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Genomic and resistome analysis of *Salmonella enterica* isolates from retail markets in Yichun city, China

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ABSTRACT

Nontyphoidal *Salmonella* (NTS) causes global outbreaks of foodborne disease. The main source of *Salmonella* for humans is animal-borne foods; however, the monitoring of *Salmonella* in the food chain via genomic platforms was limited in China. This study evaluated the prevalence, resistome, and virulome diversity of *Salmonella* strains identified from pork, retail environment, aquatic products, and poultry eggs of retail markets in Yichun city, Jiangxi province. The overall incidence of *Salmonella* was 9.4 %, with a higher contamination rate observed in pork at 13.5 %, followed by the retail environment at 7.69 %. The genomic analysis of the isolates revealed a total of fifteen distinct serovars, with serovar Enteritidis being the most prevalent (64.3 %). The phenotypic resistance analysis conducted by the broth microdilution method, revealed that 81.12 % of the isolates exhibited multidrug resistance (MDR), with high resistance to trimethoprim/sulphonamides (100 %), followed by tetracycline (99.3 %) and streptomycin (99.3 %). Genotypic analysis of antimicrobial resistance identified 80 antimicrobial-resistant genes (ARGs), with *mdf(A)*, *aph(3')-Ib*, *tet(A)*, *dfrA12*, *floR*, $bla_{TEM\text{-}1B}$, *qnrS3*, and *sul2*, conferring resistance to different antimicrobial classes, being the predominant ARGs. Additionally, forty ESBL genes, particularly critical genes such as $bla_{CTX\text{-}M}$ and $bla_{NDM\text{-}1}$, were also identified in *Salmonella* isolates. The *IncR*, *IncFIB (K)*, and *IncX1* plasmid replicons were widely prevalent and served as significant reservoirs of horizontally acquired foreign genes. Moreover, key virulence genes such as *cdtB*, *lpf* and *sef* were also detected, in addition to *Salmonella* pathogenicity islands SPI-1 and SPI-2. This study reveals the prevalence of multidrug-resistant and virulent strains of *Salmonella* serovars in the markets of Yichuan city, posing a risk of human infections. The gained knowledge provided essential baseline information that may be utilized for regular tracking of MDR *Salmonella* transmission in the food chain to minimize potential future outbreaks.

1. Introduction

The increasing global demand for animal-derived food products is a major dietary trend during this era, and it will most likely increase the possibility for colonization and dissemination of foodborne infections (e.g., *Salmonella*) [1]. The increasing emergence of *Salmonella enterica* serovars in outbreaks of human gastroenteritis infections worldwide has drawn attention to this pathogen [2–4]. The European Union ranks salmonellosis as the second most common human gastrointestinal infections, following *Campylobacter* infections [5]. Animals and their derived food products are considered as the main reservoirs for transmitting *Salmonella* to humans [6–10]. Food contamination can occur at several stages, from farm to fork and the environment where animals are grown and slaughtered, and they are mainly involved in food-borne outbreaks caused by pathogens in humans [11]. Furthermore, the expansion of global trade and the facilitation of cross-border mobility

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may contribute to the spread of contaminants and pathogenic agents in food products and susceptible humans [12,13]. Recently, The World Health Organization (WHO) has documented a widespread outbreak (from >11 countries) of MDR *S. typhimurium* ST34 infection linked to food animals and food in April 2022, indicating food safety and antimicrobial resistance concerns [14].

The widespread application of antibiotics, such as growth promotors in livestock farming, increases the emergence of antimicrobial resistance in *Salmonella* [15]. Consumption and improper handling of animal-derived products represent potential risks for the transmission of AMR *Salmonella* to humans, which may reduce the efficacy of the treatment and increase hospitalization. These MDR strains are directly linked to the increasing incidence of salmonellosis in humans [9,10,16]. According to a previous study, a high MDR pattern (86.0 %) was observed in *Salmonella* isolates, mostly from clinical sources [17]. *Salmonella* strains collected from food animals have shown resistance to quinolones and extended-spectrum β-lactamases [18]. *Salmonella* spp. and other extended-spectrum β-lactamase (ESBL) producing pathogens are becoming more common. Resistance to these key antimicrobials limits treatment options and may result in more severe clinical outcomes [3,17]. According to a previous study, antimicrobial resistance (AMR) directly caused approximately 1.27 million deaths globally and was associated with an estimated 4.95 million deaths in 2019. [19]. AMR *Salmonella* data must be monitored continuously to identify dynamic AMR patterns and detect emerging resistance genes and superbugs. Whole-genome sequencing (WGS) is an efficient approach for understanding and tackling antimicrobial resistance (AMR), genomic epidemiology, and investigating outbreaks [20].

Jiangxi province, located in southern China, is one of the major provinces for food animals in China, with numerous excellent local chicken and pig breeds [21]. This province is rich in rivers and lakes, with a humid subtropical monsoon climate, a wide range of aquatic animals, and a large population of food animals, providing a favorable habitat for *Salmonella* survival [22]. The total population of chickens in Jiangxi was 241.674 million in 2022, indicating a 4.2 % rise compared to the previous year [23]. A comprehensive study on the distribution of *Salmonella* serovars, the trend of MDR isolates, and the occurrence of β-lactamase resistance genes in food animals, their associated food products and environmental resources from Jiangxi province is lacking.

In this study, we therefore, characterized 143 *Salmonella* isolates collected from foods of animal origin, including pork, poultry eggs, aquatic products, and the retail environment in Yichun city, Jiangxi province, China through WGS. We also examined serovar diversity, AMR prevalence, virulence factors, and plasmids associated with AMR.

2. Methodology

2.1. Sample collection

The study was conducted over two years, from January 2020 to September 2021, to monitor *Salmonella* prevalence from various sources, including pork, poultry eggs, aquatic products, and the retail environment. The sample size for the current study was calculated using the following formula:

$$\text{Sample Size (N)} = z^2pq/d^2.$$

where N is the desired sample size, Z is the standard normal deviate set at 1.96, p is the estimated prevalence in the previous study (11.87 % from Zeng et al. [24] and 10.1 % to 26.5 % from Sun et al. [25] was used), q = 1-p, and d is the degree of accuracy set at 0.05. Therefore, the estimated sample size was ≤1168.

A total of 1528 food samples of animal origin, including pork (n = 746), poultry eggs (n = 230), aquatic products (n = 240), and retail environment (floor, knife, chopping board, and cages etc.) (n = 312), were randomized collected in three separate batches from five local agricultural markets across Yichun city, Jiangxi province, China. We mainly focus on major retail markets in the city, where a large number of customers seek to purchase animals and animal products. Animal food samples (≥250 g) and sterile cotton swabs from the retail environments were collected at each sampling site and stored in tightly sealed aseptic bags. The samples were immediately transferred to the microbiology laboratory at 4 °C for further processing within 2 h. All samples were analyzed qualitatively for *Salmonella* spp. using an enrichment method defined in the National Food Safety Standard of China—Food Microbiological Examination, *Salmonella* spp. (method GB 4789.4).

2.2. Isolation and identification of Salmonella spp.

Salmonella isolates were isolated and identified using previously described standard methods [26]. 10 g animal food samples and sterile swabs were initially enriched in 100 mL buffered peptone water (BPW) (Oxoid, UK) at 37 °C overnight. Subsequently, for selective enrichment, samples were further inoculated into Rappaport-Vassiliadis (MSRV) broth (Oxoid, UK) and cultured for 24 h at 42 °C. 100 uL of bacterial culture from MRSV was spread on selective media (XLD agar) (Oxoid, UK) and cultured at 37 °C overnight. Red colonies with black cores on XLD media were identified as suspected *Salmonella* colonies. For molecular confirmation, DNA was extracted from positive *Salmonella* isolates using a bacterial genome extraction kit (Beijing Solarbio Science Technology Co., Ltd., Beijing, China). Next, a conventional PCR assay targeting the *invA* gene was performed for *Salmonella* confirmation [4].

2.3. Antimicrobial susceptibility testing

The broth microdilution method was used to determine the Minimum Inhibitory Concentration (MIC) for each isolate of *Salmonella*, as previously described [27]. A total of 13 clinically important antibiotics from 8 different antimicrobial classes were used to evaluate phenotypic AMR patterns according to CLSI guidelines. The antibiotics evaluated were ampicillin (AMP), amoxicillin-clavulanic acid (AMC), sulfamethoxazole/trimethoprim (SUL), kanamycin (KAN), cefoxitin (CX), ceftiofur (CF), chloramphenicol (CHL), streptomycin (STR), gentamicin (GEN), ciprofloxacin (CIP), nalidixic acid (NAL), tetracycline (TET), and azithromycin (AZI). The data were analyzed using the Clinical and Laboratory Standards Institute (CLSI) guidelines [28]. The *Escherichia coli* ATCC 25922 strain was used for control. MDR isolates were defined as *Salmonella* strains resistant to more than three different antibiotic classes. Pan-drug resistance (PDR) was described as resistance to all drugs in all antimicrobial classes.

2.4. Whole-genome sequencing, de novo assembly, and annotation

Genomic DNA was extracted from each isolate using the Genomic DNA Extraction Kit (Promega, Beijing, China). The purity of the DNA sample was confirmed using a Nanodrop spectrophotometer. Illumina sequencing libraries were constructed using the Rapid DNA-Seq Kit (PerkinElmer., Shanghai, China) from fragmented DNA. The sequencing was carried out using a 250-bp paired-end protocol on Illumina sequencers (HiSeq/NovaSeq).

FastQC was used to assess sequencing quality, and trimmomatic v.0.30 was used to remove adapter sequence [29]. Denovo assembly was carried out using SPAdes v.4.0.1. [30]. The assembled genomes were evaluated using a quality assessment tool for genome assemblies (QUAST) for assembly quality [31]. Prokka v.1.13 [32] was used to annotate each assembly with default settings. Serotyping is the gold standard for classifying *Salmonella*. SeqSero2 v.4.6.1 was used for in silico serotyping of raw sequencing reads [33].

2.5. In silico identification of antimicrobial-resistant determinants and sequence types

Allelic profile sequence types (ST) were identified using in silico multi-locus sequence typing (MLST V2.0) [34]. Antimicrobial resistance genes (ARGs) were identified through ResFinder V4.1 and the Comprehensive Antibiotic Research Database (CARD). Antimicrobial resistance genes were screened using ResFinder with default settings. The results of both databases were combined by using gene IDs to provide a complete list of ARGs [35].

2.6. Identification of virulence genes and plasmid replicons

The virulence genes were identified using ABRicate v0.9.7 (https://github.com/tseemann/abricate) with default parameters. Plasmid Finder 2.0 was used to identify plasmids with default settings [36].

2.7. Data analysis and projection

Bar and Pie Charts were created using GraphPad Prism v9.0. Specific dynamics were identified by analyzing interactions between sampling time, host and serovar. To visualize the data, heatmaps were generated using the ggplot2 package in R programming.

3. Results

3.1. Prevalence of Salmonella serovars

During 2020–2021, a total of 143 (9.4 %) positive *Salmonella* isolates were found in 1528 samples from pork, poultry eggs, aquaculture and retail environment (Table 1). Our findings indicated that there was a significant difference ($p < 0.01$) in *Salmonella* detection among samples from diverse sources, with pork showing the greatest occurrence (13.54 %), followed by retail environment (7.69 %), aquaculture (4.17 %), and chicken eggs (3.48 %). Based on the period of sample collection, a higher frequency of *Salmonella* isolates was recovered during 2021 (14.97 %, 109/728), followed by 2020 (4.25 %, 34/800) (**Supplementary data S1**). According to in silico serotyping methods, the 143 *Salmonella* isolates belonged to 15 distinct serovars. The most prevalent serovar was Enteritidis (64.33 %, 92/143), followed by Typhimurium (6.99 %, 10/143), and *London* (4.19 %, 6/143) (Fig. 1). The findings also revealed that serovars Enteritidis and Typhimurium were the most commonly found in pork, aquaculture and the environment in this study (Fig. 1 **& Supplementary data S2**).

3.2. Antimicrobial resistance phenotype

The broth microdilution MIC assay was used to assess antimicrobial resistance in *Salmonella* isolates. The most common resistance found in isolates were against SUL (100 %, $n = 143$), TET (99.3 %, $n = 142$), STR (99.3 %, $n = 142$), AMP (98.6 %, $n = 141$), AMC (98.6 %, $n = 141$), CHL (97.9 %, $n = 140$), GEN (59.4 %, $n = 85$), and CIP (51.0 %, $n = 73$). Resistance to KAN and CX was identified in 52.4 % and 47.6 % of the isolates, respectively, while CF showed the least resistance (37.8 %) (Fig. 2a). Interestingly MDR pattern was reported in (81.1 %, $n = 116$) *Salmonella* isolates, while PDR or non-susceptibility to all antimicrobial categories, was observed in (18.88 %, $n = 27$) (Fig. 2b). Overall, pork samples had the highest frequency of MDR and PDR isolates (55.9 % & 14.7 % respectively), followed by the environment (16.8 % & 3.5 %) and aquatic products (6.3 % & 0.7 %) (Fig. 2c). There were no PDR isolates found in poultry egg samples.

Table 1
Sample summary and *Salmonella enterica* positive isolates distributed across Pork, Aquatic products, Poultry eggs and Environmental sources.

Source	Total no. of Samples	No. of Positive Samples	Positive Rate (%)	χ2 (P)
Pork	746	101	13.40	33.39 (<0.01)
Retail Environment	312	24	7.37	
Aquatic products	240	10	4.58	
Poultry eggs	230	8	4.35	
Total	1528	143	9.4	

3.3. Multidrug resistance (MDR) patterns

Furthermore, we analyzed several antimicrobial resistance patterns, such as tri-, tetra-, penta-, and hepta-drug resistance patterns (Fig. 3). The occurrence of clinically significant resistance patterns, including Tri (ACT: ampicillin, chloramphenicol, tetracycline), Tetra (ASSuT: ampicillin, streptomycin, sulfamethoxazole, tetracycline), Penta (ACSSuT: ampicillin, chloramphenicol, streptomycin, sulphonamide, tetracycline), and Hex resistance patterns (ACSSuT-AMC: ACSSuT, amoxicillin-clavulanic acid), was observed in more than 97.9 % of the isolates. ACSSuT-AMC-CIP was another common antibiotic resistance pattern observed among *Salmonella* (51.05 %) isolates. An octa-drug resistance pattern ACSSuT-AMC-CIP-AZI (ACSSuT and azithromycin) was also detected (33.57 %) in isolates (Fig. 3a**)**. These MDR patterns were also associated with the source of the isolation. ACT, ACSSuT-AMC, ASSuT-CX, ACSSuT-AMC-CIP and ACSSuT-AMC-CIP-AZI multidrug-resistant patterns were more frequent in isolates acquired from pork followed by environment, aquaculture, and poultry eggs **(**Fig. 3b**)**. In terms of phenotypic resistance to several antibiotic classes, *Salmonella* isolates obtained from foods of animal origin and retail environment exhibited increased resistance to aminoglycosides and beta-lactams **(**Fig. 3c**)**. However, *Salmonella* strains from pork or environmental samples displayed more critical AMR phenotypes than those strains isolated from poultry eggs.

3.4. Genotypic resistome of Salmonella isolates

Complete genome sequences of 143 *Salmonella* isolates were investigated to explore antibiotic resistance genes using an *in-silico* approach. Eighty genes showed resistance to ten antimicrobial groups, including β-lactams, trimethoprim, aminoglycosides, rifampicin, tetracycline, phenicol, sulfonamides, quinolones, and macrolides were found **(**Fig. 4**)**. The most detected ARGs were *floR* encoding resistance to phenicols (67.13 %; 96/143), *mdf(A)* encoding resistance to Macrolides (63.64 %; 91/143), *tet(A)* encoding resistance to tetracyclines (58.04 %; 83/143), *dfrA12* encoding resistance to trimethoprim (49.65 %; 71/143), $bla_{\text{TEM–1B}}$ encoding resistance to penicillins (43.36 %; 62/143), *aph(3′)-Ib*, encoding resistance to aminoglycosides (34.27.%; 49/143), *sul3* encoding resistance to sulfonamides (37.06 %; 53/143), and *qnrS1* encoding resistance to fluoroquinolones (41.26 %; 59/143). Forty resistant genes of beta-lactam class, including ceftriaxone-mediated ESBLs ($bla_{\text{CTX-M}}$), AmpC (bla_{CMY}, $bla_{\text{ACT-2}}$ & bla_{DHA}) β-lactamases, carbapenems-mediated ESBLs ($bla_{\text{NDM-1}}$ & bla_{OXA}), penicillin mediated ESBLs (bla_{TEM} & bla_{SHV}) were also detected. The widespread distribution of key resistance genes in isolates poses a major public health risk. Moreover, regarding the isolation source, the results showed that isolates from pork and environmental sources harbor more diversified antimicrobial resistance genes. Poultry egg samples exhibit the least incidence of AMR determinants. The study demonstrated the association between the phenotypic trend of antimicrobial resistance (AMR) and the existence of related genes **(**Fig. 3c**)**. The results indicated that the highest correlation between genotypic and phenotypic resistance was found for tetracycline (98.5 %), trimethoprim-sulfamethoxazole (97 %), and aminoglycosides (96.5 %).

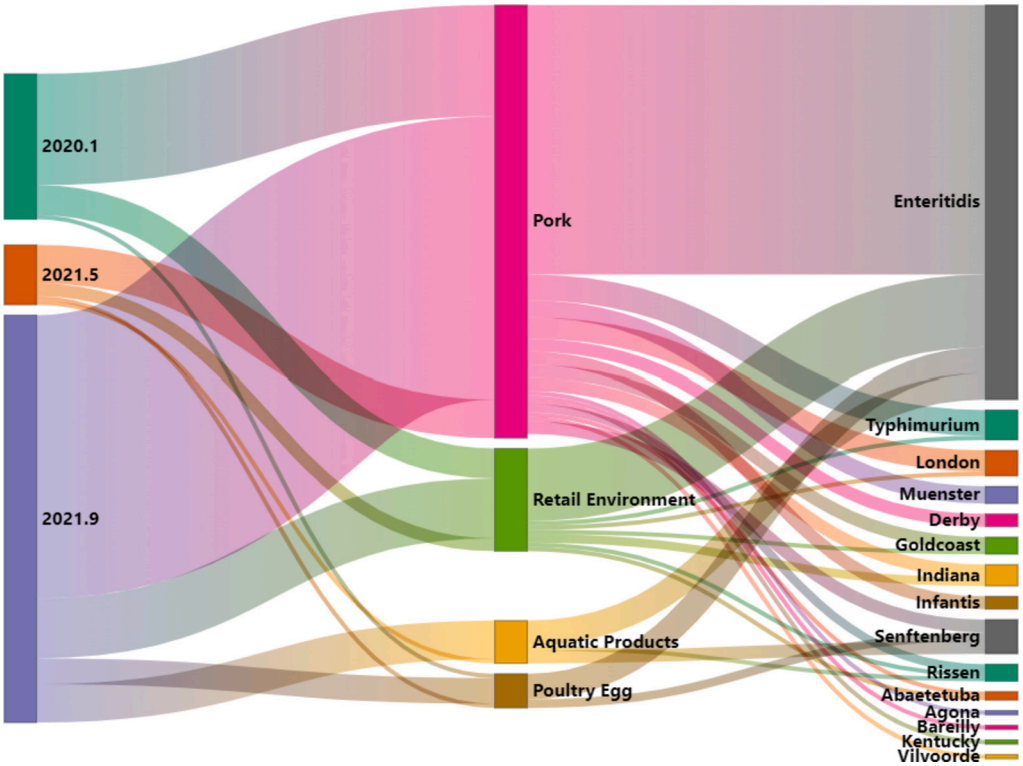

Fig. 1. A Sankey diagram demonstrating the temporal distribution of *Salmonella* serovars among pork, aquatic products, poultry eggs and retail environmental sources in Yichun. The diameter of the line is proportional to the number of isolates from a given source.

3.5. Detection of plasmid replicon using WGS

The plasmid replicons found in *Salmonella* samples were analyzed using Plasmid Finder. The results identified 33 different plasmid replicons among the 143 genomes investigated in this study (Fig. 5). The most abundant plasmid replicon identified was *IncR* (37.06 %; 53/143), followed by *IncFIB* (*K*) (27.97 %; 40/143) and *IncX1* (25.84 %; 37/143). All these strains (143/143) were positive for at least one plasmid. Our results showed that pork isolates have the most diverse plasmids (27 types), followed by environment and aquatic products (nine types of plasmids in each source), while only one plasmid replicon was identified in poultry egg isolates.

3.6. Co-existence of plasmid contigs and antimicrobial resistance genes

The co-existance of plasmid replicons and antibiotic resistance genes was evaluated Fig. 6a). The results showed that the IncQ1 plasmid, alongside the *Col3M*, *IncFIA*, *IncFIC* (*FII*), *IncFIB*(*S*), *IncX1*, *IncU*, *IncR* and *IncFII*(*S*) plasmids, are the primary carrier of antimicrobial resistance genes. The AMR genes mostly linked with *IncQ1* were $bla_{\text{TEM-1B}}$, *floR*, *aph*(*6*)-*Id*, *ant*(*3″*)-*Ia*, *aph*(*3′*)-*IIa*, *aph* (*3″*)-*Ib*, *qnrS2*, *qnrD1*, *tet*(*A*) and *sul2*, encoding resistance to the β-lactam, phenicol, aminoglycoside, quinolone, tetracycline, and sulfonamide respectively. Moreover, the plasmid replicons and ARG co-occurrences were mainly detected in pork and environmental isolates.

3.7. Invasiveness index of Salmonella isolates in different hosts

The Invasiveness Index employs DeltaBS and random forests to identify gene degradation patterns associated with invasiveness in *Salmonella*, indicating potential niche adaptation. The results suggested that the majority of isolates exhibit genetic modifications previously observed in extraintestinal infection serovars (Fig. 6b). The isolates from poultry eggs were less invasive. The results showed no significant ($p >$ 0.05) variation in invasive index among isolates from various sources.

3.8. Prediction of virulence profiles and Pathogenicity Island (PIs)

Genetic virulence characteristics were studied in 143 genomes to have a better understanding of *Salmonella* pathogenicity. VFDB and SPIFinder were used to identify virulence factors and Pathogenecity Islands (PIs) in all *Salmonella* genomes, respectively. PIs such as C63PI, SPI-1, SPI-2 SPI-5, SPI-9, SPI-14, and SPI-13 were found in all isolates. The findings revealed the identification of 105 distinct virulence genes, indicating various *Salmonella* virulence and pathogenicity pathways (Fig. 7). Furthermore, our results indicated the presence of cytolethal distending toxin (CDT) genes (*cdtB*, *pltA*, *pltB*) encoding typhoid toxin production in isolates from environment (6.99 %, 10/143), aquaculture (7.69 %, 11/143) and poultry eggs (4.19 %, 6/143). In contrast, the majority of the isolates from pork, environment, aquaculture, and poultry eggs had the virulence plasmid genes and plasmid-encoded fimbriae, which encode fimbriae that are crucial to the NTS pathogenicity. However, *Salmonella* Pathogenicity Islands 1 and 2 (SPI-1 and SPI-2) and key virulence genes were present in most *Salmonella* isolates examined in this study.

4. Discussion

NTS is a prominent cause of foodborne infection globally, with 22.8 million human cases in the Asian region each year [37–39]. Foodborne outbreaks primarily result from the consumption of contaminated food animals and their related products, particularly involving foodborne pathogens such as NTS [1,21,40]. Another concern is the ability of *Salmonella* to persist outside its host in farm environments, including manure, soil, and water [41]. China produces and consumes more than 500 million pigs annually, which makes up a significant portion of global pork consumption [42]. Jiangxi is a major animal breeding region in China, known for high-quality native chicken and pig breeds [21].

(a)

Class	Mol.	%AR	MIC range (μg/ml)									
			0.125	0.25	0.5	1	2	4	8	16	32	64	>64
Penicillins	AMP	98.6				0.7		0.7					98.6
	AMC	98.6						0.7	0.7		2.1	1.4	95.1
Cephalosporins	CF	37.8			10.5	32.2	20.3	4.2	2.8	2.1	5.6	4.2	18.2
	CX	47.6					2.8	4.9	28	16.8	7	2.8	37.8
Aminoglycosides	KAN	52.4						0.7	19.6	16.8	10.5	7	45.5
	GEN	59.4			2.1	8.4	18.2	6.3	5.6	8.4	27.3	2.1	21.7
	STR	99.3								0.7	1.4	2.1	95.8
Quinolones	NAL	58.7					0.7	7.7	16.8	16	7.7	2	49
	CIP	51.0	10.5	7.7	7	13.3	10.5	10.5	1.4	21	18.2		
Sulfonamides	SUL	100.0						0.7			32.2	0.7	66.4
Macrolides	AZI	51.0		0.7		2.1	21.7	9.1	9.8	5.6	6.3	2.1	42.7
Tetracyclines	TET	99.3							0.7			0.7	98.6
Phenicols	CHL	97.9						1.4	0.7			9.8	88.1

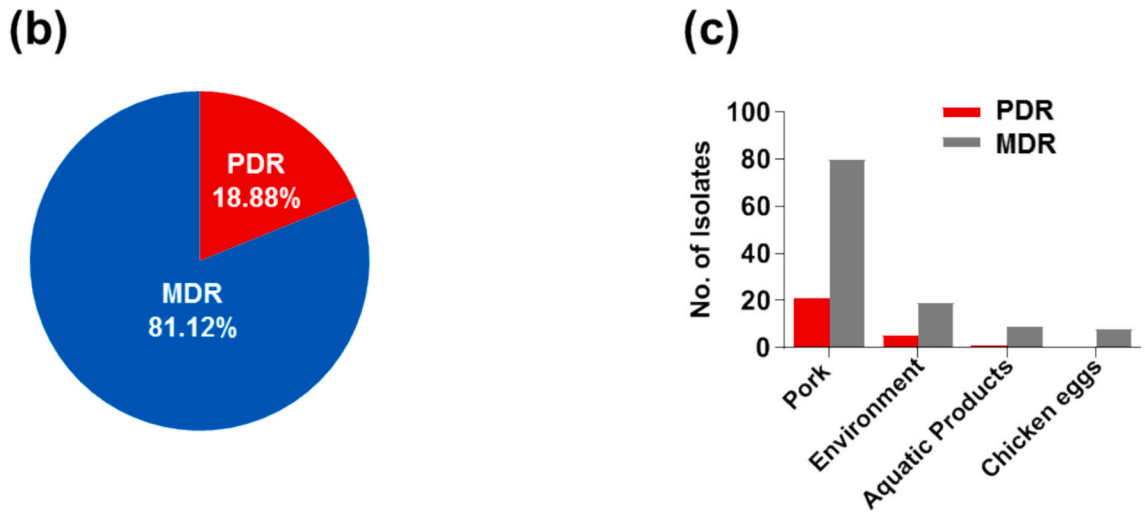

Fig. 2. Summary of overall resistance percentages of *Salmonella* isolates (n = 143) to different types of antibiotics determined by the broth microdilution method. **(a)**: The individual AMR percentage of *Salmonella* tested with 13 antibiotics. **(b)**: Percentage of *Salmonella* isolates found to be MDR and PDR in our study. **(c)**: MDR and PDR *Salmonella* isolates were found in pork, the environment, aquatic products, and poultry eggs.

Food animals and animal-derived products from Jiangxi are also distributed to other surrounding provinces such as Hunan, Guangdong, Zhejiang and Fujian. These transmission pathways also contribute to the spread of pathogens and AMR strains from farmers to dealers and consumers. Therefore, the presence of foodborne pathogens, especially *Salmonella* in Jiangxi has consequences not only at a local level but also across a wide geographical area, in relation to the One Health concept. This study investigated the prevalence, serovar distribution, multidrug-resistant profiles, and occurrence of *Salmonella* spp. in foods of animal origin and the retail environment in Yichun city from Jiangxi Province, China, collected from 2020 to 2021.

Accordingly, over 70 % of foodborne disease outbreaks in China are linked to *Salmonella* spp., with a significant number of cases associated with the consumption of foods of animal origin, particularly pork and chicken, which serve as primary reservoirs for the dissemination of *Salmonella* spp. [43]. In this study, the overall prevalence (9.4 %) of *Salmonella* in foods of animal origin and retail environment was lower than previous studies from China(12–19 %) [36,44,45] and was higher than that in Spain (8.9 %) [46] and Poland (5.5 %) [47]. In our study, the incidence of *Salmonella* in pork was higher than in previous studies from China [48,49]. In contrast, we found an incidence of *Salmonella* in retail environments, which was higher than what was found in Chongqing (6.93 %) and Shaanxi 11.3 % [50,51]. The level of contamination of aquatic products (6.99 %) and poultry eggs (5.59 %) was lower than those reported in China, Thailand and Malaysia [52–54]. Our data suggest that pork is an essential reservoir of *Salmonella* contamination, highlighting the need to monitor *Salmonella* infections in food-producing animals and the food chain supply.

Epidemiological monitoring of *Salmonella* serovars needs to be prioritized across the food system to ensure consumer safety. Our results showed that *S. enteritidis* ST11 (64.33 %) was the most common serotype found among the identified serovars, which is consistent with a previous

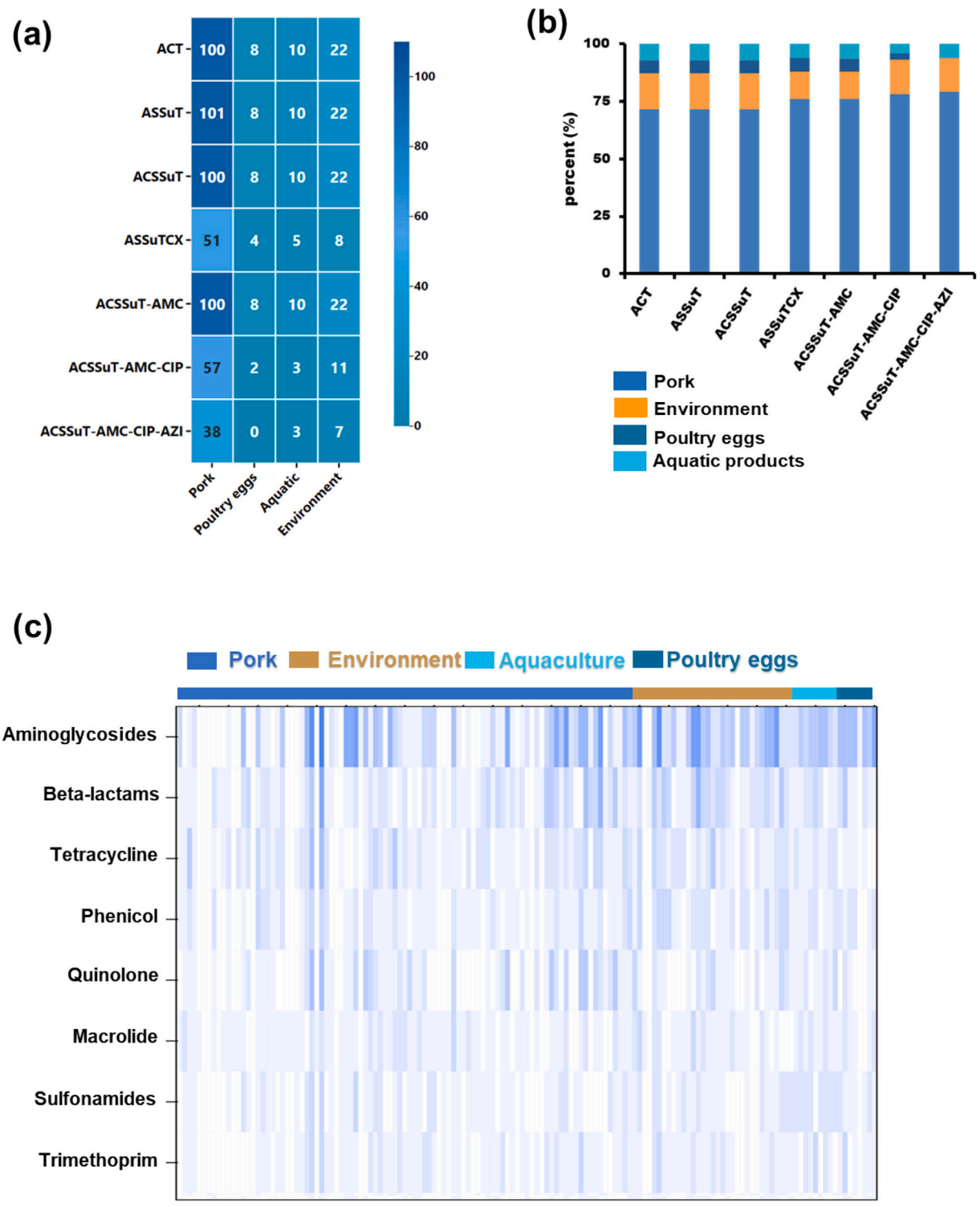

Fig. 3. Antimicrobial resistance pattern of 143 strains of *Salmonella enterica* isolated from different sources. **(a, b)**: Different antimicrobial resistance patterns of all 143 *Salmonella* isolates according to sample sources. **(c)**: The heatmap shows AMR profiles grouped by the drug class to which *Salmonella* strains isolated from pork, environment, aquaculture, and poultry eggs in China were phenotypically resistant.

study isolated from dead chicken embryos in Northern China [55]. In China, *S. enteritidis* was shown to be the most common serovar in isolates from Pork [36], chicken eggs [56], seafood [2] and the environment [57]. Furthermore, it is well-known that *S. enteritidis* is one of the primary serovars that cause salmonellosis in humans worldwide [58,59]. However, previous studies conducted in northern China revealed that the most common *Salmonella* serovars in chicken meat were Meleagridis, Senftenberg, Kentucky, Corvallis, Hadar, and Derby [60]. These variations can result from changes in temperature across different seasons, local environmental factors, and the sampling strategy. Therefore, dissemination of these strains throughout the food supply poses major risks to end consumers and may cause serious food-borne illnesses.

Conventionally, *Salmonella* infections can be treated with a variety of antibiotics. However, in recent decades, antimicrobial resistance

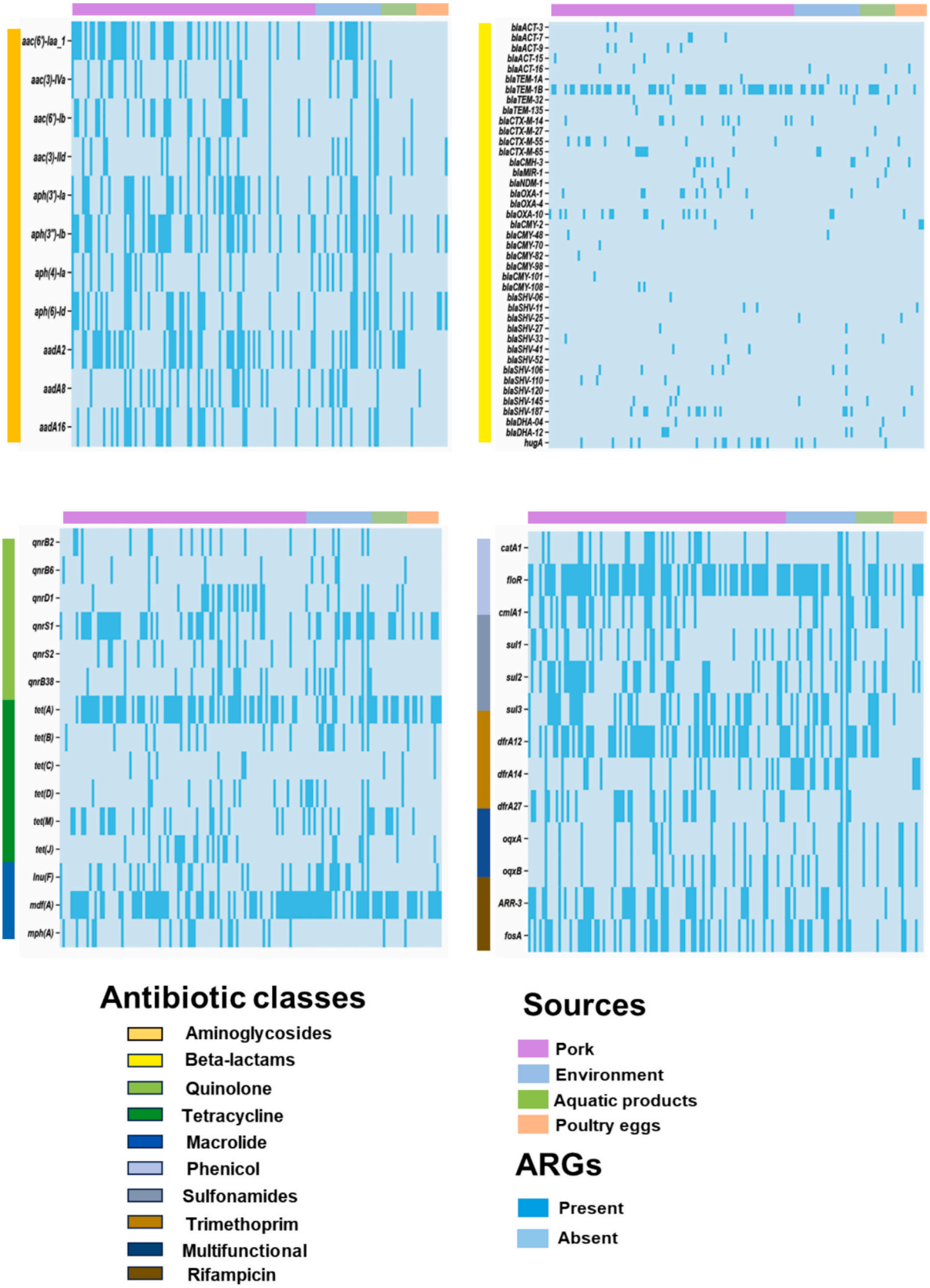

Fig. 4. The distribution of antimicrobial resistance genes (ARGs) belongs to different antimicrobial classes among 143 *Salmonella* isolates from veterinary and environmental sources. Genes detected in the genomes associated with AMR are shown on the y-axis of the graph and are grouped by drug class. The dark blue color in the heatmap represents the presence of ARGs and light blue color indicates the absence of ARGs. The strain names were shown at the top. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

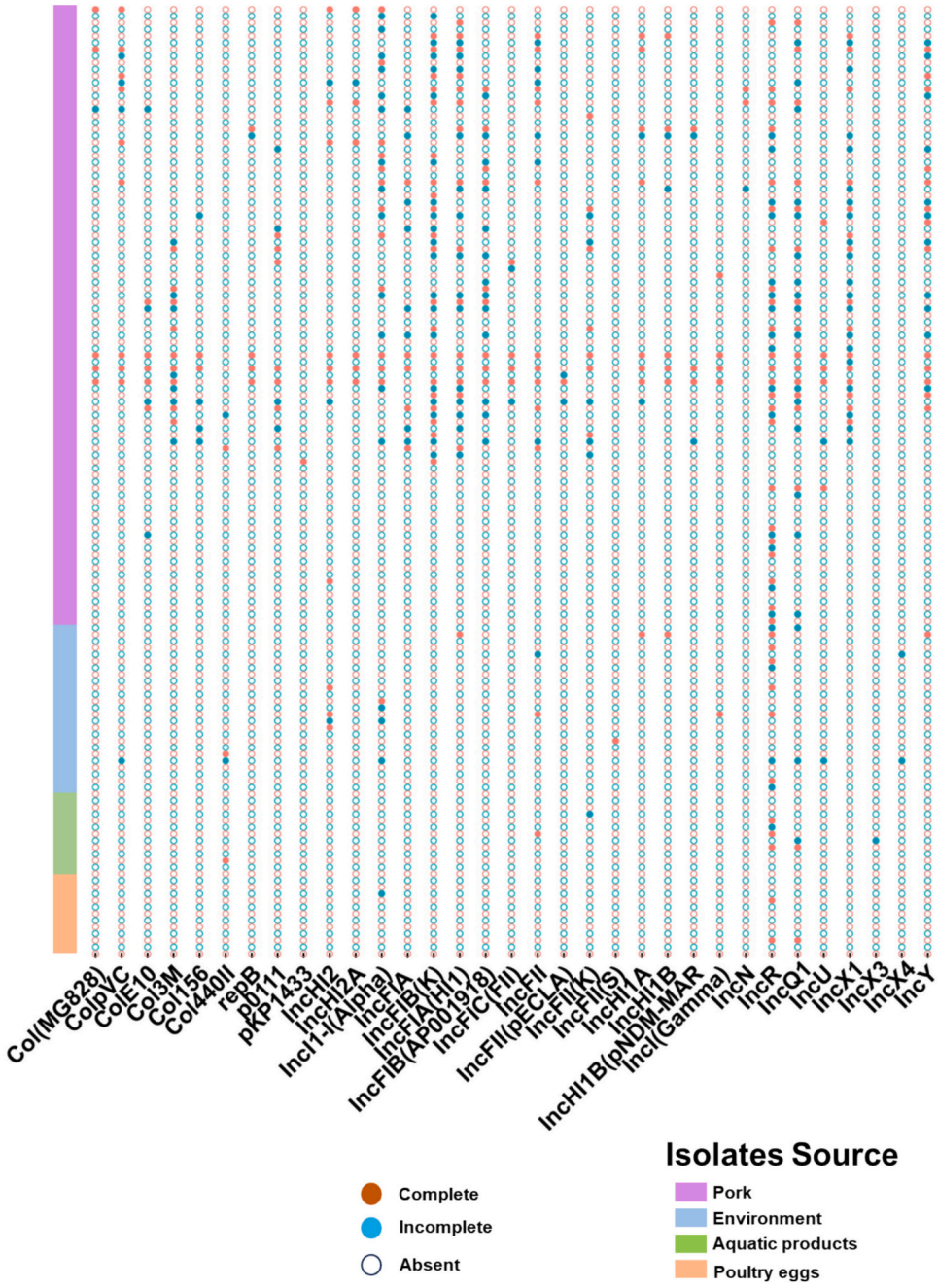

Fig. 5. Distribution of plasmid replicons among *Salmonella* strains isolated from different sources.

Salmonella has been reported globally, especially for isolates from the environment, animals, and food. Our results showed that 81.12 % of the isolates exhibited MDR to a minimum of three antimicrobial classes. According to the previous findings, *Salmonella* isolates with high resistance to tetracycline, ESBLs, quinolones, and ampicillin, have been identified worldwide in samples collected from different food sources [44,61–63]. The majority of the isolates (>90 %) identified as *Salmonella* serovars Enteritidis, Derby, London, Typhimurium, and Indiana were resistant to at least one antibiotic, which is consistent with prior findings reported in China [23]. The majority of resistant strains were isolated from pork, suggesting that pork may serve as a significant reservoir for non-typhoidal *Salmonella* MDR strains. The high prevalence of MDR among *Salmonella* spp. may provide a major hurdle to the effective treatment of *Salmonella* in China. This study reveals a high prevalence of tetra-, penta-, and hepta-resistant patterns in environmental and pork isolates, which poses a significant public health threat due to potential treatment failures after simple infections caused by MDR isolates. These findings were consistent with various global investigations demonstrating a high incidence of MDR patterns among *Salmonella* strains isolated from different sources [19,30]. The extensive use of antibiotics in the medical and veterinary sectors that resulted in a high AMR by exerting a selection pressure against the used antimicrobials. Our findings raised serious concerns for public healthcare systems, as quinolone and ESBLs antibiotics are the first-line treatment choices for human salmonellosis. Consequently, stringent policies should be implemented to reduce the utilization of essential antibiotics in livestock agriculture.

We used WGS analysis to determine the presence of several ARGs in order to obtain a comprehensive understanding of the mechanisms underlying the phenotypic resistance of the isolates. The results showed

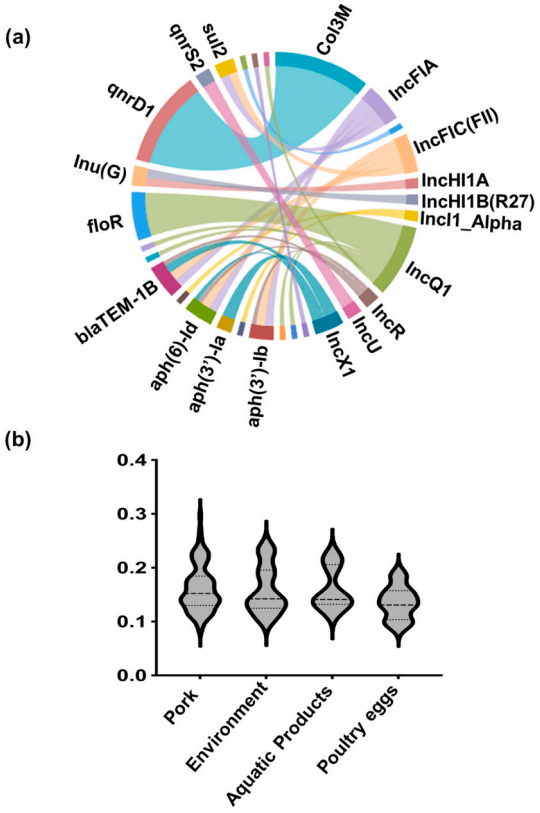

Fig. 6. Co-occurrence of common plasmid replicons, top ten detected AMR-associated genes and invasive index of *Salmonella* isolates from different sources. **(a)**: The primary source of ARGs is carried by distinct plasmid replicons. The connecting line between ARGs and plasmid replicons represents the potential carrying relationship. **(b)**: The box plot graph showed the invasive index of *Salmonella* isolates from different sources. Isolates from poultry eggs are less invasive. No statistical differences were observed among isolates from different sources.

that various determinants contributing to resistance against distinct antibiotics were identified in our sequenced strains, with each isolate containing between 1 and 23 antibiotic resistance genes (ARGs). The most detected genes were *tet(A)*, and $bla_{\text{TEM–1B}}$, these results were consistent with previous studies [64,65]. However, another Chinese investigation revealed that bla_{TEM} was dominant in isolates from chicken embryos [66]. Moreover, in our study, the detection of ESBL genes, including $bla_{\text{NDM-1}}$, $bla_{CTX\text{-}M}$, bla_{SHV}, bla_{TEM} and bla_{ACT}, from foods of animal origin and retail environment is alarming. A previous study from China identified $bla_{\text{NDM-1}}$ gene conferring carbapenem resistance in *Salmonella* isolated from a child [67]. This could be because food animals serve as *Salmonella* reservoirs, increasing the number of human cases of foodborne salmonellosis caused by MDR strains. According to a previous study, *Salmonella* isolates obtained from food animals in China in 2019 were the first reported to contain the $bla_{CTX\text{-}M\text{-}130}$ gene [68]. Our findings also illustrated that isolates from pork and environmental sources harbor more diversified ARGs than other sources. The animal protein consumption in Asia increased over threefold from 1960 to 2013 [69]. Livestock farming expanded quickly in order to satisfy this demand. Because of the high animal's population and the irrational use of antibiotics to prevent and treat diseases during animal husbandry, there is increasing selection pressure for the development of resistant bacterial strains in certain sources [48]. Therefore, there should be better surveillance of these strains since isolates from food animals can be a major carrier for the transmission of ARGs. Finally, we also found high coherence between phenotypic and genotypic resistance, particularly for aminoglycosides, trimethoprim-sulfamethoxazole, and tetracycline, which is consistent with a previous study [70]. These results are considered serious concerns to public health, leading to limited drugs of choice for the treatment of salmonellosis in humans as well as animals.

Salmonella virulence factors contribute to pathogenicity and host colonization by facilitating attachment, invasion, and replication within host cells, while evading host defenses through various mechanisms, including flagella, adhesion systems, toxins, and capsules. Virulence factors are commonly grouped within pathogenicity islands, which are typically located on mobile genetic elements like plasmids [71]. Our study identified several virulence genes primarily associated with secretion system components and fimbrial adherence determinants, which are linked to *Salmonella* pathogenicity Islands SPI-1 and SPI-2. *CDT* genes (encoding typhoid toxin production) of *pltA, pltB,* and *cdtB,* were identified in aquatic products, poultry eggs and environmental samples, which is consistent with earlier studies indicating the link of *CDT* genes with food animal isolates [72,73]. Furthermore, the *cdtB* gene was detected in NTS isolates, leading to invasive infections in humans [30,74]. The presence of virulence genes in *Salmonella* is epidemiologically associated with human salmonellosis, highlighting the necessity of establishing a surveillance program to protect public health and mitigate potential threats. The fimbrial adherence determinants (*pef* and *spV* genes) are crucial in the virulence mechanisms of NTS strains [75]. The prevalence of *Salmonella* isolates harboring numerous virulence genes in food animals and their associated products pose a significant risk to public health, since it has the potential to cause severe illness in end consumers.

The major hurdle in preventing the global dissemination of multidrug-resistant (MDR) infections is the possibility of rapid transfer of virulence factors and resistance genes across isolates. Plasmids serve as the primary means of transferring genetic information horizontally. Here, 33 distinct plasmid replicons were detected. The most abundant plasmids were *IncI1-I* (Alpha), *IncFIA* (*HI1*), and *IncR*, prevalent in pork, environments, and aquaculture. These plasmids had previously been observed in *Salmonella* isolates obtained from pork [7,76]. Interestingly, it is found that these plasmid types carry key antimicrobial resistance genes, including bla_{TEM}, *QnrS2*, *floR*, *Sul2* and *aph* (*6*)-*Id*. The isolates that possess the *spv* virulence-associated region and plasmid encoding fimbriae exhibit hypervirulence and enhance bacterial fitness [77]. Our results also showed that *Salmonella's* main antimicrobial resistance determinant carrier is *IncQ1*, along with *IncX1* and *IncI1* alpha. These results are consistent with previous findings in which isolates from China plasmids carry different antimicrobial resistance genes [77,78]. Hence, the presence of these plasmids in the isolates raises severe concerns regarding the horizontal spread of antibiotic resistance along the food chain. The burden of invasive bloodstream infections caused by MDR *S. enterica* continues to increase, especially in developing countries [75]. The genomic analysis of isolates in this study found that strains obtained from pork, the retail environment, and aquatic products had a higher invasive ability, which may have increased the risk of diarrhea. According to previous findings, most invasive *Salmonella* serovars are acquired from food, water, and the environment [79,80]. Our study has a limitation in that it was a regional investigation with a particular focus on Yichuan city, China, and the findings might not be broadly applicable. However, the high rate of *Salmonella* contamination in various food animal products and their associated environments in our study indicates that animal-derived food serves as a vehicle for the spread of MDR *Salmonella* in Jiangxi. Therefore, multidisciplinary efforts are needed to limit these MDR *Salmonella* strains with invasive capabilities in the Chinese food system. China ranks among the largest global producers and consumers of food animals, particularly pork and poultry. Consequently, there is a necessity to enhance the regulation and monitoring of antibiotic use in livestock production. Moreover, *Salmonella* contamination can be reduced by maintaining and implementing essential control procedures like good manufacturing practices (GMP) and hazard analysis and critical control point (HACCP), as well as by improving food handler/ processor training. Finally, safe food

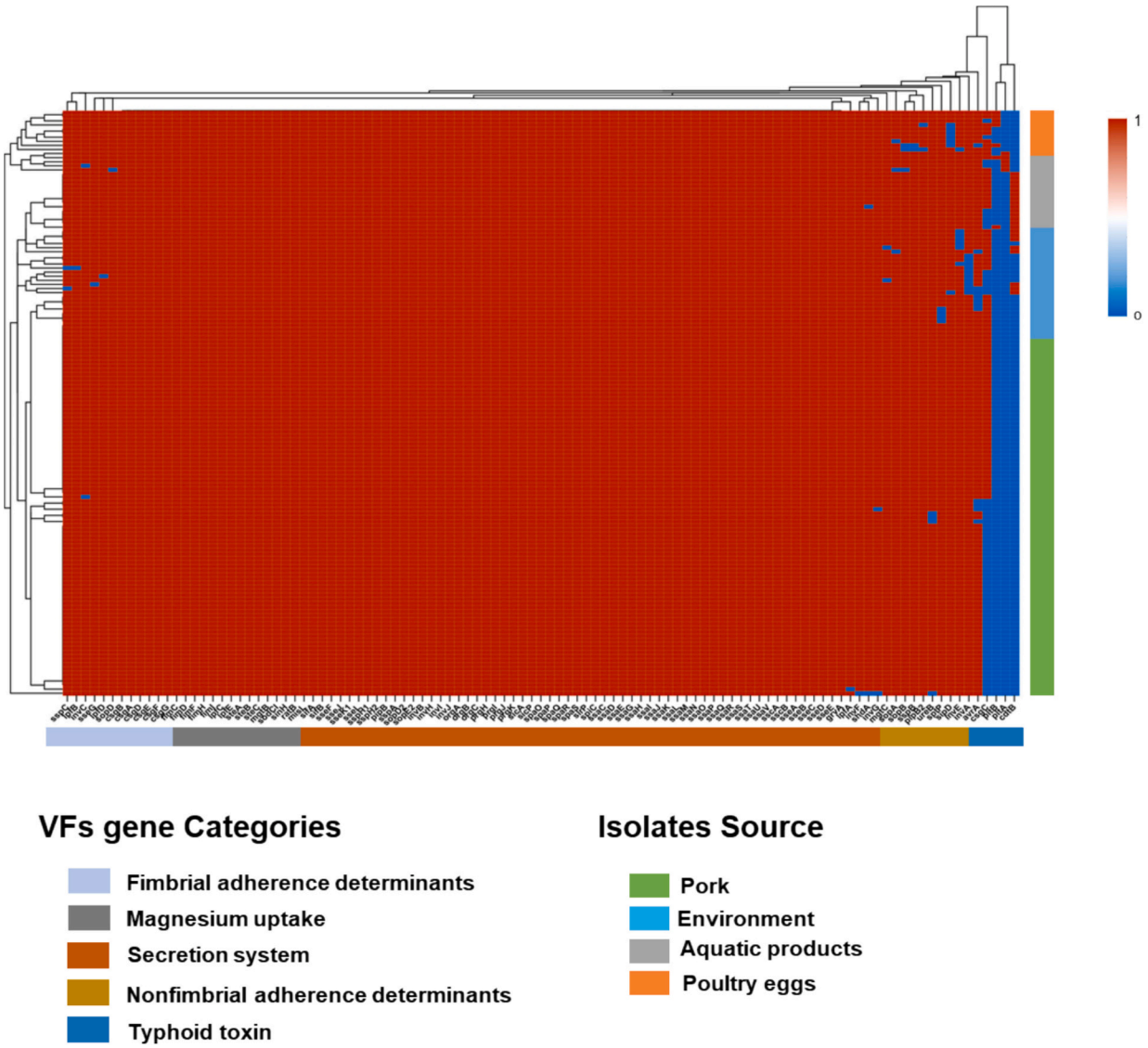

Fig. 7. Distribution of virulence genes among the studied isolates. The color of the individual cells varies with the prevalence of each virulence gene.

processing practices, including maintaining clean hands, utensils, and surfaces, separating raw from cooked foods, and cooking foods to safe minimum internal temperatures, should be considered as essential measures to prevent customers exposure to MDR foodborne pathogens.

5. Conclusion

This study investigated the prevalence, AMR genotype, virulence factors and plasmid replicons in *Salmonella* isolates from pork, poultry eggs, aquaculture and retail environments in Yichuan city, China. Our findings revealed that *S. enteritidis* was the most prevalent serovar, with a large percentage of MDR isolates harboring several AMR determinants, particularly key ESBLs genes, including $bla_{\text{CTX-M}}$ and $bla_{\text{NDM-1}}$. We also identified essential virulence genes, including fimbrial and typhoid toxin genes in addition to SPI-1 and SPI-2 PIs. Therefore, the detection of pathogenic multidrug-resistant *Salmonella serovars* from food animals and associated products is a serious concern for animal and human health. Furthermore, the generation of similar data from human clinical isolates can support a One Health strategy, assess the public health effects of *Salmonella* from food animals and related food products, and contribute to source tracing. Continuous monitoring of *Salmonella* in food animals and associated food products is essential for advising food safety practices and evaluating the outcomes of interventions, including the reduction of antimicrobial use in livestock farming. Moreover, the implementation of effective hygienic practices, including regular cleaning and disinfection of environments associated with food in markets, may serve as a viable strategy to reduce the existence of this pathogen in animal products.

CRediT authorship contribution statement

Xiaowu Jiang: Writing – original draft, Visualization, Validation, Formal analysis, Data curation. **Abubakar Siddique:** Writing – original draft, Visualization, Validation, Formal analysis, Data curation. **Li Chen:** Writing – review & editing, Investigation, Formal analysis. **Lexin Zhu:** Writing – review & editing, Visualization, Investigation. **Haiyang Zhou:** Visualization, Validation, Data curation. **Li Na:** Visualization, Validation, Data curation. **Chenghao Jia:** Visualization, Validation, Data curation. **Yan Li:** Writing – review & editing, Supervision. **Min Yue:** Writing – review & editing, Validation, Supervision, Project administration, Funding acquisition.

Declaration of competing interest

None.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.onehlt.2025.100967.

Data availability

The sequences from this study are available under NCBI BioProject No. PRJNA994834.

References

[1] O. Ehuwa, A.K. Jaiswal, S. Jaiswal, *Salmonella*, food safety and food handling practices, Foods 10 (2021) 907.
[2] M. Elbediwi, H. Pan, S. Biswas, Y. Li, M. Yue, Emerging colistin resistance in *Salmonella enterica* serovar Newport isolates from human infections, Emerg. Microb. Inf. 9 (2020) 535–538.
[3] M. Elbediwi, Y. Tang, M. Yue, Genomic characterization of ESBL-producing *Salmonella* Thompson isolates harboring mcr-9 from dead chick embryos in China, Vet. Microbiol. 278 (2023) 109634.
[4] Z. Jiang, T.M. Anwar, X. Peng, S. Biswas, M. Elbediwi, Y. Li, W. Fang, M. Yue, Prevalence and antimicrobial resistance of *Salmonella* recovered from pig-borne food products in Henan, China, Food Control 121 (2021) 107535.
[5] Z. Chen, D. Kuang, X. Xu, N. Gonzalez-Escalona, D.L. Erickson, E. Brown, J. Meng, Genomic analyses of multidrug-resistant *Salmonella* Indiana, typhimurium, and Enteritidis isolates using MinION and MiSeq sequencing technologies, PLoS ONE 15 (2020) e0235641.
[6] R.G. Ferrari, D.K.A. Rosario, A. Cunha-Neto, S.B. Mano, E.E.S. Figueiredo, C. A. Conte-Junior, Worldwide epidemiology of *Salmonella* Serovars in animal-based foods: a meta-analysis, Appl. Environ. Microbiol. 85 (2019).
[7] J. Chen, L. Huang, H. An, Z. Wang, X. Kang, R. Yin, C. Jia, X. Jin, M. Yue, One Health approach probes zoonotic non-typhoidal Salmonella infections in China: A systematic review and meta-analysis, J. Glob. Health 14 (2024) 04256.
[8] K. Ikwap, J. Erume, D.O. Owiny, G.W. Nasinyama, L. Melin, B. Bengtsson, N. Lundeheim, C. Fellström, M. Jacobson, *Salmonella* species in piglets and weaners from Uganda: prevalence, antimicrobial resistance and herd-level risk factors, Prev. Vet. Med. 115 (2014) 39–47.
[9] X. Wang, S. Biswas, N. Paudyal, H. Pan, X. Li, W. Fang, M. Yue, Antibiotic resistance in *Salmonella* typhimurium isolates recovered from the food chain through national antimicrobial resistance monitoring system between 1996 and 2016, Front. Microbiol. 10 (2019) 985.
[10] C. Wei, J. Chen, T.M. Anwar, L. Huang, W. Yang, X. Dong, Q. Chen, M. Yue, D. Yu, Genomic determinants of pathogenicity and antimicrobial resistance of nosocomial Acinetobacter baumannii clinical isolates of hospitalized patients (2019–2021) from a sentinel Hospital in Hangzhou, China, Inf. Drug Resist. (2023) 2939–2952.
[11] E.O. Igbinosa, A. Beshiru, I.H. Igbinosa, A.I. Okoh, Antimicrobial resistance and genetic characterisation of *Salmonella enterica* from retail poultry meats in Benin City, Nigeria, LWT 169 (2022) 114049.
[12] I.H. Igbinosa, C.N. Amolo, A. Beshiru, O. Akinnibosun, A.G. Ogofure, M. El-Ashker, M. Gwida, A.I. Okoh, E.O. Igbinosa, Identification and characterization of MDR virulent *Salmonella* spp isolated from smallholder poultry production environment in Edo and Delta states, Nigeria, PLoS ONE 18 (2023) e0281329.
[13] A. Siddique, Z. Wang, H. Zhou, L. Huang, C. Jia, B. Wang, A. Ed-Dra, L. Teng, Y. Li, M. Yue, The evolution of vaccines development across *Salmonella* Serovars among animal hosts: a systematic review, Vaccines 12 (2024) 1067.
[14] Q. Luo, F. Wan, X. Yu, B. Zheng, Y. Chen, C. Gong, H. Fu, Y. Xiao, L. Li, MDR *Salmonella enterica* serovar typhimurium ST34 carrying mcr-1 isolated from cases of bloodstream and intestinal infection in children in China, J. Antimicrob. Chemother. 75 (2020) 92–95.
[15] C.S. Marchello, M. Birkhold, J.A. Crump, L.B. Martin, M.O. Ansah, G. Breghi, R. Canals, F. Fiorino, M.A. Gordon, J.-H. Kim, Complications and mortality of non-typhoidal *Salmonella* invasive disease: a global systematic review and meta-analysis, Lancet Infect. Dis. 22 (2022) 692–705.
[16] B. Tang, A. Siddique, C. Jia, A. Ed-Dra, J. Wu, H. Lin, M. Yue, Genome-based risk assessment for foodborne *Salmonella enterica* from food animals in China: a one health perspective, Int. J. Food Microbiol. 390 (2023) 110120.
[17] N. Paudyal, H. Pan, X. Liao, X. Zhang, X. Li, W. Fang, M. Yue, A Meta-analysis of major foodborne pathogens in Chinese food commodities between 2006 and 2016, Foodborne Pathog. Dis. 15 (2018) 187–197.
[18] A. Siddique, S. Azim, A. Ali, S. Andleeb, A. Ahsan, M. Imran, A. Rahman, Antimicrobial resistance profiling of biofilm forming non typhoidal *Salmonella enterica* isolates from poultry and its associated food products from Pakistan, Antibiotics 10 (2021) 785.
[19] C.J. Murray, K.S. Ikuta, F. Sharara, L. Swetschinski, G.R. Aguilar, A. Gray, C. Han, C. Bisignano, P. Rao, and E. Wool, Global burden of bacterial antimicrobial resistance in 2019: a systematic analysis. Lancet 399 (2022): p. 629–655.
[20] P. Gerner-Smidt, J. Besser, J. Concepción-Acevedo, J.P. Folster, J. Huffman, L. A. Joseph, Z. Kucerova, M.C. Nichols, C.A. Schwensohn, B. Tolar, Whole genome sequencing: bridging one-health surveillance of foodborne diseases, Front. Public Health 7 (2019) 172.
[21] H. Li, M. Tan, F. Zhang, H. Ji, Y. Zeng, Q. Yang, J. Tan, J. Huang, Q. Su, Y. Huang, Diversity of avian leukosis virus subgroup J in local chickens, Jiangxi, China, Sci. Rep. 11 (2021) 4797.
[22] C. Zhang, J. Xu, T. Zhang, H. Qiu, Z. Li, E. Zhang, S. Li, Y.-F. Chang, X. Guo, X. Jiang, Genetic characteristics of pathogenic Leptospira in wild small animals and livestock in Jiangxi Province, China, 2002–2015, PLoS Negl. Trop. Dis. 13 (2019) e0007513.
[23] M.-F. Tan, H.-Q. Li, Q. Yang, F.-F. Zhang, J. Tan, Y.-B. Zeng, Q.-P. Wei, J.-N. Huang, C.-C. Wu, N. Li, Prevalence and antimicrobial resistance profile of bacterial pathogens isolated from poultry in Jiangxi Province, China from 2020 to 2022, Poult. Sci. 102 (2023) 102830.
[24] X. Zeng, S. Lv, C. Qu, L. Lan, D. Tan, X. Li, L. Bai, Serotypes, antibiotic resistance, and molecular characterization of non-typhoidal *Salmonella* isolated from diarrheic patients in Guangxi Zhuang autonomous region, China, 2014–2017, Food Control 120 (2021) 107478.
[25] T. Sun, Y. Liu, X. Qin, Z. Aspridou, J. Zheng, X. Wang, Z. Li, Q. Dong, The prevalence and epidemiology of *Salmonella* in retail raw poultry meat in China: a systematic review and meta-analysis, Foods 10 (2021) 2757.
[26] X. Kang, J. Chen, C. Jia, X. Zhou, E. Abdelaziz, M. Yue, Allelic functional variation of FimH among Salmonella enterica subspecies, Animal Dis. (2023) 3: 33.
[27] M. Mohiuddin, Z. Iqbal, A. Siddique, S. Liao, M.K.F. Salamat, N. Qi, A.M. Din, M. Sun, Prevalence, genotypic and phenotypic characterization and antibiotic resistance profile of *Clostridium perfringens* type a and D isolated from feces of sheep (Ovis aries) and goats (Capra hircus) in Punjab, Pakistan, Toxins 12 (2020) 657.
[28] CLSI, Methods for Dilution Antimicrobial Susceptibility Tests for bacteria that Grow Aerobically, Clinical and Laboratory Standards Institute, Wayne, PA, 2019.
[29] Y. Xu, X. Zhou, Z. Jiang, Y. Qi, A. Ed-Dra, M. Yue, Epidemiological investigation and antimicrobial resistance profiles of *Salmonella* isolated from breeder chicken hatcheries in Henan, China, Front. Cell. Infect. Microbiol. 10 (2020) 497.
[30] Y.-f. Qiu, R.B. Nambiar, X.-b. Xu, S.-t. Weng, H. Pan, K.-c. Zheng, and M. Yue, Global genomic characterization of *Salmonella enterica* Serovar Telelkebir. Front. Microbiol. 12 (2021): p. 704152.
[31] X. Zhou, X. Kang, J. Chen, Y. Song, C. Jia, L. Teng, Y. Tang, Z. Jiang, X. Peng, X. Tao, Y. Xu, L. Huang, X. Xu, Y. Xu, T. Zhang, S. Yu, J. Gong, S. Wang, Y. Liu, G. Zhu, C. Kehrenberg, FX. Weill, P. Barrow, Y. Li, G. Zhao, M. Yue, Genome degradation promotes Salmonella pathoadaptation by remodeling fimbriae-mediated proinflammatory response, Natl. Sci. Rev.10 (2023) nwad228.
[32] X. Kang, C. Jin, P. Gu, S. Wang, Z. Gao, C. Dai, X. Zhou, A. Siddique, H. Zhou, L. Huang, Y. Li, M. Yue, A dynamic platform for global pullorum disease and fowl typhoid, Animal Dis. 4 (2024) 39.
[33] X. Zhang, M. Payne, R. Lan, In silico identification of serovar-specific genes for *Salmonella* serotyping, Front. Microbiol. 10 (2019) 835.
[34] M. Achtman, J. Wain, F.X. Weill, S. Nair, Z.M. Zhou, V. Sangal, M.G. Krauland, J. L. Hale, H. Harbottle, A. Uesbeck, et al., Multilocus sequence typing as a replacement for serotyping in *Salmonella enterica*, PLoS Pathog. 8 (2012).
[35] A. Siddique, N. Ullah, A. Ali, A. Patel, T. Moore, S.M. Kenney, E. Ganda, A. Rahman, Draft genome sequences of 25 *Salmonella enterica* serovar Agona strains isolated from poultry and associated food products harbouring multiple antibiotic resistance genes, J. Glob. Antimicrob. Resist. 29 (2022) 131–135.
[36] Q. Liu, W. Chen, M. Elbediwi, H. Pan, L. Wang, C. Zhou, B. Zhao, X. Xu, D. Li, X. Yan, Characterization of *Salmonella* resistome and plasmidome in pork production system in Jiangsu, China, Front. Vet. Sci. 7 (2020) 617.
[37] L. Huang, H. Zhou, J. Chen, C. Jia, A. Siddique, B. Wu, H. Wang, B. Tang, F. He, G. Zhao, Impact of COVID-19-related nonpharmaceutical interventions on diarrheal diseases and zoonotic *Salmonella*, hLife 2 (2024) 246–256.
[38] Z. Wang, C. Huang, Y. Liu, J. Chen, R. Yin, C. Jia, X. Kang, X. Zhou, S. Liao, X. Jin, Salmonellosis outbreak archive in China: data collection and assembly, Sci. Data 11 (2024) 244.
[39] Z. Wang, H. Zhou, Y. Liu, C. Huang, J. Chen, A. Siddique, R. Yin, C. Jia, Y. Li, G. Zhao, Nationwide trends and features of human salmonellosis outbreaks in China, Emerg. Microb. Inf. 13 (2024) 2372364.
[40] A.C.A.D.O. Ferreira, S.L.S. Pavelquesi, E.D.S. Monteiro, L.F.S. Rodrigues, C.M.D. S. Silva, I.C.R.D. Silva, D.C. Orsi, Prevalence and antimicrobial resistance of *Salmonella* spp. in aquacultured Nile Tilapia (*Oreochromis niloticus*) commercialized in Federal District, Brazil, Foodborne Pathog. Dis. 18 (2021) 778–783.
[41] E.J. Fearnley, A. Lal, J. Bates, R. Stafford, M.D. Kirk, K. Glass, *Salmonella* source attribution in a subtropical state of Australia: capturing environmental reservoirs of infection, Epidemiol. Infect. 146 (2018) 1903–1908.
[42] C. Larson, China's Lakes of Pig Manure Spawn Antibiotic Resistance, American Association for the Advancement of Science, 2015.

[43] S. Wang, H. Duan, W. Zhang, J.-W. Li, Analysis of bacterial foodborne disease outbreaks in China between 1994 and 2005, FEMS Immunol. Med. Microbiol. 51 (2007) 8–13.
[44] L. Long, L. You, D. Wang, M. Wang, J. Wang, G. Bai, J. Li, X. Wei, S. Li, Highly prevalent MDR, frequently carrying virulence genes and antimicrobial resistance genes in *Salmonella enterica* serovar 4,[5], 12: i:-isolates from Guizhou Province, China, PLoS ONE 17 (2022) e0266443.
[45] D. Lu, J. Liu, H. Liu, Y. Guo, Y. Dai, J. Liang, L. Chen, L. Xu, P. Fu, N. Li, Epidemiological features of foodborne disease outbreaks in catering service facilities—China, 2010–2020, China CDC Weekly 5 (2023) 479.
[46] E. Doménech, A. Jimenez-Belenguer, J.A. Amoros, M.A. Ferrus, I. Escriche, Prevalence and antimicrobial resistance of listeria monocytogenes and *Salmonella* strains isolated in ready-to-eat foods in eastern Spain, Food Control 47 (2015) 120–125.
[47] A. Zadernowska, W. Chajęcka-Wierzchowska, Prevalence, biofilm formation and virulence markers of *Salmonella* sp. and Yersinia enterocolitica in food of animal origin in Poland, LWT 75 (2017) 552–556.
[48] L. Bai, R. Lan, X. Zhang, S. Cui, J. Xu, Y. Guo, F. Li, D. Zhang, Prevalence of *Salmonella* isolates from chicken and pig slaughterhouses and emergence of ciprofloxacin and cefotaxime co-resistant *S. enterica* serovar Indiana in Henan, China, PLoS ONE 10 (2015) e0144532.
[49] L. Zhang, Y. Fu, Z. Xiong, Y. Ma, Y. Wei, X. Qu, H. Zhang, J. Zhang, M. Liao, Highly prevalent multidrug-resistant *Salmonella* from chicken and pork meat at retail markets in Guangdong, China, Front. Microbiol. 9 (2018) 2104.
[50] T. Chen, J. Jiang, C. Ye, J. Xie, X. Chen, D. Xu, Z. Zeng, Y. Peng, D.-L. Hu, R. Fang, Genotypic characterization and antimicrobial resistance profile of *Salmonella* isolated from chicken, pork and the environment at abattoirs and supermarkets in Chongqing, China, BMC Vet. Res. 15 (2019) 1–8.
[51] B. Yang, D. Qu, X. Zhang, J. Shen, S. Cui, Y. Shi, M. Xi, M. Sheng, S. Zhi, J. Meng, Prevalence and characterization of *Salmonella* serovars in retail meats of marketplace in Shaanxi, China, Int. J. Food Microbiol. 141 (2010) 63–72.
[52] E.R. Atwill, S. Jeamsripong, Bacterial diversity and potential risk factors associated with *Salmonella* contamination of seafood products sold in retail markets in Bangkok, Thailand, PeerJ 9 (2021) e12694.
[53] R.R. Dewi, L. Hassan, H.M. Daud, M.F. Matori, F. Nordin, N.I. Ahmad, Z. Zakaria, Prevalence and antimicrobial resistance of *Escherichia coli*, *Salmonella* and Vibrio derived from farm-raised Red Hybrid Tilapia (Oreochromis spp.) and Asian Sea Bass (*Lates calcarifer*, Bloch 1970) on the west coast of peninsular Malaysia, Antibiotics 11 (2022) 136.
[54] X. Yang, Q. Wu, J. Zhang, J. Huang, L. Chen, S. Liu, S. Yu, S. Cai, Prevalence, enumeration, and characterization of *Salmonella* isolated from aquatic food products from retail markets in China, Food Control 57 (2015) 308–313.
[55] J. Wang, J. Li, F. Liu, Y. Cheng, J. Su, Characterization of *Salmonella enterica* isolates from diseased poultry in northern China between 2014 and 2018, Pathogens 9 (2020) 95.
[56] B. Tang, M. Elbediwi, R.B. Nambiar, H. Yang, J. Lin, M. Yue, Genomic characterization of antimicrobial-resistant *Salmonella enterica* in duck, chicken, and pig farms and retail markets in eastern China, Microbiol. Spectr. 10 (2022) e01257–e01322.
[57] Z. Wei, X. Xu, M. Yan, H. Chang, Y. Li, B. Kan, M. Zeng, *Salmonella* typhimurium and *Salmonella* enteritidis infections in sporadic diarrhea in children: source tracing and resistance to third-generation cephalosporins and ciprofloxacin, Foodborne Pathog. Dis. 16 (2019) 244–255.
[58] E.F.S. Authority, The European Union summary report on trends and sources of zoonoses, zoonotic agents and food-borne outbreaks in 2017, EFSA J. 16 (2018).
[59] D.M. Tack, Preliminary incidence and trends of infections with pathogens transmitted commonly through food—foodborne diseases active surveillance network, 10 US sites, 2016–2019, MMWR 69 (2020).
[60] X. Yang, J. Huang, Y. Zhang, S. Liu, L. Chen, C. Xiao, H. Zeng, X. Wei, Q. Gu, Y. Li, Prevalence, abundance, serovars and antimicrobial resistance of *Salmonella* isolated from retail raw poultry meat in China, Sci. Total Environ. 713 (2020) 136385.
[61] I.O. Fagbamila, E. Ramon, A.A. Lettini, M. Muhammad, A. Longo, K. Antonello, M. K. Aworh, J.K. Kwaga, P.A. Abdu, J.U. Umoh, Assessing the mechanisms of multi-drug resistant non-typhoidal *Salmonella* (NTS) serovars isolated from layer chicken farms in Nigeria, PLoS ONE 18 (2023) e0290754.
[62] A.J. Browne, M.G. Chipeta, F.J. Fell, G. Haines-Woodhouse, B.H.K. Hamadani, E. A. Kumaran, G.R. Aguilar, B. McManigal, J.R. Andrews, E.A. Ashley, Estimating the subnational prevalence of antimicrobial resistant *Salmonella enterica* serovars Typhi and Paratyphi a infections in 75 endemic countries, 1990–2019: a modelling study, Lancet Glob. Health 12 (2024) e406–e418.
[63] C. Jia, Z. Wang, C. Huang, L. Teng, H. Zhou, H. An, S. Liao, Y. Liu, L. Huang, B. Tang, M. Yue, Mobilome-driven partitions of resistance in Salmonella, mSystems 8 (2023) e0088323.
[64] I. Russo, D. Bencardino, M. Napoleoni, F. Andreoni, G.F. Schiavano, G. Baldelli, G. Brandi, G. Amagliani, Prevalence, antibiotic-resistance, and replicon-typing of *Salmonella* strains among Serovars mainly isolated from food chain in Marche region, Italy, Antibiotics 11 (2022) 725.
[65] X. Yang, J. Huang, Q. Wu, J. Zhang, S. Yang, J. Wang, Y. Ding, M. Chen, L. Xue, S. Wu, Occurrence, serovars and antibiotic resistance of *Salmonella* spp. in retail ready-to-eat food products in some Chinese provinces, LWT 154 (2022) 112699.
[66] H. An, X. Kang, C. Huang, C. Jia, J. Chen, Y. Huang, Q. Chao, Y. Li, B. Tang, M. Yue, Genomic and virulent characterization of a duck-associated Salmonella serovar Potsdam from China, Poult. Sci. 104 (2024) 104646.
[67] J. Huang, S. Deng, J. Ren, J. Tu, M. Ye, M. Wang, Characterization of a blaNDM-1-harboring plasmid from a *Salmonella enterica* clinical isolate in China, Mol. Med. Rep. 16 (2017) 1087–1092.
[68] K. Chen, E. Wai Chi Chan, S. Chen, Evolution and transmission of a conjugative plasmid encoding both ciprofloxacin and ceftriaxone resistance in *Salmonella*, Emerg. Microb. Inf. 8 (2019) 396–403.
[69] S.M. Al Hasan, J. Saulam, F. Mikami, K. Kanda, N.R. Ngatu, H. Yokoi, and T. Hirao, Trends in per capita food and protein availability at the national level of the Southeast Asian countries: an analysis of the FAO's food balance sheet data from 1961 to 2018. Nutrients 14 (2022): p. 603.
[70] A. Beshiru, I.H. Igbinosa, E.O. Igbinosa, Prevalence of antimicrobial resistance and virulence gene elements of *Salmonella* serovars from ready-to-eat (RTE) shrimps, Front. Microbiol. 10 (2019) 1613.
[71] R.A. Cheng, C.R. Eade, M. Wiedmann, Embracing diversity: differences in virulence mechanisms, disease severity, and host adaptations contribute to the success of nontyphoidal *Salmonella* as a foodborne pathogen, Front. Microbiol. 10 (2019) 1368.
[72] M. Elbediwi, Y. Tang, D. Shi, H. Ramadan, S. Xu, Y. Li, M. Yue, Genomic investigation of antimicrobial-resistant *Salmonella enterica* isolates from dead chick embryos in China, Front. Microbiol. 12 (2021) 684400.
[73] X. Zang, P. Huang, J. Li, X. Jiao, J. Huang, Genomic relatedness, antibiotic resistance and virulence traits of *Campylobacter jejuni* HS19 isolates from cattle in China indicate pathogenic potential, Front. Microbiol. 12 (2021) 783750.
[74] X. Xu, Y. Chen, H. Pan, Z. Pang, F. Li, X. Peng, A. Ed-Dra, Y. Li, M. Yue, Genomic characterization of *Salmonella* Uzaramo for human invasive infection, Microb. Genom. 6 (2020) e000401.
[75] J. Fierer, Invasive non-typhoidal *Salmonella* (iNTS) infections, Clin. Infect. Dis. 75 (2022) 732–738.
[76] Y. Liu, J. Jiang, A. Ed-Dra, X. Li, X. Peng, L. Xia, Q. Guo, G. Yao, M. Yue, Prevalence and genomic investigation of *Salmonella* isolates recovered from animal food-chain in Xinjiang, China, Food Res. Int. 142 (2021) 110198.
[77] E.A. McMillan, C.R. Jackson, J.G. Frye, Transferable plasmids of *Salmonella enterica* associated with antibiotic resistance genes, Front. Microbiol. 11 (2020) 562181.
[78] N. Lyu, Y. Feng, Y. Pan, H. Huang, Y. Liu, C. Xue, B. Zhu, Y. Hu, Genomic characterization of *Salmonella enterica* isolates from retail meat in Beijing, China, Front. Microbiol. 12 (2021) 636332.
[79] X. Kang, H. An, B. Wang, L. Huang, C. Huang, Y. Huang, Z. Wang, F. He, Y. Li, M. Yue, Integrated OMICs approach reveals energy metabolism pathways is vital for Salmonella Pullorum surival within the egg white, mSphere 9 (2024) e0036224.
[80] Y. Li, L. Teng, X. Xu, X. Li, X. Peng, X. Zhou, J. Du, Y. Tang, Z. Jiang, C. Jia, A. Muller, C. Kehrenberg, H. Wang, B. Wu, F.X. Weill, M. Yue, EMBO Mol. Med. 14 (2022) e16366.