Exact Test	<i>P</i>>0.05
Livestock	323	7	2.2	20	6.2		<i>P</i><0.05
Human	618	41	6.6	38	6.1	0.1	<i>P</i>>0.05
Periods							
2015–2019	694	30	4.3	37	5.3	0.6	<i>P</i> >0.05
2023–2024	1,539	57	3.7	116	7.5	20.6	<i>P</i> <0.001
Total	2,233	87	3.9	153	6.9	18.6	<i>P</i><0.001