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Narrative review

Circulation of extended-spectrum β-lactamase and plasmid-borne cephalosporinase-producing *Escherichia coli* from a One Health perspective: a narrative review

Guillaume Miltgen [1, 2, 3], Valentine Berti [4, 5], Milen Milenkov [6], Heike Schmitt [7, 8, †], Jaap A. Wagenaar [9, 10, 11, †], Laurence Armand-Lefevre [4, 5, *]

[1] *Laboratoire de Bactériologie, CHU Félix Guyon, Saint-Denis, La Réunion, France*
[2] *UMR Processus Infectieux en Milieu Insulaire Tropical (PIMIT), CNRS 9192, INSERM U1187, IRD 249, Université de La Réunion, Saint-Denis, La Réunion, France*
[3] *Centre Régional en Antibiothérapie (CRAtb) de La Réunion, Saint-Pierre, La Réunion, France*
[4] *Laboratoire de Bactériologie, Hôpital Bichat, AP-HP Nord, Paris, France*
[5] *Infection, Antimicrobials, Modelling, Evolution (IAME), INSERM UMR 1137, Université Paris Cité, Paris, France*
[6] *Fondation Mérieux, Lyon, France*
[7] *Centre for Infectious Disease Control, National Institute for Public Health and the Environment (RIVM), Bilthoven, The Netherlands*
[8] *Department of Biotechnology, Delft University of Technology, Delft, The Netherlands*
[9] *Faculty of Veterinary Medicine, Utrecht University, Utrecht, The Netherlands*
[10] *WHO Collaborating Centre for Reference and Research on Campylobacter and Antimicrobial Resistance from a One Health Perspective/WOAH Reference Laboratory for Campylobacteriosis, Utrecht, The Netherlands*
[11] *Wageningen Bioveterinary Research, Wageningen University & Research, Lelystad, The Netherlands*

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ABSTRACT

Background: The global rise of extended-spectrum β-lactamase (ESBL) and plasmid-borne cephalosporinase (pAmpC) producing Enterobacterales is a major health concern. Their increasing prevalence in both humans and animals underscores the need for One Health surveillance, for which *Escherichia coli* has been recognized as a key indicator. While many studies have investigated the circulation of ESBL/pAmpC-producing *E. coli* (ESBL/pAmpC-*Ec*) across human, animal, and environmental sectors, the extent to which animals contribute to human acquisition remains unclear.
Objectives: This review provides an overview of the intersectoral circulation of ESBL/pAmpC-*Ec* and evaluates the potential role of animals as a reservoir for human colonization.
Sources: Publications (2010–2024) identified through PubMed, Scopus, and Google Scholar, on ESBL/pAmpC-*Ec* circulation across human, animal, and environmental sectors (excluding studies on human-environment, animal-environment, and human-food only) were reviewed considering the included sectors, comparison methods, and geographical context.
Content: Surveillance approaches varied widely between studies, shaped by sampling strategies, geographical context, and isolated comparison methods. Advances in genomic methods have refined our understanding of ESBL/pAmpC-*Ec* circulation between sectors. Early studies, mostly conducted in high-income countries (HICs), suggested human-animal transmission based on comparisons of ESBL/pAmpC-*Ec* sequence types, resistance genes, and plasmid replicons. However, these findings were challenged by the introduction of more discriminating comparison methods such as whole-genome sequencing, which revealed a largely compartmentalized circulation of ESBL/pAmpC-*Ec* in HICs. Similar studies in low- and middle-income countries (LMICs) shifted this paradigm, demonstrating frequent cross-sectoral transmission across humans, animals, and the environment. Many authors also highlighted the likely underestimated role of plasmids in the circulation of ESBL/pAmpC genes.
Implications: Despite the heterogeneity of the studies, two distinct scenarios emerged: predominantly intrasectoral ESBL/pAmpC-*Ec* circulation in HICs and significant intersectoral circulation in LMICs. These findings underscore the need for region-specific antimicrobial resistance control strategies, focusing on

* Corresponding author: Laurence Armand-Lefevre, IAME INSERM UMR 1137 Université Paris Citésite Xavier Bichat, 16 rue Henri Huchard, 75018 Paris, France.
E-mail address: laurence.armand@aphp.fr (L. Armand-Lefevre).
† These authors contributed equally to this work.

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limiting human-to-human transmission in HICs and enhancing sanitation and biosecurity in LMICs.
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Introduction

The global rise of antimicrobial resistance (AMR) is a major public health concern, with multidrug-resistant bacteria contributing significantly to morbidity and mortality worldwide [1]. Among these bacteria, third-generation cephalosporin-resistant Enterobacterales, particularly those producing extended-spectrum β-lactamase (ESBL) and plasmid-borne cephalosporinase (pAmpC), are the most prevalent [2]. Although these two resistance mechanisms differ in their enzymatic characteristics and spectrum, both are predominantly plasmid-mediated and share a high potential for dissemination [3–5]. Over the past two decades, the emergence of CTX-M-type ESBL and their dissemination in the community has largely replaced older ESBL such as TEM and SHV, which were primarily confined to health care settings [6,7]. This shift has driven a steady increase in the prevalence of ESBL-producing Enterobacterales, with global human carriage estimated at 14% in 2015 and an annual increase of 5.4% over the past 20 years, a trend that has also reached the animal sector [8,9]. Since the 2000s, infectious diseases have been recognized as a global issue affecting human, animal, and environmental health, leading to the One Health concept [10]. More recently, the One Health approach has been applied to AMR with strong support of the Quadripartite Alliance (Food and Agriculture Organization, United Nations Environment Programme, WHO, and World Organization for Animal Health), highlighting the need for integrated global surveillance [11]. *Escherichia coli* has been recognized as a key indicator due to its high prevalence in human infections, its presence as a commensal in human and animal gut, and its persistence in the environment [12–15]. Moreover, ESBL/pAmpC-*Ec* is a major contributor to global mortality [16]. For years, researchers have speculated about the sources of ESBL/pAmpC-*Ec* acquisition in humans, particularly the contribution of animals and food. Clarifying these pathways is essential for effectively addressing the rise of ESBL/pAmpC-*Ec* infections in humans.

This review assesses the potential intersectoral circulation of ESBL/pAmpC-*Ec* and evaluates the extent to which animals may serve as a source for the general population. We examined relevant studies and tracked the evolution of hypotheses over time, taking note of differences in methodology and study location.

Methods

We searched PubMed, Scopus, and Google Scholar for relevant publications, published from 2010 to 2024, on ESBL/pAmpC-*Ec* cross-sectoral circulation, using the following keywords (or abbreviations): *E coli*, extended-spectrum β-lactamase, acquired or plasmid-borne AmpC, third-generation cephalosporin-resistance, humans, patients, farmers, animals, chickens, livestock, farms, food, environment, water, wastewater, and sewage. Given that both ESBL and pAmpC mechanisms involve plasmid-mediated resistance to third-generation cephalosporins and that many studies have investigated them together, we chose to consider ESBL/pAmpC-*Ec* jointly. As our aim was to investigate the role of animals, either directly or via the environment, in the risk of human acquisition of ESBL/pAmpC-*Ec*, studies including only human-environment, animal-environment, and human-food chain were excluded. Retained studies were classified according to three main criteria: (a) whether whole genome sequencing (WGS) was used to compare *E. coli* isolates, (b) the number of sectors included, i.e. human-animal or human-animal-environment, and (c) the country in which the study was conducted, classified as low and middle-income or high-income, according to the current World Bank classification [17]. We also included relevant risk factors and modelling studies. Studies with fewer than 20 isolates or in languages other than English were excluded. In total, 58 studies were included in this review.

Results

Transmission of ESBL/pAmpC E. coli strains

One Health studies prior to the use of WGS

Studies at the human–animal interface. From 2010 to 2017, many studies investigated livestock as potential reservoirs for ESBL/pAmpC-*Ec* transmission to humans, both in the general population and specific high-risk groups. Most used strain comparison based on ESBL/pAmpC resistance genes, phylogenetic groups, and sequence type (ST) [18–21]. Only a few studies used more discriminatory typing methods, such as pulsed-field gel electrophoresis (PFGE), primarily in European high-income countries (HICs), including The Netherlands and Spain [22–24]. A high prevalence of ESBL/pAmpC-*Ec* was observed in animals, particularly poultry, and less in humans [19,25]. CTX-M type enzymes predominated, with some shared between humans and animals, and others more common in animals (CTX-M-1, TEM-52, CMY-2) or in humans (CTX-M-15). STs were highly diverse, with ST131 dominating in humans. Potential animal-human transmission, mainly from chickens and pigs, was suggested based on shared ST and resistance gene combinations (e.g. ST131/CTX-M-9 or CTX-M-15, ST10/CTX-M-1 or TEM-52, ST58/CTX-M-1), sometimes supported by similar plasmid replicons and virulence genes [5,18,20,26]. Most studies concluded that findings suggested intersectoral transmission, with cross-sectoral clusters more frequently observed in at-risk populations, such as farm workers and their families. However, some studies using PFGE to compare human and animal isolates reported more contrasting results [22,24]. Cortés et al. [22] found that, despite shared ESBL/pAmpC enzymes, STs, and virulence genes among *E. coli* isolates from poultry, pigs and human clinical samples, only two (ST648/CTX-M-32) of 166 isolates had the same PFGE pulsotype. Similarly, in 2013, Kluytmans et al. [24] re-analysed 145 *E. coli* isolates from Overdevest et al. [20] using PFGE and identified only one clonally related pair among 30 cross-sectoral isolates.

Studies at the human–animal-environment interface. Between 2017 and 2021, six studies covering all three sectors were published, including three in HICs [27–32]. Dorado-Garcia et al. [29] analysed over 27 000 isolates from 35 studies in The Netherlands, comparing the distribution of ESBL/AmpC genes and plasmid replicons across 22 reservoirs. They found significant similarities between farmer and farm animal isolates, while human (general

population) isolates clustered with those from surface water and wild birds, remaining distinct from those from farm animals or food. Day et al. [31] sequenced the genome of 936 ESBL-*E. coli* isolated from bacteraemia, human faeces, sewage, and livestock, but compared them only using ST, serotype and ESBL genes. Minimal overlap was found between human and animal sectors, except for ST10 isolates. However, within ST10, serotypes remained reservoir specific [31]. These two studies confirmed the sectorized circulation of ESBL/pAmpC-*Ec* in HICs, with distinct transmission cycles showing minimal overlap: one involving food producing animals and farmers, and another the general population and the environment. During this period three studies were conducted in low- and middle-income countries (LMICs) (Thailand, India, and Bangladesh) [27,30,32]. As in HIC studies, two suggested cross-sectoral circulation of ESBL/pAmpC-*Ec* based on shared CTX-M genes, phylogroups, and/or ST [27,32]. However, Tansawai et al. [30] (Thailand), using PFGE, found that only two of 32 human isolates matched chickens or environmental profiles, suggesting that while animal-human transmission occurs, it remains rare.

In their 2015 review, Lazarus et al. [33] questioned whether ESBL/pAmpC-*Ec* infections originate from food-producing animals and pointed out that, although there is some evidence of human-animal transmission, larger-scale studies using highly discriminatory methods such as WGS are needed to accurately quantify its intensity and extent.

One Health studies using WGS

Studies at the human–animal interface. While contact with farm animals was a recognized risk factor for ESBL/pAmpC-*Ec* colonization, WGS-based comparisons between animal and farmer isolates have yielded mixed results. Van Hoek et al. [34] confirmed six of 8 suspected cross transmissions from chicken farms using WGS (<10 *cg*MLST alleles difference), and Aworh et al. [35,36] identified 30 closely related isolates among 97 (<30 SNPs) in farmers, cattle and abattoir effluents. In contrast, de Been et al. [37] reanalysed isolates from Leverstein van Hall et al. [18] incorporating human clinical isolates, and found that all isolates, including five human-poultry pairs (previously indistinguishable by MLST, ESBL genes, and pMLST), differed by over 1263 SNPs, suggesting that earlier studies using low-resolution methods may have overestimated animal-human transmission [37]. At the population level, numerous studies, mostly in HICs, including clinical/commensal human and farm animal isolates, confirmed these findings and concluded that ESBL/pAmpC-*Ec* of animal origin contribute minimally to human isolates [38–42]. This was supported by findings that (a) the predominant STs differed significantly between human and animal reservoirs and (b) cross-sectoral STs such as ST10, ST38, or ST88 formed distinct reservoir-adapted subpopulations. Ludden et al. [38] (UK) identified only two closely related patient-cattle pairs (<15 SNPs) among 1948 *E. coli* isolates, including 297 ESBL/pAmpC-*Ec* from bloodstream infections, cattle, and meat. Similarly, studies from Nigeria, Laos, Thailand, and Vietnam found very few clonally related isolates between sectors (e.g. Truong et al. identified a single strain shared between a farmer and chickens among 486 isolates from healthy individuals, farmers, and chickens) [43–47].

This paradigm held until two studies from LMICs, Cambodia (2019) and Tanzania (2020), provided the first evidence of multiple cross-transmission of ESBL-*Ec* between poultry, meat, fish, and the human community using WGS [48,49]. Nadimpalli et al. [48] identified ST10, ST48, and ST189/CTX-M-55 strains shared between fish, meat, and humans (clinical and commensal isolates) through phylogenetic analysis combined with resistance gene and AMR profile data, while Büdel et al. [49] observed ST361/CTX-M-15 and ST1585/CTX-M-14 strains shared between poultry, chicken meat, and healthy individuals (<15 SNPs). These human-animal strain circulation patterns were later confirmed by studies in other LMICs, including China, Ecuador, Ghana, and Nigeria [50–53], while findings from Kenya were more nuanced [54].

Studies at the human–animal-environment interface. Studies from HICs covering all three sectors confirmed the human-animal findings, with the exception of Falgenhauer et al., [55] who reported clonal dissemination of an ST410/CTX-M-15 ESBL-*Ec* strain across humans, livestock, and farm environment. Studies in Canada and Reunion Island (France) confirmed host specificity for ESBL/AmpC enzymes and STs, with CTX-M-14, CTX-M-15, CTX-M-27, and ST131 again being predominant in human clinical isolates, whereas CTX-M-1 was predominant in cattle, with no strain overlap between sectors (<10 cg or *wg*MLST alleles) [41,56]. Martak et al. [57] conducted a study in five HICs using an innovative model comparing isolates from food in long-term care facilities (representing production animals and derived food products) and sewage/polluted rivers (representing human excreta) and similarly noted compartmentalization between these two sectors [57].

Here again, three recent studies conducted in LMICs (Brazil and Madagascar) produced markedly different results, identifying numerous cross-sectoral clusters between humans, animals and the environment [58–60]. In Madagascar, ST48-ST450-ST3489/CTX-M-15 strains (<40 SNPs) and in Brazil, ST410/CTX-M-15, ST648/CTX-M-14 (>98% homology) were shared between the three sectors. Milenkov et al. demonstrated that 30% of isolates were shared between chickens and humans and 12% between all three sectors (<40 SNPs) [60]. Authors highlighted the role of the environment in animal-human transmission [60,61].

Some studies also observed shared human-animal ESBL/pAmpC-*Ec* strains (e.g. ST131/CTX-M-14, ST410/CTX-M-15, ST38/CTX-M-27, and ST405/CMY-2) [62] associated with direct contact with companion animals or wildlife exposure to human waste from sewers and landfill sites [4,63–66].

Transmission of mobile genetic elements carrying ESBL/pAmpC-encoding genes

Almost all included studies mentioned the role of mobile genetic elements, such as plasmids, in the circulation of ESBL/pAmpC genes between sectors. Prior to WGS, researchers hypothesized cross-sectoral transmission of plasmids carrying ESBL/pAmpC genes based on the presence of similar enzymes and plasmids [18,25,29,67]. Short-read sequencing has enhanced evidence of this circulation through methods such as contig comparison, in silico plasmid reconstruction, and typing tools (e.g. Placnet, MLplasmids) [37,40,41,47,59,61,68,69]. A wide range of plasmids, mainly IncF types, as well as IncH, IncI, IncN, IncX, or IncY, were identified as vectors of ESBL/pAmpC genes. For a few suspected cases of plasmid transmission, some studies added long-read sequencing to provide more definitive evidence. Studies conducted in HICs suggested that only a small fraction of plasmids was transmitted between human and animal isolates, with Ludden et al. [38] estimating the proportion shared between sectors at 5%. Studies from The Netherlands and Reunion Island showed the circulation of IncI-$bla_{\text{CTX-M-1}}$ (ST7 and ST3) plasmids suggesting transmission from animals to humans, given the markedly higher prevalence of this enzyme in animals [37,41,69]. Cross-transmissions of IncK-$bla_{\text{CMY-2}}$, IncI-$bla_{\text{CTX-M-15}}$ or IncFII-$bla_{\text{CTX-M-55}}$ plasmids have also been documented [37,38,70]. Interestingly, Milenkov et al. [60] used extensive long-read sequencing and demonstrated significant circulation of some IncF plasmids (F31/36:A4 B1 and F-:A-B53) and of a highly conserved IncY plasmid

Table 1
Studies investigating circulation of ESBL/pAmpC *Escherichia coli* strains and plasmids between humans and animals ($N = 37$)

Study	Year of sampling	Country	HIC/ LMIC	Sampling location	Type of isolates	Number of isolates	Human sampling	Animal sampling	WGS	Isolate typing and comparison	Plasmid typing and comparison	Conclusion (Remark)
Cortés et al. [22]	2003	Spain	HIC	Regional	ESBL, pAmpC	166	Patients (clinical isolates)	Livestock (pig, poultry)	N	MLST, phylogenetic groups, PFGE, serotype	None	Compartmentalization
Mora et al. [23]	1991-2010	Spain	HIC	Regional	ESBL	67	Patients (clinical isolates)	Livestock (chicken, turkey), wildlife (birds)	N	MLST, phylogenetic groups, PFGE, serotype	None	Interconnection
Overdevest et al. [20]	2009	Netherlands	HIC	Regional	ESBL	158	Patients (clinical isolates/rectal swabs)	Chicken meat	N	Micro array, MLST	None	Interconnection
Leverstein van Hall et al. [18]	2009-2010	Netherlands	HIC	Local (animal)/ National (human)	ESBL	525	Patients, community (clinical isolates/ rectal swabs)	Chicken meat, livestock (poultry)	N	MLST, R genes (micro array)	pMLST, plasmid replicons	Interconnection
Dierikx et al. [19]	2009	Netherlands	HIC	National	ESBL, pAmpC	54	Risk group (farmers; rectal swabs)	Chicken meat, livestock (broiler)	N	MLST, R genes	pMLST	Interconnection
Kluytmans et al. [24]	2008-2009	Netherlands	HIC	Regional	ESBL	145	Patients (clinical isolates/rectal swabs)	Chicken meat	N	MLST, phylogenetic groups, PFGE	Plasmid replicons	Limited transmission (based on isolates from Overdevest et al.)
Voets et al. [79]	2009-2010	Netherlands	HIC	Local (animal)/ National (human)	AmpC	577	Patients, community (clinical isolates/ rectal swabs)	Chicken meat	N	MLST, R genes (multiplex PCR)	Plasmid replicons	Interconnection
Bortolaia et al. [67]	2009-2011	USA	HIC	Regional	pAmpC	68	Community	Pets (cat, dog)	N	None	pMLST	Compartmentalization (only CMY-two plasmids analysis)
de Been et al. [37]	2006-2011	Netherlands	HIC	Local (animal)/ National (human)	ESBL, pAmpC	32	Patients, community (clinical isolates)	Chicken meat, livestock (broiler)	Y	SNPs	SNPs	Compartmentalization (partly based on isolates from Leverstein van Hall et al. and Voets et al.)
Huijbers et al. [25]	2010-2011	Netherlands	HIC	*Not specified*	ESBL, pAmpC	133	Risk group (farmers)	Livestock (broiler)	N	MLST, phylogenetic groups, R genes	pMLST	Interconnection
Wang et al. [68]	2009-2011	Switzerland	HIC	*Not specified*	ESBL	9 (16 plasmids)	Risk group (farmers; stools)	Livestock (chicken, lamb)	Y	None	SNPs	Interconnection -plasmids (human: staff from eat-processing companies)
Schaufler et al. [63]	2011-2014	Germany	HIC	Local	ESBL	68	Patients (clinical isolates)	Pets (dog), wildlife (birds)	Y	SNPs	None	Interconnection (only ST410 isolates analysis)
Day et al. [26]	2005-2009	Germany, Netherlands, United Kingdom	HIC	International	ESBL	353	Community (clinical isolates)	Livestock (cattle, pig, poultry, turkey), pets (cat, dog)	N	MLST, R genes	pMLST	Compartmentalization
Dang et al. [21]	2015	Vietnam	LMIC	Regional	ESBL	517	Risk group (farm workers; stools)	Livestock (pig)	N	R genes	None	No clear conclusion.
Ludden et al. [38]	2001-2015	United Kingdom	HIC	Regional	ESBL (and 3GC-S)	297 (1948 in all)	Patients (clinical isolates)	Livestock (cattle, chicken, pig, turkey), various meat	Y	SNPs	SNPs	Compartmentalization (human isolates only from bloodstream infections)

(*continued on next page*)

Table 1 (*continued*)

Study	Year of sampling	Country	HIC/ LMIC	Sampling location	Type of isolates	Number of isolates	Human sampling	Animal sampling	WGS	Isolate typing and comparison	Plasmid typing and comparison	Conclusion (Remark)
Nguyen VT et al. [44]	2012-2013	Vietnam	LMIC	Local	ESBL	486	Risk group (farmers; rectal swabs), community.	Livestock (chicken, pig)	Y	SNPs	None	Compartmentalization
Falgenhauer et al. [50]	2015	Ghana	LMIC	Local	ESBL	74	Patients (children; stools)	Livestock (poultry)	Y	SNPs	None	Interconnection
Valcek et al. [69]	2014-2015	Danemark, (Australia, France, Netherlands)	HIC	International	ESBL	12 (22 plasmids)	Patients (clinical isolates)	Livestock (broiler, chicken, pig), various meat	Y	None	SNPs	Interconnection - plasmids transmission (human isolates only from bloodstream infections)
Nadimpalli et al. [48]	2015-2016	Cambodia	LMIC	Local	ESBL	196	Patients, community (clinical isolates; rectal swabs)	Chicken/fish/ pork meats	Y	Phylogeny	None	Interconnection
Alzayn et al. [39]	2017-2018	United Kingdom	HIC	Local	AmpC	45	Community (urine samples)	Livestock (dairy cattle)	Y	SNPs	None	Compartmentalization
Van Hoek et al. [34]	2010-2012	Netherlands	HIC	*Not specified*	ESBL, pAmpC	22	Risk group (farmers)	Livestock (broiler)	Y	cgMLST	None	Interconnection (based on isolates from Huijbers et al.)
Büdel et al. [49]	2018	Tanzania (Zanzibar)	LMIC	Local	ESBL	56	Community (rectal swabs)	Chicken meat, livestock (poultry)	Y	cgMLST, microarray, rep-PCR	None	Interconnection
Hong et al. [4]	2018-2019	South Korea	HIC	*Not specified*	ESBL, pAmpC	221	Risk group (pet owners; rectal swabs)	Pets (cat, dog)	N	PFGE	None	Limited transmission (human cohabiting with pets)
Toombs-Ruane et al. [62]	2015-2017	New Zealand	HIC	Regional	ESBL, pAmpC	125	Patients (clinical isolates), risk group (pet owners; rectal swabs)	Pets (cat, dog)	Y	SNPs	None	Interconnection (human isolates only from urinary-tract infections)
Salinas et al. [51]	2018	Ecuador	LMIC	Local	ESBL	264	Community (children; stools)	Livestock (chicken), pets (dog)	Y	SNPs	None	Interconnection
Hounmanou et al. [40]	2015-2018	Vietnam	LMIC	Regional	ESBL, pAmpC	114	Risk group (farmers)	Livestock (pig)	Y	SNPs	SNPs	Compartmentalization (partly based on isolates from Dang et al.)
Truong et al. [45]	2018	Vietnam	LMIC	Regional	ESBL	74	Risk group (farm workers; stools)	Livestock (pig)	Y	SNPs	SNPs	Compartmentalization
Moser et al. [46]	2018	Laos	LMIC	Local	ESBL	49 (109)	Community, travellers (rectal swabs)	Chicken meat, livestock (poultry)	Y	Microarray, rep-PCR, SNPs	SNPs	Limited transmission (only 49 of the 109 *E. coli* were compared by WGS)
Giufrè et al. [5]	2016-2017	Italy	HIC	National	ESBL	925	Patients (clinical isolates)	Livestock (cattle, pig, poultry)	N	MLST, phylogenetic groups, R genes	None	Compartmentalization (human isolates only from blood and urines samples)
Muloi et al. [54]	2015-2016	Kenya	LMIC	Local	ESBL, pAmpC (and 3GC-S)	1338 (all isolates)	Community (faecal swabs)	Livestock (cattle, goat/ sheep, pig, poultry, rabbit),	Y	SNPs, cgMLST	None	Limited transmission (study design based on all 3GC-R and 3GC-S isolates)

								wildlife (bat, birds, rodents)				
Sealey et al. [42]	2019-2020	United Kingdom	HIC	Local	ESBL, pAmpC	396	Patients (clinical isolates)	Livestock (dairy cattle), pets (dog)	Y	SNPs	SNPs	Compartmentalization (human isolates only from urines samples)
Olorunleke et al. [47]	2019	Nigeria	LMIC	Regional	ESBL (pAmpC)	157	Risk group (in-contact humans; hand swabs)	Livestock (cattle, chicken, goat, pig, sheep)	Y	SNPs	SNPs	Compartmentalization but plasmid transmission
Nagy et al. [64]	2016-2017	Hungary	HIC	Local	ESBL	20	Community (stools), patients (clinical isolates)	Wildlife (rook)	Y	cgMLST	Plasmid replicons	Compartmentalization
Li et al. [52]	2021	China	LMIC	Regional	ESBL (and 3GC-S)	194	Patients (clinical isolates)	Livestock (chicken)	Y	MLST, phylogenetic groups, R genes, SNPs	Plasmid replicons	Interconnection
Jesumirhewe et al. [53]	2017	Nigeria	LMIC	Regional	ESBL	16	Community (urine/nasal samples), patients (clinical isolates)	Livestock (poultry)	Y	cgMLST	None	Interconnection
Menezes et al. [65]	2018-2020	Portugal/United Kingdom	HIC	International	ESBL, pAmpC	229	Risk group (pets owner; stools)	Pets (cat, dog)	Y	rep-PCR, SNPs	None	Limited transmission
Walas et al. [66]	2020	USA	HIC	Local	ESBL (and 3GC-S)	7	Community (stools)	Pets (dog)	Y	SNPs	Plasmid replicons	Compartmentalization (regarding ESBL isolates)

The conclusion column summarizes the main conclusion of each author, categorized as compartmentalization: no evidence of strain transmission, interconnection: significant strain transmission, limited transmission, or no clear conclusion.

3GC-R, third-generation cephalosporin-resistant; 3GC-S, third-generation cephalosporin-susceptible; ESBL, extended spectrum β-lactamase, HIC, high income country; LMIC, low-middle income country; MLST, multi-locus sequence typing; N, no; pAmpC, plasmid borne cephalosporinase; PFGE, pulsed-field gel electrophoresis; SNPs, single nucleotide polymorphisms; R genes, resistance genes; WGS, whole genome sequencing; Y, yes.

Table 2
Studies investigating circulation of ESBL/pAmpC *Escherichia coli* strains and plasmids among humans, animals and the environment ($N = 18$)

Study	Year of sampling	Country	HIC/LMIC	Sampling location	Type of isolate	Number of isolates	Human sampling	Food/animal sampling	Environmental sampling	WGS	Isolate typing and comparison	Plasmid typing and comparison	Conclusion (Remark)
Falgenhauer et al. [55]	2009-2014	Germany	HIC	National	ESBL	436	Patients, community	Livestock (broiler, cattle, horse, swine), pets (dog)	Farm environments	Y	SNPs	SNPs	Interconnection (only ST410 isolates analysis and farm environments)
Purohit et al. [27]	2014	India	LMIC	Local	ESBL (and 3GC-S)	115	Community (children)	Livestock (cattle, goat, hen, horse), pets (dog)	Household drinking, source water, waste water	N	R genes	None	Interconnection
Runcharoen et al. [43]	2014-2015	Thailand	LMIC	Local	ESBL	149	Patients	Farm environments (proxy)	Canals, hospital effluents	Y	SNPs	Not for ESBL genes	Compartmentalization (only farm environments)
Ojer-Usoz et al. [28]	2009-2012	Spain	HIC	Local	ESBL	448	Patients	Foods: cheese, fish, meat (poultry, pork), vegetables	Farm beds, rivers, wastewater	N	MLST	None	Compartmentalization
Dorado-Garcia et al. [29]	2005-2015	Netherlands	HIC	National	ESBL, pAmpC	5808	Community, patients risk group (farmers)	Livestock (beef, broiler, calf, chicken, hen, pig, turkey), pets (dog), wildlife (birds)	Surface and wastewaters	N	Modelisation (R genes, MLST, plasmids)	Plasmid replicons	Compartmentalization for general population - Interconnection for at risk populations (samples of 35 - studies, >27 000 samples)
Tansawai et al. [30]	2013-2014	Thailand	LMIC	Local	ESBL	159	Risk group (farmers, family members)	Livestock (chicken, duck)	Farm environments	N	PFGE	None	Interconnection - (only farm environments)
Day et al. [31]	2013-2014	United Kingdom	HIC	National	ESBL	936	Community, patients	Livestock (cattle, chicken, meat), vegetables/ fruits	Sewage, slurry	Y	R genes, MLST	None	Compartmentalization
Adator et al. [56]	2014-2016	Canada	HIC	Local	ESBL	162	Patients	Livestock (cattle)	Beef processing plant, sewage, streams	Y	SNPs	Plasmid replicons	Compartmentalization
Aworh et al. [35]	2018-2019	Nigeria	LMIC	Local	ESBL	37	Risk group (poultry/chicken markets workers)	Livestock (chicken, poultry)	Farm/live bird markets wastewater	Y	R genes, MLST	None	No clear conclusion.
Rousham et al. [32]	2017	Bangladesh	LMIC	Local	ESBL (and carbapenem-R)	540	Community, risk group (poultry-exposed workers)	Livestock (poultry)	Drinking water, farm wastewater	N	R genes	None	No clear conclusion.
Nguyen MN et al. [70]	2014-2015	Vietnam	LMIC	Local	ESBL	235	Patients	Livestock (chicken, pig)	Slaughterhouse environments (surface, water)	Y	R genes, cg/ wgMLST, SNPs	SNPs (bla_{CTX-M})	Compartmentalization (transposable elements analysis)
Miltgen et al. [41]	2015-2018	France	HIC	Regional	ESBL	410	Community, patients	Livestock (cattle, chicken, pig, small ruminants)	Sewage, human/animal wastewater	Y	cgMLST	SNPs	Compartmentalization

Martak et al. [57]	2018-2019	France, Germany, Netherlands, Spain, Switzerland	HIC	International	ESBL	254	—	Food (from LTCFs kitchen and supermarkets)	Sewage and wastewater	Y	cgMLST	None	Compartmentalization (sewers and polluted rivers as a proxy of human contamination)
Fuga et al. [58]	2010-2019	Brasil	LMIC	National	ESBL, pAmpC (and carbapenem-R)	167	Patients	Food (meat, seafood, vegetables), livestock (cattle, chicken/ poultry, horse, turkey), pets (cat, dog), wildlife (anteater, elephant, fish, ocelot, owl, penguin, vulture)	Freshwater, seawater, soil, surface water	Y	SNPs	pMLST	Interconnection
Aworh et al. [36]	2020	Nigeria	LMIC	Local	ESBL	97	Risk-group (abattoir workers)	Livestock (beef cattle)	Abattoir environments	Y	SNPs	SNPs	Limited transmission (only abattoir environments)
Gay et al. [59]	2018	Madagascar	LMIC	Local	ESBL	512	Community	Livestock (cattle, chicken, duck, goose, horse, pig, turkey), pets (cat, dog)	Drinking water	Y	SNPs	SNPs	Interconnection
Flatgard et al. [61]	2017	Bangladesh	LMIC	Local	ESBL (and carbapenem-R)	117	Community, risk group (poultry-exposed workers)	Chicken meat, livestock (poultry)	Drinking water, farm wastewater	Y	SNPs	SNPs	Interconnection (based on isolates from Rousham et al.)
Milenkov et al. [60]	2018-2019	Madagascar	LMIC	Regional	ESBL	277	Community (pregnant women), patients	Livestock (chicken)	Slaughterhouse effluents, surface water, wastewater	Y	SNPs	SNPs	Interconnection

The conclusion column summarizes the main conclusion of each author, categorized as compartmentalization: no evidence of strain transmission, interconnection: significant strain transmission, limited transmission, or no clear conclusion.
3GC-R: third-generation cephalosporin-resistant; 3GC-S: third-generation cephalosporin-susceptible; carbapenem-R: carbapenem-resistant; ESBL: extended spectrum β-lactamase; HIC: high income country; LMIC: low-middle income country; LTCFs: long-term care facilities; MLST: multi-locus sequence typing; N: no; pAmpC: plasmid borne cephalosporinase; PFGE: pulsed-field gel electrophoresis; R genes: resistance genes; WGS: whole genome sequencing; Y: yes.

across all three sectors in Madagascar. Although this review focuses on *E. coli*, plasmids also circulate across other Enterobacterales [71]. They can be acquired by species such as *Klebsiella pneumoniae* or *Enterobacter cloacae*, which may subsequently spread in health care settings and contribute to multidrug-resistant infections [72–74]. In their recent review, Castañeda-Barba et *al*. [75] concluded that plasmids represent a cornerstone of AMR dissemination, both between bacterial species and across ecological sectors.

Risk factor and modelling studies

In addition to genomic studies, risk factor and modelling studies have enriched the discussion. Mughini-Gras et al. [76] used a source attribution model based on 35 Dutch studies (2005-2017) to quantify community sources of ESBL/pAmpC-*Ec* carriage. They found that person-to-person transmission accounted for 61%, secondary contact with high-risk groups (e.g. travellers and farmers) for 7%, food for 19%, pets for 8%, and environmental exposure through freshwater bathing for 3%. Although this study is the first to quantify the sources of ESBL/pAmpC-*Ec* acquisition, these results are limited to a single HIC, restricting broader generalization. Conversely, studies in LMICs linked ESBL/pAmpC-*Ec* human colonization to untreated drinking water, open defecation, shared toilets, and poor hand hygiene [77]. A large-scale study in Malawi also associated carriage with high-density urban housing and households where animals interacted with food or were kept indoors. Interestingly, the rainy season has been identified as a risk factor for both human and animal colonization in some studies [60,78].

Challenges and prospects

This narrative review provided an overview of the circulation of ESBL/pAmpC-*Ec* from a One Health perspective, highlighting how hypotheses regarding the contribution of animals to human carriage or infection have evolved over time, shaped by methodological advances and geographical context.

The heterogeneity of the studies is evident, with variations in sample types, geographical and temporal scales, and methods (Tables 1 and 2). Human isolates originate from a variety of sources, including healthy carriers, clinical samples, and infections, further complicating interpretation. Indeed, the diversity of commensal strains is greater than that of clinical strains, which are overrepresented by virulent types. Human and animal isolates have sometimes been collected at different times and locations, further hindering circulation analysis [18,23,79]. Detection of ESBL/pAmpC-*Ec* was generally based on culture but using different selective media, following or not an enrichment step. A standardized methodology for ESBL/pAmpC-*Ec* surveillance within a One Health framework is thus needed. To address this, WHO has developed the Tricycle Protocol, a simplified, multisectoral surveillance approach targeting ESBL-*Ec* in the three main sectors: humans (community carriage and bloodstream infections), the food chain (poultry at slaughter) and the environment [80]. The implementation of a standardized protocol should provide highly

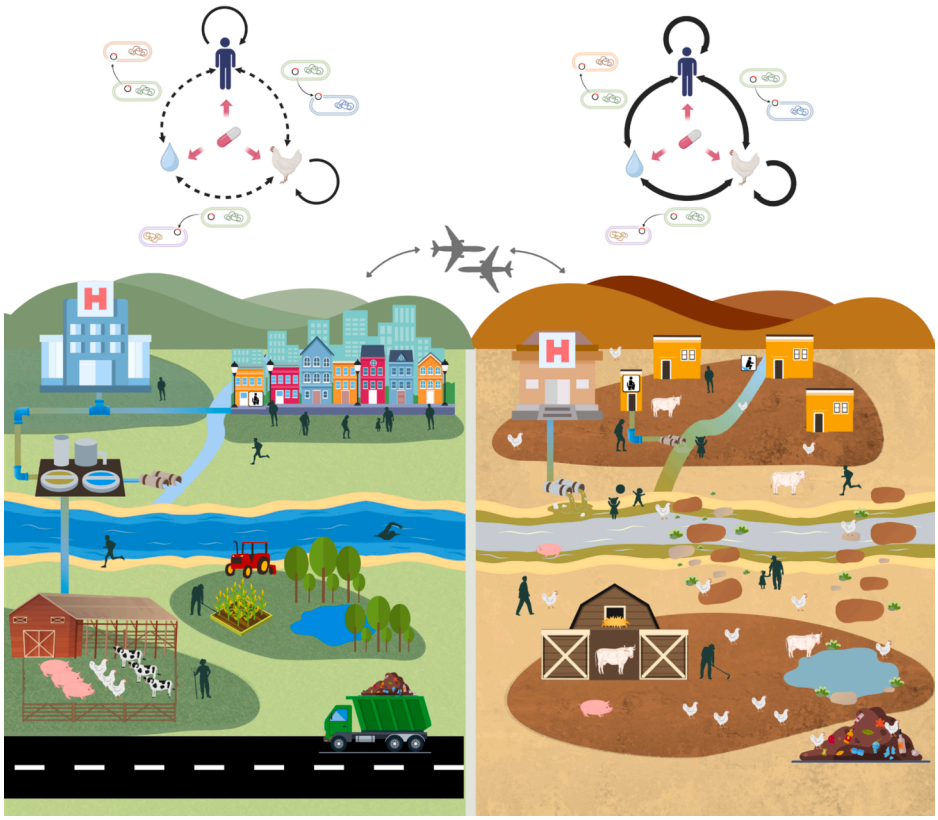

Fig. 1. Two-part figure illustrating the intra- and intersectoral transmission patterns of extended-spectrum β-lactamase and plasmid-borne cephalosporinase-producing *E. coli* in high-income (left) and low-income and middle-income (right) countries. This diptych highlights key differences related to the socioeconomic context, including the management of human and animal waste, access to sanitation and drinking water, and the organisation of livestock farming and agriculture, as well as the resulting potential human exposures. The circles above show transmission routes of bacteria and plasmids: dotted lines indicate low transmission, thin solid lines moderate transmission, and thick solid lines high transmission; fade arrows indicate plasmid transmission between isolates. The figure was created using Canva and BioRender softwares (Agreement numbers PA28ULKCS3 and KU28ULKJMA).

comparable data on global ESBL/pAmpC-*Ec* prevalence and circulation.

Prior to the use of WGS, the circulation of ESBL/pAmpC-*Ec* was assessed using genomic markers such as ESBL enzymes, STs, plasmid replicons, and to a lesser extent PFGE profiles. These methods lacked discriminatory power, often leading to erroneous conclusions about human-animal transmission. WGS is now the reference method, but its interpretation remains challenging due to inconsistencies in comparison approaches and strain similarity thresholds [81,82]. Indeed, defining a universal SNP or allele cut-off is complex, as the threshold for defining relatedness between isolates depends on the spatio-temporal scale of the study, the evolutionary rate of the strains, and the sequencing technology used. Recent studies advocate instead for context-specific thresholds [60,82].

Despite these limitations, two distinct scenarios emerge in the studies reviewed. In HICs, where hygiene measures are well developed in all sectors, health systems are regulated, food production is controlled, livestock farms are structured and located outside urban areas, and access to running water and sanitation systems minimizes environmental risks, the direct link between sectors appears limited (Fig. 1). However, human, animal, and environmental health remain deeply interconnected, with the use of antibiotics, biocides, and pesticides impacting this balance. By contrast, LMICs face distinct challenges. The uncontrolled use of antibiotics creates selection pressure, driving the emergence and persistence of resistance. Factors such as close human-animal contact, with farm animals often living in or near households, limited access to water hindering proper hand hygiene, and highly contaminated environments contribute to the spread of resistant strains across sectors (Fig. 1) [83–85].

Interestingly, in HICs, human colonization was dominated by extraintestinal virulent *E. coli* from B2 and D phylogroups (e.g. ST 131, ST1193, or ST73), which were rarely shared with animals. In contrast, in LMICs, ESBL/pAmpC-*Ec* cross-sectoral circulation was primarily driven by commensal strains from A and B1 phylogroups [8,33,38,40,62]. Some STs appear to have a greater ability to circulate across sectors. For example, ST10, ST38, ST69, ST410, ST450, and ST648 have been identified in both humans and animals, without necessarily implying genetic relatedness between isolates [5,25,31,50,58,60,86]. However, in contexts of close contact, particularly between humans and companion animals, human-associated clones such as ST131 or ST73 have also been detected in the latter [4,52,58,60].

While our review primarily focused on ESBL/pAmpC-*Ec* identified from asymptomatic carriage or extraintestinal infections, several intestinal pathogenic *E. coli* pathotypes (InPEC), including shiga-toxin producing (STEC) or enterohaemorrhagic *E. coli* (EHEC), may be associated with ESBL-production [87,88]. However, to date, no outbreaks of ESBL-producing InPEC of confirmed animal origin have been reported.

Many studies have examined the cross-sectoral circulation of ESBL/pAmpC-*Ec* strains, but fewer have focused on that of mobile genetic elements, particularly resistance gene-carrying plasmids [75]. Beyond the human and animal microbiota, the environment serves as both a reservoir and an important site for resistance gene exchange [89]. The role and burden of plasmids in the spread of AMR remain poorly quantified and underestimated, and the mechanisms underlying their persistence and propagation are still largely unclear [75].

In a broader context, global changes, including climatic events and population migration, may accelerate the spread of ESBL/pAmpC-*Ec* through epidemic clones or mobile genetic elements, highlighting the need for coordinated global surveillance of antibiotic resistance [90,91].

Conclusion

Surveillance of ESBL/pAmpC-*Ec* circulation remains a complex challenge requiring a One Health approach. The heterogeneity of existing studies highlights the need for standardized surveillance protocols to provide robust and reliable data for effective interventions. The two identified transmission models underscore the importance of tailoring AMR control programs to regional contexts and priorities. While antibiotic stewardship must be implemented or maintained across all sectors and countries, efforts in LMICs should include improved sanitation, wastewater management and food chain/livestock biosecurity. By contrast, HICs should prioritize reducing human-to-human transmission in health care facilities and the community.

Credit author contribution statement

Guillaume Miltgen and Laurence Armand-Lefevre: Conceptualization. Guillaume Miltgen, Valentine Berti, and Milen Milenkov: Literature search. Guillaume Miltgen, Valentine Berti, Milen Milenkov, and Laurence Armand-Lefevre: Reviewed the full-text articles included in the review. Guillaume Miltgen and Laurence Armand-Lefevre: Writing- Original draft preparation. Valentine Berti: Created illustrations. Heike Schmitt and Jaap A. Wagenaar: Interpretation and Manuscript Revision. Laurence Armand-Lefevre: Supervision, Writing- Reviewing and Editing. All authors contributed to the final version of the manuscript and approved it for publication.

Transparency declaration

Potential conflict of interest

The authors declare that they have no conflicts of interest.

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