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Global distribution of *mcr*-carrying bacteria: an analysis of genomic data

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Abstract

Background Mobilized colistin resistance (*mcr*) gene has emerged as a major driver of colistin resistance. Therefore, this study aimed to determine the distribution of *mcr*-variants and *mcr*-carrying genomes deposited in the NCBI database by sample collection periods and across continents, countries, genera, species, and ecosystems.

Methods In this database mining study, the keyword “*mcr*” was used to identify all *mcr*-carrying genomes deposited in the NCBI Pathogen Detection database until June 07, 2025, 12h15 GMT. A purely descriptive approach was used in this study, and percentages were calculated by dividing the number of an event by the total number of events (percentage = $n/N \times 100$).

Results Of the 2422739 whole genomes registered in the NCBI database, 18785 (0.78%) carried complete *mcr* variant sequences. Seventy-seven *mcr* subvariants were detected, including mostly *mcr-1.1* (9431/18785; 50%), and *mcr-9.1* (5971/18785; 32%). *Mcr-9.1* was the most frequently detected subvariant in several genera, including *Serratia* spp. (17/17; 100%), *Cronobacter* spp. (155/160; 97%), and *Pluralibacter* spp. (19/20; 95%), whereas *mcr-1.1* was the most commonly detected subvariant in *Escherichia* and *Shigella* spp. (8235/9678; 85%). Regarding geographical distribution, *mcr-1.1* was the most observed subvariant in Asia (6759/9033; 75%) and Europe (1886/4680; 40%), whereas *mcr-9.1* was the most identified in America (2982/4017; 74%) and Oceania (546/771; 71%). In Africa, *mcr-10.1* (52/160; 33%), and *mcr-1.1* (50/160; 31%) were the most frequent subvariants. *Mcr*-carrying genomes deposited in the NCBI database were distributed across ecosystems, including humans ($n=8185$), animals ($n=4521$), the environment ($n=468$), and food ($n=48$). The sample collection years for *mcr*-carrying bacteria ranged from 1953 to 2025, and the distribution of *mcr*-carrying genomes was as follows: 1953–1990 ($n=49$), 1991–1999 ($n=47$), 2000–2009 ($n=704$), 2010–2019 ($n=12810$), and 2020–2025 ($n=4297$). Another key finding was that 705 of the 18785 *mcr*-carrying genomes deposited in the NCBI database (3.8%) harbored multiple *mcr* genes, including 693 and 12 genomes co-carrying two and three *mcr* genes, respectively.

Conclusion *Mcr*-carrying bacteria represent a significant One Health concern because of their major role in colistin resistance and potential for global dissemination. Key actions, such as global surveillance, One Health monitoring, and appropriate stewardship, should be taken to preserve the efficacy of colistin for decades.

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Keywords Antimicrobial resistance, Colistin resistance, One Health, Polymyxins, Systematic analysis, Whole-genome sequencing

Introduction

The mitigation of antimicrobial resistance (AMR) has become a priority for the World Health Organization (WHO) [1], and last-resort antibiotics constitute a glimmer of hope for treating multidrug-resistant (MDR) and extensively drug-resistant (XDR) bacteria - associated infections worldwide [2]. Last-resort antibiotics include mainly carbapenems, tigecycline, vancomycin, daptomycin, and polymyxins (i.e., colistin and polymyxin B) [3]. However, in recent years, bacterial isolates resistant to these drugs have been increasingly reported worldwide [4, 5]. In this regard, the WHO has classified carbapenem-resistant *Enterobacterales* as critical priority pathogens [6], for which few therapeutic options are available. Therefore, despite its possible nephrotoxicity, colistin remains a ultimate last-resort antibiotic for treating carbapenem-resistant bacteria-associated infections [7–9].

Nevertheless, in recent years, colistin-resistant clones have been reported worldwide [10–12], and animal and environmental ecosystems are considered reservoirs and vectors of transmission to humans [13–15]. In the past, colistin resistance in *Enterobacterales* was commonly associated with the inactivation/mutation of *mcrB* [16, 17]. More recently, the transferable mobilized colistin resistance (*mcr*) genes have emerged as major contributors to colistin resistance alongside the traditional mutations in *mcrB*, *phoPQ*, and *pmrAB* [18]. In 2015, the first *mcr* gene case was reported in *Escherichia coli* isolated from pigs in China [19]. Currently, more than ten *mcr* gene variants have been reported worldwide, with the Asian continent being the primary location of *mcr*-carrying bacteria [20]. *Mcr* encodes a phosphoethanolamine transferase that transfers phosphoethanolamine (pEtN) to the lipid A portion of the lipopolysaccharide (LPS) in the bacterial outer membrane, neutralizing the negative charge to which colistin binds to. This modification prevents colistin from displacing essential divalent cations, such as Mg^{2+} and Ca^{2+} , and inserting them into the cell membrane, thereby stopping colistin-induced destabilization and bactericidal effects [18]. In contrast to the inactivation/mutation of *mcrB* (that is chromosomally mediated), the potential for the dissemination of *mcr* genes is very high because *mcr* is mainly transferable by horizontal transfer via mobile genetic elements (MGE) such as plasmids, transposons, and integrons [21]. The situation is further alarming due to reports of the co-carriage of other resistance genes such as carbapenemases and extended-spectrum beta-lactamases (ESBL) on *mcr*-resistance plasmids from some bacterial isolates in some

parts of the world thereby likely to render the efficacy of these last lines of antibiotics questionable [22–24].

Mcr genes can be detected in isolates using polymerase chain reaction (PCR) or whole-genome sequencing (WGS) approaches. PCR methods are limited in the detection of *mcr* variants carried by the isolates because only the *mcr* variants for which primers are used can be detected, and novel variants may remain undetectable. Although the limitations of WGS (high financial cost and uneven global availability), it has the advantage of accurately detecting all known *mcr* variants and subvariants carried by the isolates and even detecting novel *mcr* variants and subvariants [25].

Numerous WGS studies have detected *mcr* variants and subvariants worldwide. However, comprehensive analyses including thousands of genomes, and summarizing the global distribution of *mcr*-carrying bacteria based on genomic data remain scarce. In addition, strong data, such as continental, regional, and national trends, and trends according to ecosystems and species, are lacking. In this study, the primary objective was to determine the percentage of *mcr*-carrying genomes deposited in the NCBI Pathogen Detection database. In addition, we determined the distribution of *mcr* variants by sample collection period and across continents, countries, genera, species, and ecosystems.

Methods

Search strategy

This database mining study focused on the NCBI Pathogen Detection database, as it is a major resource for genomic data and a highly relevant and important database for biomedical and life sciences research. The database search was performed on June 07, 2025 (12:15 GMT) using the following link "<https://www.ncbi.nlm.nih.gov/pathogens/antimicrobial-resistance>". This study represents a cross-sectional analysis of the NCBI Pathogen Detection database at a single time point, and the date and time of access define the version of the dataset analyzed, as the database is continuously updated. Therefore, replication of this study at a different time point may yield different absolute numbers due to ongoing database updates. The keyword "*mcr*" was used to identify all genomes deposited in the NCBI Pathogen Detection database and carrying an *mcr* variant or subvariant. No additional filters were applied in order to maximize sensitivity and ensure the inclusion of all potential *mcr*-carrying genomes. Retrieved entries were subsequently screened based on predefined eligibility criteria, including the presence

of complete *mcr* sequences and the availability of WGS data.

Eligibility criteria

- Only genomes carrying *mcr* genes obtained through WGS were included.
- Only *mcr* genes with 100% sequence identity and coverage were included to ensure high specificity and avoid inclusion of partial, truncated, or ambiguous sequences.
- Genomes obtained through partial genome sequencing were excluded.
- All WGS genomes that reported partial *mcr* sequences were excluded.
- Duplicate genomes were identified and excluded.
- Two authors (KMD and TB) evaluated whether the genomes met the inclusion criteria of the review, and disagreements were resolved through discussions.

Data extraction

Three authors extracted the data, and disagreements were resolved through discussions. For all the included genomes, the following subgroup data were extracted: organism group, location where the strains were isolated, strain ID, BioSample ID, host, isolation source (sample from which the strains were isolated), sample collection date, WGS accession number, assembly number, and *mcr* variant or subvariant. Multiple *mcr* genes in the same genome (same subvariant or different subvariant) were considered and included in the estimation of the proportions to avoid miscalculations. All these informations were recorded in a Microsoft Excel 2016 v2.0 file. A data curation step was performed prior to analysis, including removal of duplicate genomes and verification of meta-data fields. Metadata completeness was assessed, and entries with missing information were retained and categorized as ‘not available’, without any imputation.

Statistical analyses

A purely descriptive approach was used in this study, and percentages were calculated by dividing the number of an event by the total number of events (percentage = $n/N \times 100$). Subgroup percentages were also calculated at the *mcr* subvariants level, specie and genus levels, country and continent levels, ecosystem and sub-ecosystem levels, and at the sample collection period levels. *Escherichia* and *Shigella* were grouped together following the structure of the NCBI Pathogen Detection database and due to their close phylogenetic relationship, as *Shigella* spp. are phylogenetically nested within the *Escherichia coli* lineage and are often considered part of the *Escherichia coli-Shigella* complex.

Results

Selection of the genomes

The NCBI Pathogen Detection database search generated 2422739 bacterial whole-genomes. Subsequently, 2400561 whole genomes without *mcr* genes were excluded. Duplicated genomes and whole genomes carrying partial *mcr* genes ($n=3393$) were also excluded. The remaining 18785 bacterial whole genomes with a complete *mcr* gene were therefore included in this study (Supplementary File).

Distribution of *mcr*-carrying genomes deposited in the NCBI pathogen detection database

A total of 18785 WGS genomes carrying a complete *mcr* gene were identified in the NCBI Pathogen Detection database (Supplementary File) out of 2422739 WGS genomes available (0.78%). A total of 77 *mcr* variants and subvariants were detected, including mainly *mcr*-1.1 (9431/18785; 50%), *mcr*-9.1 (5971/18785; 32%), *mcr*-9.2 (1202/18785; 6%), and *mcr*-10.1 (664/18785; 4%) (Table 1).

Mcr-carrying genomes across species and genera

A total of 31 bacterial species carrying *mcr* variants were recorded in the NCBI Pathogen Detection database, and all were Gram-negative bacteria. Species included mostly *E. coli* and *Shigella* (9678), *Salmonella enterica* (3224), *Enterobacter hormaechei* (1870), *Enterobacter cloacae* (1317), and *Klebsiella pneumoniae* (910) (Table 2). Fifteen genera of *mcr*-carrying bacteria were represented. The most frequent genera were *Escherichia* and *Shigella* spp. (9678), *Enterobacter* spp. (4003), *Salmonella* spp. (3224) and *Klebsiella* spp. (1067) (Table 3).

Mcr-9.1 was the most frequently detected subvariant in several genera, including *Serratia* spp. (17/17; 100%), *Cronobacter* spp. (155/160; 97%), *Pluralibacter* spp. (19/20; 95%), *Citrobacter* spp. (248/297; 84%), *Kluyvera* spp. (10/14; 71%), and *Enterobacter* spp. (2634/4003; 65%). In contrast, *mcr*-1.1 was the most commonly detected subvariant in *Escherichia* and *Shigella* spp. (8235/9678; 85%). In *Klebsiella* spp., *mcr*-9.1 (418/1067; 39%) and *mcr*-1.1 (253/1067; 24%) were the most commonly detected subvariants. In *Salmonella* spp., *mcr*-9.1 (1862/3224; 58%) and *mcr*-1.1 (1035/3224; 32%) were also the most identified subvariants. In *Acinetobacter* spp., *mcr*-4.3 (9/10; 90%) was the most frequently identified subvariant, whereas *mcr*-4.9 (3/4; 75%) was the most frequently detected in *Vibrio* spp. In *Providencia* spp., *mcr*-8 (11/15; 73%) was the most frequently detected, whereas *mcr*-5.1 was the only subvariant identified in *Pseudomonas* spp. (11/11; 100%). In *Aeromonas* spp., *mcr*-3 was the most commonly identified (256/264; 97%), whereas *mcr*-5 was the only subvariant identified in *Morganella* spp. (Fig. 1 and Supplementary File).

Table 1 Distribution of *mcr* variants and subvariants in genomes deposited in the NCBI Pathogen Detection database

Variants and sub-variants of <i>mcr</i>	<i>mcr</i> variant	Total <i>mcr</i> genome	Percentage
<i>mcr</i> -1.1	9431	18785	50%
<i>mcr</i> -9.1	5971	18785	32%
<i>mcr</i> -9.2	1202	18785	6%
<i>mcr</i> -10.1	664	18785	4%
<i>mcr</i> -3	306	18785	1.6%
<i>mcr</i> -3.1	266	18785	1.4%
<i>mcr</i> -9	219	18785	1.2%
<i>mcr</i> -1	190	18785	1%
<i>mcr</i> -5.1	143	18785	0.8%
<i>mcr</i> -8.1	137	18785	0.7%
<i>mcr</i> -3.5	134	18785	0.7%
<i>mcr</i> -1.26	133	18785	0.7%
<i>mcr</i> -8.2	67	18785	0.4%
<i>mcr</i> -4.3	60	18785	0.3%
<i>mcr</i> -3.2	50	18785	0.3%
<i>mcr</i> -1.32	48	18785	0.3%
<i>mcr</i> -10	46	18785	0.2%
<i>mcr</i> -3.39	40	18785	0.2%
<i>mcr</i> -1.2	37	18785	0.2%
<i>mcr</i> -2.1	33	18785	0.18%
<i>mcr</i> -3.4	26	18785	0.13%
<i>mcr</i> -4.6	25	18785	0.13%
<i>mcr</i> -8	24	18785	0.13%
<i>mcr</i> -1.5	20	18785	0.1%
<i>mcr</i> -4.2	18	18785	0.1%
<i>mcr</i> -3.17	14	18785	0.07%
<i>mcr</i> -2.3	13	18785	0.07%
<i>mcr</i> -3.21	12	18785	0.06%
<i>mcr</i> -3.20, <i>mcr</i> -3.3	11	18785	0.06% *
<i>mcr</i> -1.7, <i>mcr</i> -3.40	10	18785	0.05% *
<i>mcr</i> -5	9	18785	0.05%
<i>mcr</i> -1.18, <i>mcr</i> -3.24	8	18785	0.04% *
<i>mcr</i> -3.16, <i>mcr</i> -3.19	7	18785	0.04% *
<i>mcr</i> -3.11	6	18785	0.03%
<i>mcr</i> -1.12, <i>mcr</i> -1.27, <i>mcr</i> -11.1, <i>mcr</i> -3.6	5	18785	0.03% *
<i>mcr</i> -3.22, <i>mcr</i> -4	4	18785	0.02% *
<i>mcr</i> -1.19, <i>mcr</i> -1.8, <i>mcr</i> -10.3, <i>mcr</i> -3.27, <i>mcr</i> -3.41, <i>mcr</i> -4.1, <i>mcr</i> -4.9, <i>mcr</i> -8.3	3	18785	0.02% *
<i>mcr</i> -1.11, <i>mcr</i> -1.33, <i>mcr</i> -10.2, <i>mcr</i> -2.8, <i>mcr</i> -3.23, <i>mcr</i> -3.25, <i>mcr</i> -3.9, <i>mcr</i> -4.5, <i>mcr</i> -5.3	2	18785	0.01% *
<i>mcr</i> -1.28, <i>mcr</i> -1.31, <i>mcr</i> -1.34, <i>mcr</i> -1.37, <i>mcr</i> -1.4, <i>mcr</i> -1.6, <i>mcr</i> -1.9, <i>mcr</i> -2, <i>mcr</i> -3.12, <i>mcr</i> -3.26, <i>mcr</i> -3.28, <i>mcr</i> -3.29, <i>mcr</i> -3.38, <i>mcr</i> -3.42, <i>mcr</i> -8.4, <i>mcr</i> -9.3	1	18785	0.005% *

*: for each *mcr* variant or subvariant**Table 2** Distribution of *mcr*-carrying genomes across bacterial species

Species	<i>mcr</i> -carrying genomes
<i>Escherichia coli</i> and <i>Shigella</i>	9678
<i>Salmonella enterica</i>	3224
<i>Enterobacter hormaechei</i>	1870
<i>Enterobacter cloacae</i>	1317
<i>Klebsiella pneumoniae</i>	910
<i>Enterobacter kobei</i>	314
<i>Citrobacter freundii</i>	297
<i>Enterobacter roggenkampii</i>	225
<i>Enterobacter asburiae</i>	223
<i>Aeromonas salmonicida</i>	177
<i>Cronobacter</i>	160
<i>Klebsiella oxytoca</i>	157
<i>Aeromonas veronii</i>	75
<i>Enterobacter ludwigii</i>	27
<i>Pluralibacter gergoviae</i>	20
<i>Serratia marcescens</i>	17
<i>Providencia alcalifaciens</i>	15
<i>Kluyvera intermedia</i>	14
<i>Pseudomonas aeruginosa</i>	11
<i>Aeromonas hydrophila</i>	10
<i>Acinetobacter baumannii</i>	10
<i>Enterobacter mori</i>	9
<i>Enterobacter bugandensis</i>	7
<i>Enterobacter chengduensis</i>	5
<i>Enterobacter sichuanensis</i>	3
<i>Vibrio cholerae</i>	3
<i>Aeromonas sobria</i>	2
<i>Enterobacter cancerogenus</i>	2
<i>Enterobacter intestihominis</i>	1
<i>Morganella morganii</i>	1
<i>Vibrio parahaemolyticus</i>	1

Table 3 Distribution of *mcr*-carrying genomes across bacterial genera

Genera	Number of species in the genus	<i>mcr</i> -carrying genomes
<i>Escherichia</i> and <i>Shigella</i> spp.	1	9678
<i>Enterobacter</i> spp.	12	4003
<i>Salmonella</i> spp.	1	3224
<i>Klebsiella</i> spp.	2	1067
<i>Citrobacter</i> spp.	1	297
<i>Aeromonas</i> spp.	4	264
<i>Cronobacter</i> spp.	1	160
<i>Pluralibacter</i> spp.	1	20
<i>Serratia</i> spp.	1	17
<i>Providencia</i> spp.	1	15
<i>Kluyvera</i> spp.	1	14
<i>Pseudomonas</i> spp.	1	11
<i>Acinetobacter</i> spp.	1	10
<i>Vibrio</i> spp.	2	4
<i>Morganella</i> spp.	1	1

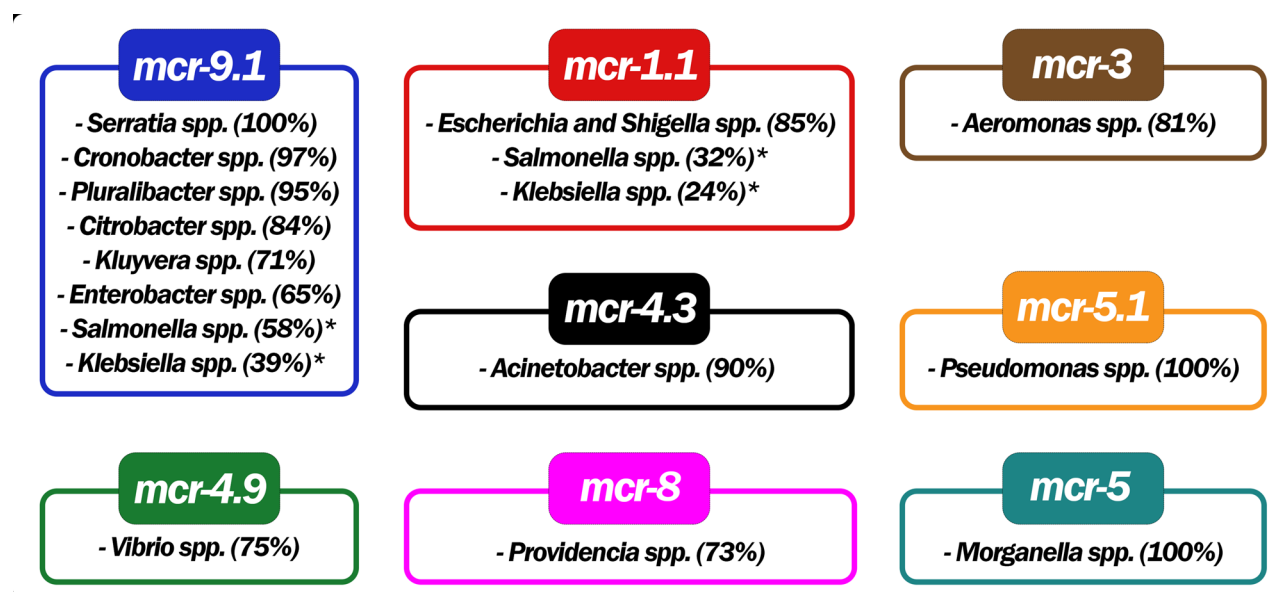


Fig. 1 Distribution of *mcr* variants and subvariants in genomes deposited in the NCBI Pathogen Detection database by genus: The most observed *mcr* variants and subvariants in each of the 15 genera. *: The two most observed *mcr* variants and subvariants were reported for *Salmonella* spp. and *Klebsiella* spp

Among the genomes deposited in the NCBI Pathogen Detection database, several *mcr* subvariants were found exclusively in some species: *mcr-3.17* ($n=14$), *mcr-3.3* ($n=11$), *mcr-3.16* ($n=7$), *mcr-3.6* ($n=5$), *mcr-3.27* ($n=3$), *mcr-3.41* ($n=3$), *mcr-3.25* ($n=2$), *mcr-3.9* ($n=2$), *mcr-3.38* ($n=1$), *mcr-3.42* ($n=1$) were exclusively found in *Aeromonas* spp. In addition, *mcr-10.3* ($n=3$) and *mcr-10.2* ($n=2$) were exclusively found in *Enterobacter* spp. *Mcr-3.11* ($n=6$), *mcr-3.22* ($n=4$), *mcr-3.23* ($n=2$), *mcr-3.26* ($n=1$), *mcr-3.28* ($n=1$), *mcr-8.3* ($n=3$), *mcr-8.4* ($n=1$), *mcr-9.3* ($n=1$) were exclusively found in *Klebsiella* spp., whereas *mcr-1.19* ($n=3$), *mcr-1.6* ($n=1$), were exclusively found in *Salmonella* spp. Moreover, *mcr-4.9* ($n=3$) was found exclusively in *Vibrio* spp. (Supplementary File).

Distribution of *mcr*-carrying genomes across countries and continents

The 18785 *mcr*-carrying genomes were from 97 countries worldwide, including 33 in Europe, 29 in Asia, 17 in America, 16 in Africa, and two in Oceania. The highest number of *mcr*-carrying genomes deposited in the NCBI Pathogen Detection database was recorded in Asia (9033), followed by Europe (4640), America (4057), Oceania (771), and Africa (160). The collection country of 124 *mcr*-carrying bacteria has not been submitted to the NCBI Pathogen Detection database. At the country level, the five countries with the highest number of *mcr*-carrying genomes deposited in the NCBI Pathogen Detection database were China (6263), the USA (3163), the United

Kingdom (1322), Australia (747), and Thailand (726) (Supplementary File).

The most common *mcr* subvariant in genomes deposited in the NCBI Pathogen Detection database in Asia was *mcr-1.1* (6759/9033; 75%), followed by *mcr-9.1* (844/9033; 9%). In Europe, the most detected *mcr* subvariants were *mcr-1.1* (1886/4680; 40%), *mcr-9.1* (1541/4680; 33%), and *mcr-9.2* (763/4680; 16%). In America, *mcr-9.1* was the most detected (2982/4017; 74%), followed by *mcr-1.1* (642/4017; 16%). In Oceania, the most common was *mcr-9.1* (546/771; 71%), followed by *mcr-9.2* (151/771; 20%). In Africa, it was rather *mcr-10.1* (52/160; 33%), followed by *mcr-1.1* (50/160; 31%), and *mcr-9.1* (37/160; 23%) (Supplementary File).

Distribution of *mcr*-carrying genomes across ecosystems and sub-ecosystems

Mcr-carrying genomes deposited in the NCBI Pathogen Detection database were represented by ecosystems as follows: humans (8185), animals (4521), the environment (468), and food (48). The sub-ecosystems with the highest number of *mcr*-carrying genomes deposited in the NCBI Pathogen Detection database were mammals (including humans) (10473), birds (1919), water (384), and fish (183). A total of 5563 *mcr*-carrying genomes were deposited in the NCBI Pathogen Detection database without any information on the ecosystem of origin (Table 4).

Table 4 Distribution of *mcr*-carrying genomes deposited in the NCBI Pathogen Detection database at the sub-ecosystem level

Sub-ecosystems	<i>mcr</i> -carrying genomes
Invertebrate	113
Fish	183
Environment (not specified)	73
Food (not specified)	38
Bird	1919
Water	384
Animal (not specified)	14
Reptile	4
Mammals (including human)	10473
Tree	1
Cereal	1
Manure	6
Sewage	4
Fruit	4
Meat	5
NA	5563

NA: sub-ecosystem data not deposited in the NCBI Pathogen Detection database

Table 5 Distribution of *mcr* genomes in bacteria isolated from human biological systems

Human body systems and sub-systems	<i>mcr</i> -carrying genomes
Digestive tracts	2326
Urinary tracts	953
Blood systems and pericardium	622
Respiratory tracts	539
Wounds	152
Peritoneal and retroperitoneal fluids	79
Multiple location pus	67
Liver and bile duct	40
foot, hands, bones, toes	31
Hospital tools and devices*	15
Skin and related tissues	14
Central nervous system	11
Genital tracts	7
Uncommon samples**	3
Ear, nose, and throat	1
TOTAL	

*Hospital tools and devices: Urine catheter, deep venous catheter, tracheoflex, bronchoscope, colonoscope, endoscope, ureteroscope

**Uncommon samples: Neoplasm, hydatid fluid, umbilical cord

Distribution of *mcr*-carrying genomes deposited in the NCBI pathogen detection database from human samples

In this study, we found that *mcr*-carrying bacteria were isolated from almost all human biological systems, including mostly the digestive ($n=2326$), urinary ($n=953$), blood ($n=622$), and respiratory ($n=539$) systems. Interestingly, *mcr*-carrying bacteria have been isolated from hospital tools and devices ($n=15$), central nervous system samples ($n=11$), and uncommon samples such as neoplasm, hydatid fluid, and umbilical cord ($n=3$) (Table 5).

Distribution of *mcr*-carrying genomes across sample collection periods

The sample collection years for *mcr*-carrying bacteria ranged from 1953 to June 07, 2025, and the distribution of *mcr*-carrying genomes was as follows: 1953–1990 ($n=49$), 1991–1999 ($n=47$), 2000–2009 ($n=704$), 2010–2019 ($n=12810$), and 2020–2025 ($n=4297$). In addition, 878 *mcr*-carrying genomes were deposited without referencing the sample collection year.

Genomes with multiple *mcr* genes

A total of 705 of the 18785 *mcr*-carrying genomes deposited in the NCBI Pathogen Detection database, (3.8%), harbored multiple *mcr* genes. A total of 693 genomes co-carried two *mcr* genes, whereas the remaining 12 co-carried three *mcr* genes. The most frequent pattern of multiple *mcr* genes in the genomes included (*mcr*-9.1 + *mcr*-9.2) = (137/705; 19%), (*mcr*-9.2 + *mcr*-9) = (106/705; 15%), and (*mcr*-9.1 + *mcr*-9) = (89/705; 13%) (Supplementary File).

Genomes with multiple *mcr* genes were observed in nine of the 15 genera. The highest percentage of genomes with multiple *mcr* genes was observed in *Pluralibacter* spp. (11/20; 55%) and *Aeromonas* spp. (42/264; 15.9%). Genomes with multiple *mcr* genes were also observed in the following key genera: *Escherichia* and *Shigella* spp. (324/9678; 3.3%), *Enterobacter* spp., (173/4003; 4.3%), *Klebsiella* spp., (61/1067; 5.7%), and *Salmonella* spp., (78/3224; 2.4%) (Supplementary File).

At the ecosystem level, the highest percentage of genomes with multiple *mcr* genes was observed in environmental samples (62/468; 13.2%), followed by human samples (348/8185; 4.3%) and animal samples (142/4521; 3.1%) (Supplementary File).

Genomes with multiple *mcr* genes have been observed in 40 countries across five continents including Oceania (59/771; 7.7%), Europe (228/4640; 4.9%), Asia (302/9033; 3.3%), Africa (5/160; 3.1%), America (103/4057; 2.5%) and eight genomes without continent data (Supplementary File).

The highest percentage of genomes with multiple *mcr* genes was observed in the sample collection periods of 2010–2019 (542/12810; 4.2%), and 2020–2025 (114/4297; 2.7%). Bacteria with multiple *mcr* genes were not isolated during the sample period of 1953–1990 (Supplementary File).

Discussion

In this review, a total of 18785 *mcr*-carrying bacterial whole genomes were deposited in the NCBI Pathogen Detection database, indicating the widespread distribution of *mcr*-carrying bacteria. Even if the proportion of *mcr*-carrying genomes in the NCBI Pathogen Detection database was low, (0.78%), the large number of

77 *mcr*-variants suggests a continual genetic evolution of *mcr* genes worldwide. In addition, the percentage of *mcr*-carrying genomes in the NCBI Pathogen Detection database (0.78%), reflects the distribution of sequenced genomes rather than the true population-level prevalence.

At the species level, Shi et al. [26] and Liu et al. [27], respectively, corroborated our findings by reporting *mcr*-1 as the most predominant *mcr* variant (86.1%) in *E. coli* isolates and *mcr*-1 and *mcr*-9 as the dominant *mcr* variants in *mcr*-positive *K. pneumoniae* isolates.

The *mcr*-carrying bacteria were collected from 97 countries worldwide and from all five continents. This suggests that *mcr*-carrying bacteria are no longer a region- or continent-related issue but a global concern that must be addressed in every part of the globe. At the continent level, Asia showed the highest number of *mcr*-carrying genomes deposited in the NCBI Pathogen Detection database, likely reflecting differences in sequencing intensity and surveillance strategies rather than the true epidemiological burden. The number of *mcr*-carrying genomes in each continent needs to be interpreted cautiously, as the high number of *mcr*-carrying genomes observed in Asia may be influenced by the level of surveillance of colistin-resistant bacteria and the type of bacteria (pathogenicity/AMR level) subjected to WGS and deposited in the NCBI Pathogen Detection database. In addition, the low number of *mcr*-carrying genomes in Africa and Oceania may partially result from the low number of genomes deposited in the NCBI Pathogen Detection database on these continents. Similar to this study, Martiny et al. [28] found that *mcr*-1 was less widely spread worldwide (America, Asia, and Europe) than *mcr*-9 (Africa, America, Asia, Europe, Oceania, the Atlantic Ocean, and the Pacific Ocean). Another key finding of this study was that Nordic countries, such as Finland ($n=5$), Norway ($n=22$), Iceland ($n=1$), and Sweden ($n=14$), had the lowest number of *mcr*-carrying genomes deposited in the NCBI Pathogen Detection database in Europe. Several European scientific reports have reported that Nordic countries have the lowest antimicrobial consumption (mg/kg estimated biomass) in food-producing animals in Europe [29], and no sales of colistin for animals have been routinely reported in Finland, Iceland, and Norway in the last two decades, in contrast to other European countries [29, 30]. The very low number of *mcr*-carrying genomes observed in these countries appears to be a possible consequence of the non-use of colistin in food-producing animals in these countries.

In this study, *mcr*-carrying bacteria were isolated from all ecosystems, including humans, animals, the environment, and food, as also reported by Shi et al. [26]. Bacteria carrying *mcr* genes are known to have broad host

ranges. Previous research has documented the presence of *mcr*-carrying strains in various ecological settings, such as water (71% of samples), animal feces (51%), and food products (36%) [31]. Furthermore, Furlan et al. [32] highlighted the emergence of *mcr*-1 and *mcr*-9 in companion animals, emphasizing the importance of enhanced monitoring through a One Health-based surveillance. Common reservoirs (environmental sources, food chains, and human activities) further promote cross-niche transmission [13]. The extensive host range of *mcr* genes can be attributed to its potential evolutionary changes in the animal gastrointestinal tracts (GIT) owing to the prolonged use of colistin as a growth promoter. This gene can then be transferred to humans via the food chain, direct contact with animals, or through contamination of freshwater and seawater systems, leading to the contamination of vegetables and seafood products. The persistence of *mcr* in the human GIT microflora can result in further contamination of water systems through the disposal of wastewater containing human feces [31]. Therefore, the mitigation of *mcr*-carrying bacteria and colistin resistance by predominantly targeting the environmental and animal ecosystems could yield efficient results, as evidenced by the ban on colistin as a growth promoter and antimicrobial therapy for animals in several countries [33–35]. In bacterial emergency infections, such as sepsis, pneumonia, and meningitis, probabilistic antimicrobial therapies are often administered before the isolation of the implicated bacteria and the availability of antibiotic susceptibility testing (AST) results. With the dangerous spread of carbapenem-resistant bacteria worldwide, colistin, although potentially nephrotoxic, has become a last-line empirical treatment for emergency bacterial infections. However, this study revealed more than one thousand *mcr*-carrying bacteria isolated from these emergency bacterial infections, suggesting numerous cases of emergency infections without any efficient probabilistic antimicrobials. Another key aspect was the isolation of numerous *mcr*-carrying bacteria on hospital tools and devices, such as urine catheters, deep venous catheters, tracheoflex, bronchoscopes, colonoscopes, endoscopes, and ureteroscopes, calling for better implementation of patient safety and cleaning-disinfection protocols and appropriate advertisement for the prevention and mitigation of healthcare-associated infections (HAIs).

Another key point was that *mcr*-carrying bacteria have been spreading worldwide for approximately six decades before the first characterization of *mcr* gene by Liu et al. in 2015 [19]. In fact, the registered sample collection periods in the NCBI Pathogen Detection database revealed that *mcr*-carrying bacteria have been circulating at least since 1950s. Similar to this study, a previous study [36] also traced the origins of *mcr* genes back to

the 1960s, far from the official first characterization of an *mcr* gene in 2015.

Another key observation in this study was that (3.8%) of the genomes co-harbored two or three *mcr* genes. Whether the multiple *mcr* genes were located on the same or different plasmids, the presence of multiple *mcr* genes in the genomes can enhance colistin resistance and accelerate its rapid, horizontal, and global spread of colistin resistance [37]. In addition, the fact that genomes with multiple *mcr* genes were observed in key species such as *Escherichia* spp. and *Shigella* spp., *Klebsiella* spp., *Enterobacter* spp., *Salmonella* spp., and *Acinetobacter* spp. required particular attention and further monitoring. Moreover, the fact that genomes with multiple *mcr* genes were observed in all five continents, in both human-animal-environment ecosystems highlights the complexity of colistin resistance and the importance of tackling the rise of colistin resistance globally through the One Health concept.

Limitations of this study

Although this study reported *mcr*-carrying bacteria in 97 countries, many countries with *mcr*-carrying bacteria may have not been included in this study because we focused only on WGS genomes submitted to the NCBI Pathogen Detection database. The inclusion of *mcr* resulting from PCR analysis or WGS genomes not registered in the NCBI Pathogen Detection database may have added weight to these findings. Another limitation was the database bias. In fact, the NCBI repository is subject to strong geographic, clinical, and temporal biases, including the overrepresentation of high-income countries and clinically significant pathogens. The apparent predominance of *mcr*-carrying genomes in Asia, in human samples, and during the period of 2010–2019 may be due to a difference in sequencing intensity rather than true epidemiological differences. Therefore, these biases should be considered when interpreting the data reported in the present study. Furthermore, the use of a strict threshold (100% identity and coverage) may have excluded some legitimate *mcr* variants with lower similarity or incomplete sequences. Moreover, inconsistencies and variability in metadata reporting across NCBI submissions (e.g., geographic origin, host, and sampling context) may have affected the accuracy of subgroup analyses. The availability of these data would have provided more accurate findings, and reflected the real distribution of *mcr*-carrying genomes across subgroups.

Conclusion

This study provides a clear overview of the global distribution of *mcr*-carrying genomes deposited in the NCBI Pathogen Detection database. The overall proportion of *mcr*-carrying genomes was very low and Asia had the

highest number of *mcr*-carrying genomes deposited in the NCBI Pathogen Detection database. In addition, this study revealed that *mcr-1.1* and *mcr-9.1* were the most represented *mcr* subvariants in the NCBI Pathogen Detection database, and several *mcr* variants and subvariants were specific to certain continents, species, and genera. Moreover, this study revealed that *mcr*-carrying bacteria were present in every ecosystem, calling for a One Health action. We hope that key actions, such as global surveillance, One Health monitoring, and appropriate stewardship, will be taken to preserve the efficacy of colistin for decades.

Supplementary Information

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Supplementary Material 1.

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Clinical trial

Not applicable.

Authors' contributions

KMD, FPS and MC conceptualized the study. KMD, FPS, EEI, TB, and DK collected and extracted the data. KMD, EEI, TB analyzed data. KMD and FPS drafted the original manuscript. FPS, DK, BSB, SD, AEK, and MC substantively revised and edited the manuscript. All authors have made intellectual contributions to the work and approved the final version of the manuscript for submission.

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Data availability

The datasets supporting the conclusions of this article are included within the article and its Supplementary files.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

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Competing interests

The authors declare no competing interests.

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