One Health 21 (2025) 101171

Contents lists available at ScienceDirect

One Health

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

What are we eating?. Detection of antibiotic resistance mechanisms in frozen chicken nuggets imported from Brazil

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ARTICLE INFO

Keywords:
Nuggets
Frozen food
Antibiotic resistance
Metagenomics
One health

ABSTRACT

The rise of antibiotic resistance is a growing challenge, affecting humans, the environment, and animals. Under the One Health framework, this study investigated resistance mechanisms to critically important antibiotics in frozen chicken nuggets imported from Brazil.

Eighty nugget samples were cultured on selective media containing ceftriaxone, ciprofloxacin, or colistin. Isolates were identified using MALDI-TOF, and antibiotic susceptibility was assessed by disk diffusion. Eight samples were also analyzed using shotgun metagenomic sequencing processed through the SqueezeMeta pipeline.

Nineteen Enterobacterales resistant mainly to β-lactams and to a lesser extent, to quinolones and aminoglycosides, were identified. Eight *Pseudomonas* spp. were recovered, including one *P. fulva* resistant to colistin. Metagenomics revealed predominant Firmicutes, (*Bacillaceae*, *Lactobacillaceae*, and *Paenibacillaceae*) with low γ-Proteobacteria levels.

Additionally, we detected resistance genes against several antibiotics.

This study highlights the role of imported food in spreading AMR and the value of combining metagenomics with conventional microbiology to strengthen One Health surveillance.

1. Introduction

Antibiotics are crucial for treating severe diseases. However, their overuse in human and veterinary medicine has promoted multidrug-resistant microorganisms (MDR-M) driven by mechanisms such as enzyme inactivation, target modification, and diminished permeability. Antimicrobial resistance (AMR) is a global threat to humans, animals, and the environment's health, and can spread via food, water, and trade. AMR and food are pillars of the "One Health" concept supported by the WHO and related agencies. In humans, MDR-M infections increase morbidity and mortality, hospital stays, and healthcare costs [1]. However, the highest consumption of antibiotics occurs in animal husbandry (80 %), with further increases expected by 2030 [2]. This generates therapeutic challenges in the veterinary field and facilitates the selection and transmission of MDR-M or resistance genes to humans through livestock. Foodborne pathogens like *Salmonella* spp. and *Escherichia coli* are considered major threats [3].

These microorganisms can cause economic losses in animal production, as observed in Norway, where chicken sales dropped 20 % due to resistant *E. coli* [4]. Food can act both as a substrate and vehicle for enteropathogens and other bacteria harboring resistance genes which may transfer them to the human microbiota [3].

In Uruguay, our group previously studied resistance genes like *rmtG* and *mcr9* in imported chicks [5]. We aimed to investigate resistance mechanisms in frozen food from Brazil as a potential route for critical AMR gene entry.

2. Materials and methods

2.1. Sampling and pre-enrichment of chicken nuggets for microbiological analysis

Eighty chicken nuggets samples imported from Brazil were studied during an 8-month period, in 2022. Chicken nuggets corresponding to five different brands (named A-E) were acquired from local supermarkets, and refrigerated and processed within 24 h. Each sample was homogenized in 100 mL of LB broth, pre-enriched at 37 °C for 18–24 h, and subsequently processed.

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https://doi.org/10.1016/j.onehlt.2025.101171
Received 20 May 2025; Received in revised form 4 August 2025; Accepted 15 August 2025
Available online 21 August 2025

2.2. Sampling and bacterial analysis

Pre-enriched samples were inoculated (100 μL) onto McConkey agar with/without ceftriaxone (1 mg/L), ciprofloxacin (0.25 mg/L), or colistin (3 mg/L), and on trypticase soy agar (Oxoid). Plates were incubated at 37 °C for 24 [6].

Up to five colony types per sample were identified using MALDI-TOF (Bruker, USA) with Biotyper v3.1 and the MBT Library. Species-level identification was accepted for scores ≥ 2.0, and genus-level for scores between 1.7 and 2.0, following standard formic acid extraction protocols.

Antibiotic susceptibility was tested by Kirby-Bauer disk-diffusion on Mueller-Hinton agar (Oxoid, UK), following CLSI M100–32 guidelines [6]. Control strain *Escherichia coli* ATCC 25922 was included and plates were incubated at 35 ± 2 °C for 18 h.

Susceptibility to ampicillin, cefuroxime, amoxicillin-clavulanic acid, ceftriaxone, ceftazidime, cefepime, imipenem, meropenem, ciprofloxacin, enrofloxacin, amikacin, gentamicin, and trimethoprim-sulfamethoxazole was tested by disk diffusion. Colistin MIC was determined by colistin agar test (CAT). Results and ESBL/AmpC screening were interpreted according to CLSI M100–32 guidelines.

Finally, PCR was performed to detect plasmid-mediated resistance genes, including: *mcr1–9*, *qnrA-E* and *aac(6')Ib-cr*, and plasmid-mediated AmpC β-lactamases and ESBL. DNA was extracted using a thermal shock method, and PCR reactions were carried out with specific primers previously described (Supplementary Table 1). PCR products were analyzed by gel electrophoresis on 1 % agarose gels [5].

2.3. gDNA extraction and sequencing

Eight chicken nugget samples underwent metagenomic analysis. Samples N8 and N9 (brand B), N11 and N42 (brand A), N40 (brand C), and N49 (brand D) yielded Gram-negative bacilli on MacConkey agar, while N26 and N77 (brand B) showed growth only on TSA. Genomic DNA was extracted using the QIAamp Fast DNA Stool Mini Kit (Qiagen, USA) and quantified using a Qubit fluorometer (ThermoFisher Scientific, USA). Subsequently, DNA samples were sent to Macrogen, Inc. for quality control, library preparation, and NovaSeq sequencing (Illumina).

2.4. Metagenomic and in silico analysis

Raw Fastq files were processed with SqueezeMeta v1.6.3 in co-assembly mode using Megahit, whereas the binning step was performed using Maxbin and Concoct [7]. Results were analyzed with the SQMtools R package. Binned Fasta files were analyzed for antibiotic resistance genes using AMRFinderPlus 4.0 [8]. The generated bins were further processed using CheckM v1.1.6, following a lineage-specific workflow [9], and DAS_Tool v1.1.7 with a score threshold = 0.4 [10].

3. Results

3.1. Identification of critically priority pathogens and antibiotic susceptibility in food samples

Eighty nugget samples were analyzed. All grew on TSA, and 14 also on McConkey lactose (±antibiotic). Nineteen enterobacterial isolates were recovered from antibiotic-supplemented media, *Citrobacter freundii* (*n* = 6), *Escherichia coli* (*n* = 2), *Serratia* spp. (*n* = 5), *Enterobacter asburiae* (n = 2), *Enterobacter vulneris* (*n* = 1), *Enterobacter cloacae* (n = 1), *Enterobacter kobei* (n = 1), and *Klebsiella variicola* (n = 1). All were resistant to ampicillin, others showed resistance to cefuroxime (*n* = 15), ceftriaxone (*n* = 3), ceftazidime (n = 3), amoxicillin-clavulanic acid (n = 3), ciprofloxacin (*n* = 1), enrofloxacin (n = 3), and amikacin (n = 1). (Supplementary Table 2).

Eight *Pseudomonas* species (recovered from 4 samples) were identified: *Pseudomonas putida* (*n* = 5), *P. fulva* (*n* = 2), and *P. monteilii* (*n* = 1). All isolates were susceptible to the tested antibiotics, except for one *P. fulva* resistant to colistin (MIC > 4 μg/mL by CAT).

No ESBLs were detected phenotypically, and PCR assays revealed no plasmid-mediated AmpC β-lactamase, PMQR, or *mcr* genes.

3.2. Metagenomic characterization of the food sample

3.2.1. Bacterial identification

gDNA from eight samples was sequenced for metagenomic analysis. Firmicutes dominated (>45 %), mainly *Bacillaceae*, *Lactobacillaceae*, and *Paenibacillaceae*, with *Bacillus*, *Leuconostoc*, *Weissella*, and *Paenibacillus* as predominant genera.

Proteobacteria were detected at low levels (0.01–1.5 %), mainly *Enterobacteriaceae*, *Moraxellaceae*, *Aeromonadaceae*, *Vibrionaceae*, and *Pseudomonadaceae*. Detected species included *E. coli*, *K. pneumoniae*, and *A. baumannii* (Fig. 1).

The generated Metagenome-Assembled Genomes (MAGs) were evaluated for completeness and contamination based on single-copy gene (SCG) markers (Table 1). The resulting high and mid-quality bins were assigned to several bacterial groups like *Enterobacteriaceae*, *Streptococcus*, *Paenibacillaceae*, *Clostridiales*, *Bacillus*, and *Lactobacillales*; accordingly, such MAGs showed SCG completeness values >70 %, and generally low contamination values.

3.2.2. Antibiotic resistance mechanisms

The AMRFinderPlus pipeline detected genes conferring resistance to: β-lactams, chloramphenicol, fosfomycin, lincomycin, macrolides, quaternary ammonium compounds, aminoglycosides, tetracycline, and glycopeptides (Table 1).

The *Enterobacteriaceae* MAG carried $bla_{\text{CTX-M-15}}$ and *mdfA*, whereas most resistance genes were found in MAGs assigned to Gram-positive taxa like *Paenibacillaceae* and *Bacillus*, matching the dominant microbial profile. However, some resistance genes could not be linked to any specific bin and were designated as unbinned AMR genes (Table 1).

4. Discussion

Antibiotics are essential for human health, animal welfare, and food production. However, their use contributes to antimicrobial resistance, jeopardizing medicine, food security, and environmental safety. A One Health approach is crucial to mitigating this threat.

The importance of detecting Enterobacterales in frozen products lies in their role as reservoirs of resistance genes, which could be transferred to other microorganisms in the environment or in the host's microbiota. Although no transferable resistance genes to β-lactams, colistin, and fluoroquinolones were found by conventional methods, the isolated microorganisms showed intrinsic resistance to these agents. Notably, *C. freundii*, *E. coli* and *K. variicola* are known for their pathogenicity and their content of AMR genes [10].

The presence of *Pseudomonas* spp. is relevant, as they are environmental reservoirs of resistance genes. *Pseudomonas fulva*, found in soil and food, can acquire and transfer such genes. Although rarely pathogenic, its ability to colonize diverse environments makes it a potential reservoir of resistance to other pathogens [11].

After being implemented in 2009, food metagenomics has allowed rapid analysis of bacterial and metabolic pathways using foodomic databases. Studies tackling MAGs from various foods reported an abundance of *Lactobacillaceae* and *Streptococcaceae* in dairy products, along with *Bifidobacterium* and *Propionibacterium* in fermented foods [12].

In our samples, *Lactobacillaceae*, *Bacillaceae* and *Paenibacillaceae* were the most frequently identified families. The prevalence of *Firmicutes* was expected due to their role in food fermentation and preservation [13]. Particularly, the genera *Bacillus*, *Leuconostoc* and *Paenibacillus* are commonly found in heat-processed, chilled and frozen poultry products. The predominance of Firmicutes in poultry is typical in

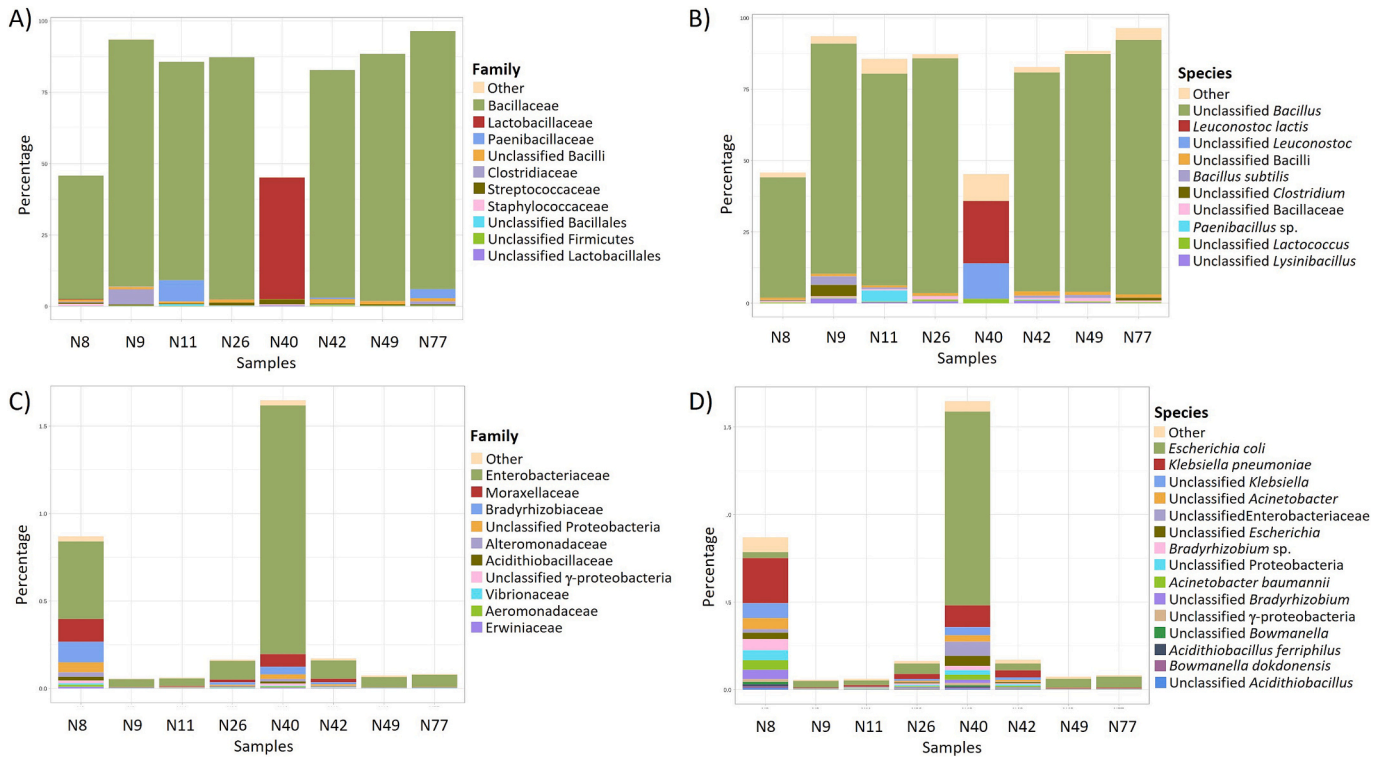

Fig. 1. Main microorganisms detected by metagenomic analysis of frozen chicken nuggets. Panels A and B correspond to microbial families and species belonging to the phylum *Firmicutes*, respectively; Panels C and D correspond to microbial families and species belonging to the phylum *Proteobacteria*, respectively. Samples N8 and N9 (brand B), N11 and N42 (brand A), N40 (brand C), and N49 (brand D) yielded bacterial growth on MacConkey (i.e.: Gram-negative bacilli); samples N26 and N77 (brand B) only yielded growth on TSA plates.

post-processing stages, as highlighted in microbiome studies of meat products, that show a shift toward Firmicutes dominance after slaughter and chill, with *Bacillus* sp., among others species, prevailing in post-processing stages [14,15].

Furthermore, *Bacillus* and *Paenibacillus* spp. are spore-forming and highly thermotolerant bacteria capable of surviving industrial cooking and refrigeration processes [16]. Therefore, their presence may reflect the residual microbiota remaining after industrial processing.

Conversely, Gram-negative families like *Enterobacteriaceae* and *Moraxellaceae* were detected at low levels, suggesting a likely spillover from chicken gut during processing.

Nevertheless, we acknowledge that post-processing contamination (during handling, packaging, or cold chain storage) may have also contributed to the observed microbial profile. Further studies would be necessary to distinguish between these possibilities.

According to the latest WOAH report, 62 % of antibiotics used on terrestrial food-producing animals were tetracyclines, penicillins and macrolides. Interestingly, 61 % (17/28) of the detected resistance genes conferred resistance to the aforementioned families [17].

Among these we detected, i) class A, B and D β-lactamase genes (e.g., $bla_{\text{CTX-M-15}}$), ii) macrolide-resistance genes (*ermD*, *mphK*, *mef(A)*); iiI) tetracycline-resistance genes (*tet(A)*, *tet(L)*, *tet(M)*, *tet(S)*, *tet(45)*); furthermore, we also detected genes conferring resistance to antibiotics rarely used in veterinary medicine such as aminoglycosides (*aadK*, *satA*), lincosamides (*lnu(G)*), and chloramphenicol (*cat86*).

Given the abundance of Gram-positive bacteria in our samples, the detection of genes conferring resistance to lincosamides, macrolides, streptogramins, and glycopeptides was not unexpected, since such genes are typically found in those microorganisms [18].

The reconstruction of MAGs allowed the construction of tentative associations between resistance genes and bacterial taxa, revealing potential AMR reservoirs in our samples. Most MAGs belonged to *Paenibacillaceae*, *Clostridium*, Lactabacillales and *Bacillus*, consistent with the predominance of Firmicutes and explaining the prevalence of the associated AMR genes. Of particular interest was the occurrence of $bla_{\text{CTX-M-15}}$ in the *Enterobacteriaceae* bin, suggesting a possible transmission of ESBL genes through food. However, limitations in bin quality and contamination restrict the strength of some taxonomic assignments, highlighting the need for deeper sequencing in future studies.

In our region, Brazil is the largest consumer of antibiotics linked to food production of animal origin, occupying second place on a worldwide scale [2]. In this scenario, reports of enterobacteria carrying antibiotic resistance genes in Brazilian chicken meat sold in European supermarkets are not surprising [2,5].

Furthermore, in Uruguay, we have detected the same AMR genes in one-day-old chicks imported from Brazil circulating in local broiler farms [5]. Notably, $bla_{\text{CTX-M-2}}$, $bla_{\text{CTX-M-8}}$, $bla_{\text{CTX-M-15}}$, $bla_{\text{CMY-2}}$, *qnrB2,* and *qnrB19* have also been found in human samples [19].

In this sense, we highlight the detection in frozen food of $bla_{\text{CTX-M-15}}$, an extended-spectrum β-lactamase commonly found in Enterobacterales present in humans and farm animals, as we reported in previous studies. Moreover, $bla_{\text{CTX-M}}$ alleles are one of the most epidemiologically relevant β-lactam resistance mechanisms worldwide due to their association with mobile genetic elements [5,20].

Conversely, *lnu* (lincosamide nucleotidyl-transferases) have been detected in microorganisms of human and animal origin. Interestingly, *lnu(G)* was first discovered in *E. faecium* within transposon Tn*6260*, and later detected on a plasmid in an NDM-1-producing *Proteus sp* isolate of animal origin [21,22]. These findings highlights the alarming risk of co-selecting multiple AMR mechanisms through improper antibiotic use.

Taken together, our findings underscore the potential dissemination of resistance genes via international food trade. Differences in antimicrobial policies between Brazil and our country may explain the presence of resistant microorganisms in imported food. In this sense, supported by national surveillance programs and aligned with export requirements for high-level markets such as the European Union,

Table 1
Taxonomic MAGs and AMR genes identified.

Bin	Marker Lineage	Unique SCGs	Redundant SCGs	Size (bp)	Contigs	N50	SCG completeness (%)	SCG redundancy	Contamination (%)	AMR genes
concoct.108. contigs	*Enterobacteriaceae*	51	0	4,937,291	203	48,402	100	0	2.15	$bla_{CTX-M-15}$, *mdfA*
concoct.13. contigs	*Streptococcus*	51	0	2,075,379	166	22,461	100	0	3.06	–
concoct.121. contigs	*Paenibacillaceae*	51	1	5,239,509	126	76,075	100	2	2.53	–
Maxbin.040. contigs	*Clostridium*	51	1	2,397,747	96	57,839	100	2	0.04	–
Maxbin.062. contigs	*Paenibacillaceae*	50	2	5,209,152	396	44,055	98	4	1.19	–
concoct.90_sub. contigs	*Clostridiales*	51	4	5,411,840	259	30,744	100	8	3.10	*tet(a), mef (A), lnu(G), mph(N)*
Maxbin.070. contigs	*Paenibacillaceae*	48	1	6,142,295	246	145,970	94	2	4.55	*tet(L)*
concoct.57_sub. contigs	*Paenibacillaceae*	50	6	6,652,595	534	20,174	98	12	11.79	*aadK*
Maxbin.073_sub. contigs	*Paenibacillaceae*	45	7	4,250,905	283	61,157	88	14	25.72	
Maxbin.047. contigs	*Bacilli*	39	4	6,145,525	1793	5399	76	8	15.22	*blaZ, satA, vanR-A, tet (L)*
Maxbin.038. contigs	*Bacillus*	33	1	3,787,333	1415	3184	65	2	24.33	–
Maxbin.077. contigs	*Lactobacillales*	32	1	1,289,356	545	2691	63	2	9.40	–
Maxbin.050. contigs	*Bacilli*	37	6	14,414,661	4693	4043	73	12	23.97	*satA, vanS-F, dfrG*
Maxbin.069_sub. contigs	*Bacteria*	44	13	3,555,457	495	21,097	86	25	53.89	–
Maxbin.058_sub. contigs	*Lactobacillales*	33	4	183,071,294	84,906	2345	65	8	63.03	bla_{BPU-1}
concoct.23_sub. contigs	*Bacteria*	45	13	8,691,418	3661	2650	88	25	45.05	*fosB1*
Maxbin.034. contigs	*Bacillus*	30	3	5,178,609	1129	9592	59	6	29.26	*mphK, aadK, vmlR*
Maxbin.043. contigs	*Paenibacillaceae*	25	0	2,073,868	737	3457	49	0	3.85	*ant(6)-Ia, tet (L)*
concoct.114_sub. contigs	*Bacteria*	37	9	806,010	156	7142	73	18	13.53	–
concoct.131_sub. contigs	*Lactobacillales*	24	0	2,165,742	476	6665	47	0	3.39	–
Maxbin.046_sub. contigs	*Paenibacillaceae*	25	1	5,419,823	618	27,878	49	2	3.42	*satA, aadK*
–	–	–	–	–	–	–	–	–	–	**clbA, lsa (D), ermD, cat86, qacH, tet(M), clbC*

SCG: Simple-copy genes; *: Unbinned AMR genes.

Uruguay has introduced stricter controls on the use of critically important antibiotics in animals intended for human consumption [23,24]. Accordingly, the use of antibiotics as growth promoters in Uruguay has been banned since 2011 (Decree 98/011), as well as the use of colistin in veterinary products since 2019 (Decree 141/019). As previously stated, Brazil is one of the largest consumers of veterinary antimicrobials, particularly tetracycline, penicillins and macrolides used for treatment and prophylactic purposes [2]. Conversely, Brazil implemented in 2019 the plan named AgroPrevine, in an attempt to strengthen measures for the prevention and control of antimicrobial resistance, which differs from Uruguay's model, characterized by earlier implementation and tighter antibiotic use controls [25]. These differences may facilitate the entry of resistant bacteria and antimicrobial resistance genes through imported food products, so regional surveillance strategies must be taken into consideration.

Finally, even though the industrial application of metagenomic studies is limited, the adoption of such an approach could enhance food safety and quality by optimizing the detection of hazardous microorganisms along the processing chain, thus surpassing traditional methods and strengthening public health strategies.

CRediT authorship contribution statement

Nicolás F. Cordeiro: Methodology, Investigation, Formal analysis, Writing – review & editing. **Nadia Coppola:** Methodology, Investigation. **Federica Ferreira:** Methodology, Investigation. **Inés Bado:** Validation, Supervision, Project administration, Investigation, Funding acquisition, Formal analysis, Conceptualization, Writing – original draft. **Rafael Vignoli:** Writing – review & editing.

Funding

This work was supported by Agencia Nacional de Investigación e Innovación, Proyecto de investigación aplicada Fondo María Viñas, FMV_3_2020_1_162024, Uruguay

Disclosure statement

No competing financial interests are declared.

English language editing assistance was provided by ChatGPT (OpenAI, GPT-4, 2025 version).

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.onehlt.2025.101171.

Data availability

Data will be made available on request.

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