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Copeticona-Callejas, C., Jimenez, S., Torrez-Mamani, A. et al (2026). Prevalence of enteric pathogens in mothers and children from communities in the La Paz River Basin Bolivia; associations with water, sanitation, and hygiene conditions. *Journal of Water and Health*, 24(2): 239-263. <http://dx.doi.org/10.2166/wh.2026.243>

N.B. When citing this work, cite the original published paper.

## Prevalence of enteric pathogens in mothers and children from communities in the La Paz River Basin Bolivia; associations with water, sanitation, and hygiene conditions

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 VI, 0009-0007-3660-5836

### ABSTRACT

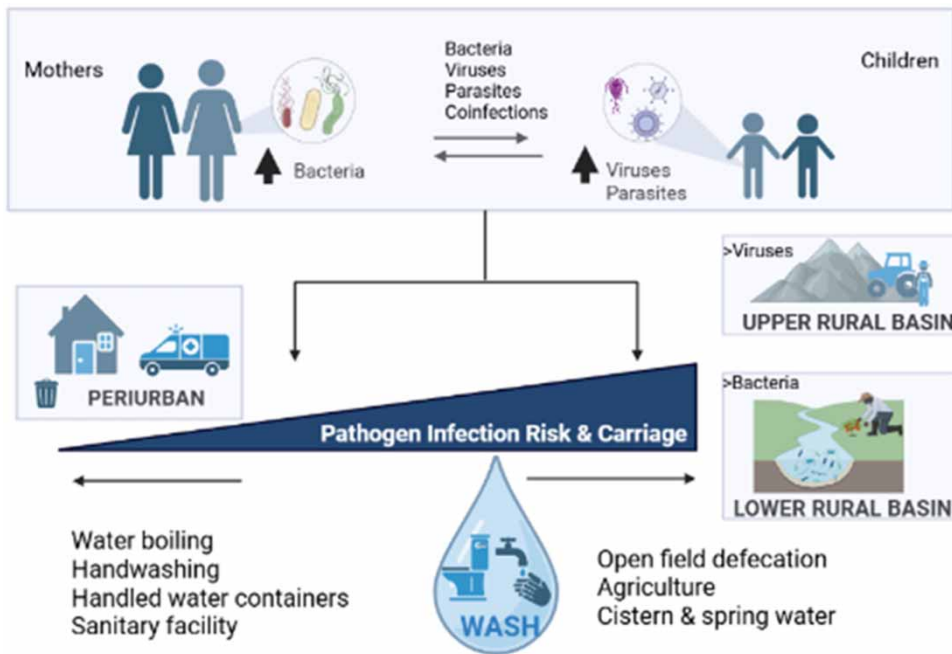
Enteric infections remain a major public health challenge in low- and middle-income countries, disproportionately affecting young children. We conducted a cross-sectional study to characterize the prevalence of enteropathogens among mothers and children from peri-urban and rural communities in the La Paz River Basin Bolivia, and to examine associations with water, sanitation, and hygiene (WASH) conditions. Fecal samples were analyzed by real-time PCR to detect 21 viral, bacterial, and parasitic pathogens, alongside household surveys and water quality assessments. Sixteen pathogens were detected, 85% of participants carried at least one pathogen, with frequent coinfections. The most prevalent pathogens were *Helicobacter pylori*, adenovirus, EPEC, *Giardia lamblia*, and *Shigella*. Pathogen carriage was higher in rural than in peri-urban settings, with bacterial infections predominating in the lower basin and viral infections in the upper basin. Children carried more viral and parasitic pathogens, while mothers had more bacterial pathogens. Significant mother–child concordance was observed for several pathogens, supporting shared household exposures. Enteric pathogen carriage was strongly associated with drinking water source, sanitation practices, housing quality, and hygiene behaviors, particularly reliance on cistern/spring water, open defecation, and inadequate hand hygiene. These findings highlight a substantial and heterogeneous burden of enteric infections, underscoring the need for integrated WASH interventions.

**Key words:** enteric pathogen carriage, hygiene practices, mothers-children, rural settings WASH

### HIGHLIGHTS

- High burden of enteric pathogens in La Paz River Basin households.
- Rural households showed higher bacterial, viral & parasitic carriage than peri-urban settings.
- Children more often carried viral and parasitic infections; mothers, bacterial.
- Unsafe cistern water linked to *Shigella*, diarrheagenic *E. coli*, & *Giardia* while open field defecation to ETEC.
- Findings highlight the need for integrated WASH interventions.

## GRAPHICAL ABSTRACT



## INTRODUCTION

Enteric infections caused by a broad range of viruses, bacteria, and parasites are leading causes of morbidity globally, disproportionately affecting children under five years of age in low-resource settings (Wang *et al.* 2025). These pathogens include highly transmissible viral agents (e.g., norovirus, rotavirus), toxin-producing bacteria and invasive bacteria (e.g., diarrheagenic-*Escherichia coli*, *Shigella*), and environmentally persistent protozoa and helminths (e.g., *Giardia*, *Cryptosporidium*, *Ascaris*) (Kotloff *et al.* 2013; Platts-Mills *et al.* 2015; Fauziah *et al.* 2022). Infections may manifest as acute diarrheal disease or remain asymptomatic, particularly in endemic settings with repeated exposure (Liu *et al.* 2016). Importantly, even asymptomatic infections can contribute to environmental enteric dysfunction (EED), which is strongly associated with long-term sequelae, including chronic malnutrition, stunted growth, and impaired cognitive development (Humphrey 2009; Budge *et al.* 2019). The prevalence and impact of these infections vary across regions, and reflect the complex interplay between pathogens, host factors, and cumulative exposure within contaminated environments (Korpe & Petri 2012; Ngunjiri *et al.* 2014; Kyu *et al.* 2025).

Transmission risk is amplified in settings characterized by overcrowding, limited caregiver education, and inadequate water, sanitation, and hygiene (WASH) infrastructure (Knee *et al.* 2018; Colston *et al.* 2020; Wolf *et al.* 2023). Under these conditions, widespread fecal contamination of water, food, soil, hands, and household surfaces facilitates multiple overlapping fecal-oral pathways, enabling repeated exposure of both mothers and children to diverse enteric pathogens (Pickering *et al.* 2011; Brown *et al.* 2013; WHO 2015; Sclar *et al.* 2016; Penakalapati *et al.* 2017; Goddard *et al.* 2020; Mertens *et al.* 2024). From early childhood onward, mothers and primary caregivers play a central role in this transmission dynamic, as daily activities such as hand washing routines, food preparation, infant feeding, and child feces management directly influence exposure risk (Caruso *et al.* 2010; Soe *et al.* 2024; Suparmi *et al.* 2025). As a result, the mother-child dyad represents a key epidemiologic unit within households, characterized by shared environmental exposures and close physical contact that may facilitate pathogen circulation. Indeed, studies have shown that mothers and children may share enteric pathogens (Mattioli *et al.* 2014; Odetoyn *et al.* 2016; Belina *et al.* 2023), reflecting common exposures and potential transmission among them. In this context, caregiver hygiene practices are relevant not only for child protection but also for limiting ongoing exposure and repeated infection within the household (Mattioli *et al.* 2014; Paulos *et al.* 2024). Consequently, the burden of enteric infection in children is shaped by both environmental contamination and associated hygiene practices. Accurate characterization of this burden requires sensitive diagnostic tools. Molecular methods like the quantitative polymerase

chain reaction (qPCR) provide critical insights into pathogen load, coinfections, and transmission dynamics not captured by conventional surveillance (Liu *et al.* 2016). However, the application of such tools remains limited in many low-resource settings, contributing to a substantial underestimation of enteric infection prevalence.

These diagnostic and public health challenges are accentuated in LMIC such as Bolivia, where diarrheal diseases remain among the leading causes of child mortality and morbidity (INE 2016), and access to WASH services is limited and marked by substantial urban-rural disparities (Bancalari & Martinez 2018; UNICEF & WHO 2021). To address this critical data gap, this study used quantitative PCR to assess the prevalence and pathogen load of 21 viral, bacterial, and parasitic enteric pathogens in mother-child pairs from rural and peri-urban communities in the La Paz River Basin (Palca, Achocalla, and Mecapaca municipalities), Bolivia. We further examined the associations between molecular pathogen detection and key demographic and WASH indicators to identify potential modifiable risk factors and inform targeted public health interventions.

## METHODS

### Study setting and population

The municipalities included in this study are located in the La Paz River Basin in the highlands of Bolivia, which exhibits a pronounced altitudinal and socioenvironmental gradient (INE 2012; SEI 2022). Palca and Mecapaca, which are situated in the upper and lower parts of the basin at approximately 3,700–4,100 and 2,100–2,800 m above sea level, respectively, are entirely rural and characterized mostly by subsistence agriculture. In contrast, Achocalla, located in the peri-urban part of the basin at approximately 3,700 m above sea level, is closer to the metropolitan area of La Paz and has better access to urban infrastructure, with only approximately 16% of the population living in rural areas (Figure 1; Supplementary Table S1).

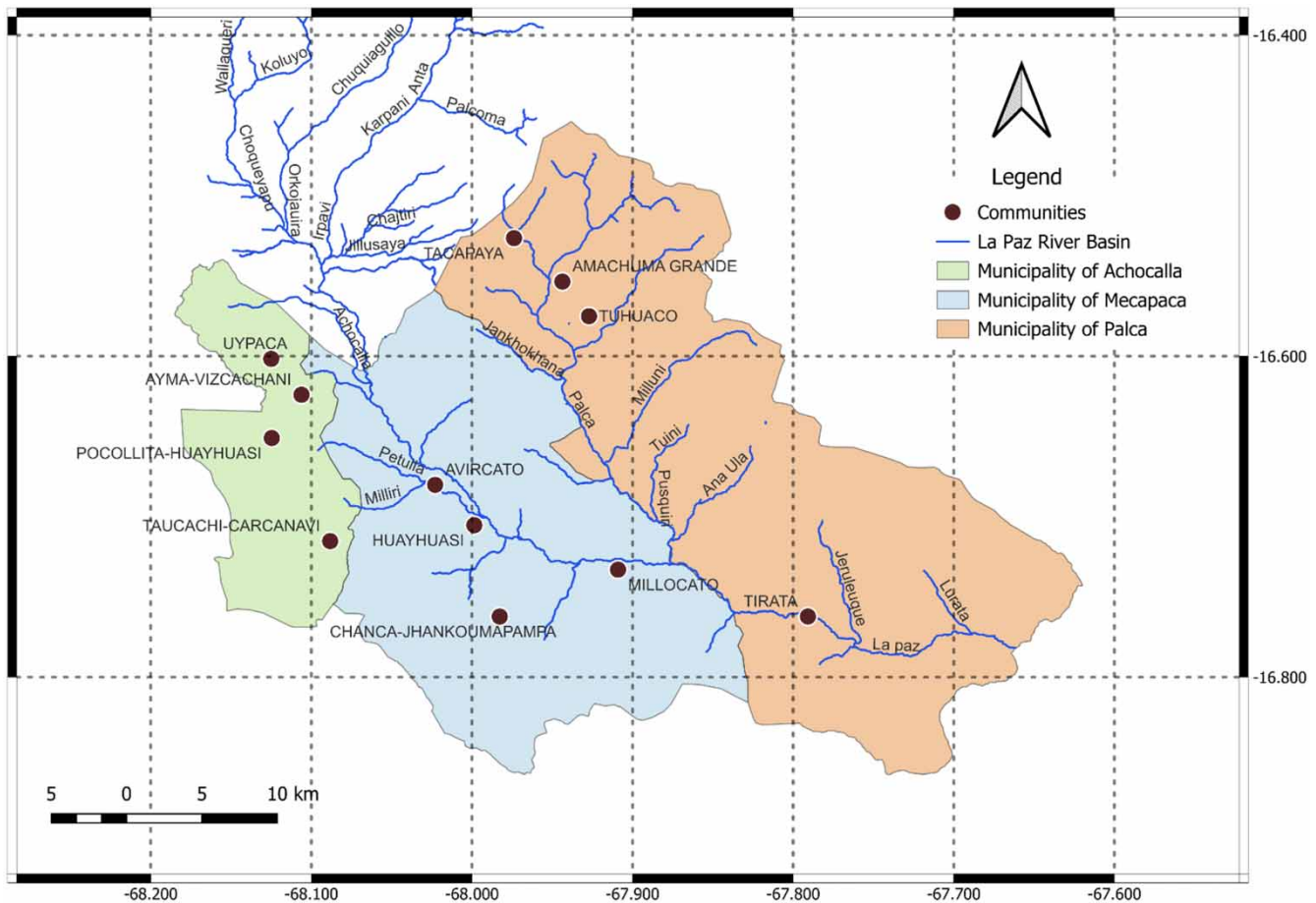
Both peri-urban and rural communities face limited access to safe water and sanitation, a situation worsened by contamination of riparian areas of the La Paz River with untreated urban wastewater. This water is frequently used for crop irrigation, supplying the large cities of La Paz and El Alto and posing a substantial public health risk (Cisneros *et al.* 2015; Poma *et al.* 2016; Guzman-Otazo *et al.* 2019). The combination of inadequate basic services and basin-wide contamination further degrades water sources, creating a high-risk scenario for public health.

### Sample collection, demographic, and WASH data

Between May and September 2022, a total of 171 survey responses and 376 fecal samples were collected from mothers and their preschool children (average  $3.12 \pm 1.75$  years old) across municipalities within the La Paz River watershed. Verbal informed consent was obtained from all participants after an explanatory session with community members and prior to survey administration and sample collection. The survey gathered information on sociodemographic characteristics, housing conditions (based on the quality of roofing, walls, and floors), access to healthcare and education, household overcrowding, episodes of diarrhea in children (defined as  $\geq 3$  loose stools within 24 hours), and practices related to water access, treatment, sanitation, and hygiene. Stool samples were collected and transported under cold chain conditions to the Instituto de Biología Molecular y Biotecnología (IBMB) and stored at  $-70^\circ\text{C}$  until further analysis. Samples from children with current or recent diarrhea (within the preceding week) were excluded from the analysis to focus on asymptomatic enteric pathogen carriage. This exclusion aimed to minimize potential bias related to acute diarrheal episodes, which are known to cause transient increases in pathogen shedding.

### Analysis of water samples for human consumption

Four-hundred-milliliter samples of drinking water (potable, cistern, and spring) were collected in plastic bottles from the community supply source. Potable water was defined as piped tap water supplied through private household connections; cistern water was defined as stored water, obtained from water trucks; and spring water was defined as untreated water collected directly from natural springs originating from surrounding mountainous areas. In-situ values of pH, temperature ( $^\circ\text{C}$ ), and electrical conductivity ( $\mu\text{S}/\text{cm}$ ) (Oakton Instruments, Vernon Hills) were recorded (Duncan *et al.* 2007). The physicochemical and microbiological analyses were conducted at the Laboratorio de Calidad Ambiental (LCA), Universidad Mayor de San Andrés, following the criteria established by the *Standard Methods* and the Environmental Protection Agency (EPA) (Bridgewater *et al.* 2017) as well as the 2022 WHO guidelines for drinking water quality (WHO 2022). The physicochemical characteristics evaluated were total alkalinity (mg  $\text{CaCO}_3/\text{L}$ ), calcium (mg/L), free cyanide (mg/L), chlorides (mg  $\text{Cl}/\text{L}$ ), BOD-5 (mg/L), COD (mg/L), total hardness (mg  $\text{CaCO}_3/\text{L}$ ), magnesium (mg/L), nitrates (mg  $\text{N-NO}_3/\text{L}$ ), nitrites



**Figure 1** | Study area and community distribution within the La Paz River basin. Map of the study area showing the locations of the peri-urban, upper rural, and lower rural communities across Achocalla, Palca, and Mecapaca municipalities within the La Paz River basin.

(mg N-NO<sub>2</sub>/L), sodium (mg/L), dissolved solids (mg/L), sulfates (mg/L), arsenic (mg/L), cadmium (mg/L), copper (mg/L), iron (mg/L), manganese (mg/L), mercury (mg/L), nickel (mg/L), lead (mg/L), zinc (mg/L), soluble phosphorus (P-PO<sub>4</sub><sup>3-</sup> mg/L), and potassium (mg/L). The microbiological characteristics evaluated were total coliforms (MPN/100 mL), fecal coliforms (MPN/100 mL), and *Escherichia coli* (MPN/100 mL).

### Sample processing

Fecal specimens were prepared as 10% (w/v) suspensions in phosphate-buffered saline (PBS; pH 7.4) (Steyer *et al.* 2016). For each mother-child pair, 300 µl of suspension was used for total nucleic acid extraction with the QIAmp DNA Stool Mini (Qiagen, Germany), following the manufacturer's instructions. The resulting extract was used for the detection of both DNA targets and RNA viruses. Nucleic acid concentrations were quantified by measuring the absorbance at 260 nm using a NanoDrop spectrophotometer (NanoDrop Technologies, Wilmington, DE, USA).

Pathogens were detected via real-time PCR on a CFX96 Touch Real-Time PCR Detection System (Bio-Rad Laboratories, Hercules, CA, USA). RNA targets were amplified using the SOLIScript<sup>®</sup> 1-step Multiplex Probe Kit (SOLIS BIODYNE, USA), while DNA targets were amplified with HOT FIREPol Probe qPCR Mix Plus (no ROX), 5x (SOLIS BIODYNE, USA). All qPCR and RT-qPCR assays were performed using specific primers and probe, and thermal cycling conditions as specified in the original references, with details provided in Supplementary Table S2.

For each pathogen, a standard curve was first generated to validate the quantitative performance of the assay. Serial dilutions of positive controls derived from previously confirmed positive samples, quantified using a Qubit<sup>™</sup> fluorometer (Thermo Fisher Scientific, USA), were analyzed by real-time PCR. This curve was used to calculate the relative copy

number of the pathogen in test samples, as previously described (Lappan *et al.* 2021). Subsequently, the diagnostic cycle threshold (Ct) cut-off value was determined based on the limit of detection (LOD). The mean Ct value and standard deviation (SD) at the LOD were calculated, and the cut-off was defined as the mean Ct + 2SD, rounded to the nearest integer. Samples with Ct values above this threshold were considered negative (Caraguel *et al.* 2011).

### Data analysis

Analyses were performed in R version 4.5.0. Associations between regional categories, sociodemographic factors, and WASH variables were assessed via multiple correspondence analysis (MCA) (Khangar & Kamalja 2017) and binomial logistic regression (Dunn & Smyth 2018). Crude and adjusted odds ratios (ORs and aORs) with 95% confidence intervals (CIs) were calculated for enteric pathogens in relation to geographical settings, drinking water sources, and mother–child status, with generalized linear logistic models and *p* values corrected for multiple comparisons via the Benjamini–Hochberg false discovery rate (FDR). Associations between log-transformed enteric pathogen target copy numbers and these categories were evaluated via generalized linear models assuming a Gaussian distribution with an identity link function and FDR-corrected *p* values. Coinfections were evaluated via binomial generalized linear models adjusted for mother–child status and geographic settings and visualized as networks.

For the family-based pathogen transmission analyses, only households including a mother and one child were considered. Pathogen concordance between mothers and children was evaluated via Cohen's kappa coefficient (McHugh 2012). Central-ity metrics were derived from a co-occurrence network representing simultaneous pathogen detection within families. Their significance was assessed through 1,000 random permutations to obtain empirical *p* values. Relationships between average physicochemical and microbiological water parameters, survey data, and enteric pathogens were assessed via Spearman correlations. Associations between enteric pathogens and demographic or WASH indicators were further examined via beta-binomial regression models with a logit link implemented via the glmmTMB package (Brooks *et al.* 2017), with crude and adjusted ORs calculated by geographical setting and FDR-corrected *p* values.

## RESULTS

### Access to WASH services and sociodemographic characteristics

The study population exhibited limited access to essential water, sanitation, and hygiene (WASH) services, with marked differences across settings (Table 1; Supplementary Table S3). Overall, only 19% of the households had access to safe drinking water, and 61% to basic sanitation. Conditions were notably better in peri-urban communities where 78% of households treated their water, and open defecation was uncommon (4%) (Table 1). In contrast, in rural areas, 41% of households did not treat their drinking water, and nearly half (47%) practiced open defecation. In addition, a majority of respondents reported inadequate hygiene practices, with 68% not washing their hands after contact with animal feces and 60% after changing diapers or cleaning latrines (Supplementary Table S3).

In the Upper Basin, socioeconomic vulnerability was pronounced: 41% of residents had low educational attainment, 48% lived in overcrowded households (>6 persons), 89% lacked access to medical centers, and 82% reported relying on traditional medicine (Table 1). In the Lower Basin, 83% of households depended on agriculture, and more than half of them (57%) lacked access to basic sanitation (Supplementary Table S3).

Multiple correspondence analysis (MCA) identified three main vulnerability clusters, accounting for 60% of the total variance. These clusters were primarily structured by geographical setting (peri-urban, lower basin, upper basin), drinking water source (potable, spring, or cistern), and housing quality (low, moderate, or good). When behavioral variables such as water treatment and defecation practices were included, the proportion of explained variance decreased to 41%, highlighting the heterogeneous nature of these behaviors (Figure 2). Despite this, spatial patterns remained evident: the lower basin separated from peri-urban zones along Dimension 1, while the upper basin diverged along Dimension 2. Overall, peri-urban clusters aligned with safer WASH practices and better infrastructure, whereas rural clusters were characterized by higher-risk conditions, including untreated water, open defecation, and inadequate hygiene systems.

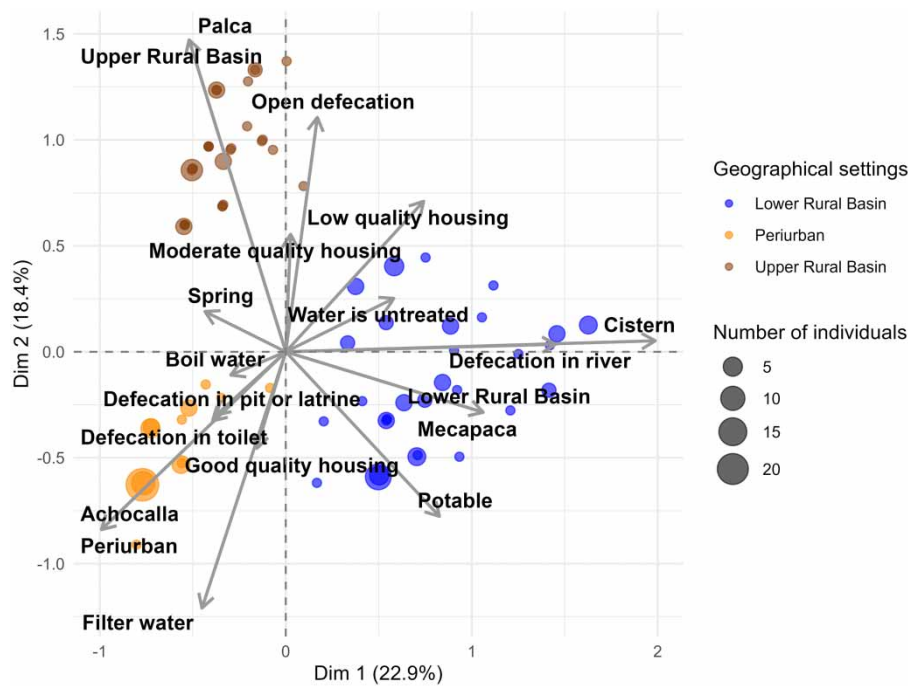
### Prevalence of enteric pathogens in the study population

Sixteen of the 21 enteric pathogens evaluated were detected in fecal samples from the study population (Figure 3). Overall, 85% of the participants carried at least one pathogen, with an average of two pathogens per individual (Table 2). The most

**Table 1** | Demographic and WASH characteristics by upper and lower rural basins and peri-urban settings

Features		Peri-urban (n = 55; 32.16%), ref. n (%)	Upper Rural Basin (n = 44; 25.73%)		Lower Rural Basin (n = 72; 42.11%)		Total (n = 171) n (%)
Indicator	Level		n (%)	OR (CI 95%)/aOR (CI 95%)	n (%)	OR (CI 95%)/aOR (CI 95%)	
DEMOGRAPHICS							
Occupation	Homemaker	52 (94.55)	44 (100)	n.s.	64 (88.89)	n.s.	160 (93.57)
	Agriculture	26 (47.27)	27 (61.36)	n.s.	60 (83.33)	5.58 [2.47–12.60] ***/ <b>5.71 [2.42–13.51]**</b>	113 (66.08)
	Livestock	7 (12.73)	8 (18.18)	n.s.	6 (8.33)	n.s.	21 (12.28)
	Business	14 (25.45)	5 (11.36)	n.s.	14 (19.44)	n.s.	33 (19.30)
WATER							
Drinking water treatment	Yes (Boil/Filter)	43 (78.18)	31 (70.45)	n.s.	38 (52.78)	0.29 [0.13–0.64]*/ <b>0.36 [0.15–0.83]</b>	112 (65.50)
	No	11 (20.00)	13 (29.55)	ref.	34 (47.22)	ref.	58 (33.92)
Water drawing container: with a handle	Yes	29 (52.73)	12 (27.27)	n.s.	17 (23.61)	0.28 [0.13–0.59]*/ <b>0.28 [0.13–0.61]*</b>	58 (33.92)
	No	2 (3.64)	14 (31.82)	ref.	36 (50.00)	ref.	52 (30.41)
SANITATION							
Sanitary facility	Yes	48 (82.27)	27 (61.36)	0.17 [0.05–0.50]**/ <b>0.26 [0.08–0.81]</b>	30 (41.67)	0.08 [0.03–0.21] ***/ <b>0.08 [0.03–0.24]</b> ***	105 (61.40)
	No	5 (9.09)	17 (38.64)	ref.	41 (56.94)	ref.	63 (36.84)
Defecation site	Open field/river	2 (3.64)	17 (38.64)	16.69 [3.59–77.58] **/ <b>9.79 [2.03–47.25]</b>	38 (52.78)	29.62 [6.70–130.86] ***/ <b>27.11 [5.95–123.61]***</b>	57 (33.33)
	Latrine or well	15 (27.27)	9 (20.45)	n.s.	11 (15.28)	n.s.	35 (20.47)
	Toilet	36 (65.45)	18 (40.91)	n.s.	22 (30.56)	0.23 [0.11–0.49]**/ <b>0.24 [0.11–0.51]**</b>	76 (44.44)
HYGIENE							
Handwashing after touching animal feces	Yes	31 (56.36)	15 (34.09)	n.s.	22 (30.56)	0.31 [0.15–0.66]*/ <b>0.32 [0.15–0.70]</b>	68 (39.77)
	No	22 (40.00)	29 (65.91)	ref.	50 (69.44)	ref.	101 (59.06)

OR, odds ratio; aOR, adjusted odds ratio for education and housing quality (bold values indicate aOR); 95% CI, 95% confidence interval. The peri-urban group is the reference (ref.). Significance *p* value, \**p* < 0.05, \*\**p* < 0.01, \*\*\**p* < 0.001; n.s., not significant; n, number of individuals.



**Figure 2** | Multiple correspondence analysis (MCA) based on community-level demographic and WASH indicators. MCA plot showing community-level vulnerability patterns based on geographical setting, housing quality, drinking water source, water treatment, and defecation site. The communities in the lower rural basin are located near the La Paz River, which receives untreated urban wastewater. The point size indicates the number of individuals represented.

prevalent pathogens were *Helicobacter pylori* (34%), adenovirus (28%), enteropathogenic *Escherichia coli* (EPEC, *eae*: 27%), *Giardia lamblia* (26%), and *Shigella* spp. (22%) (Figure 3 and Table 2).

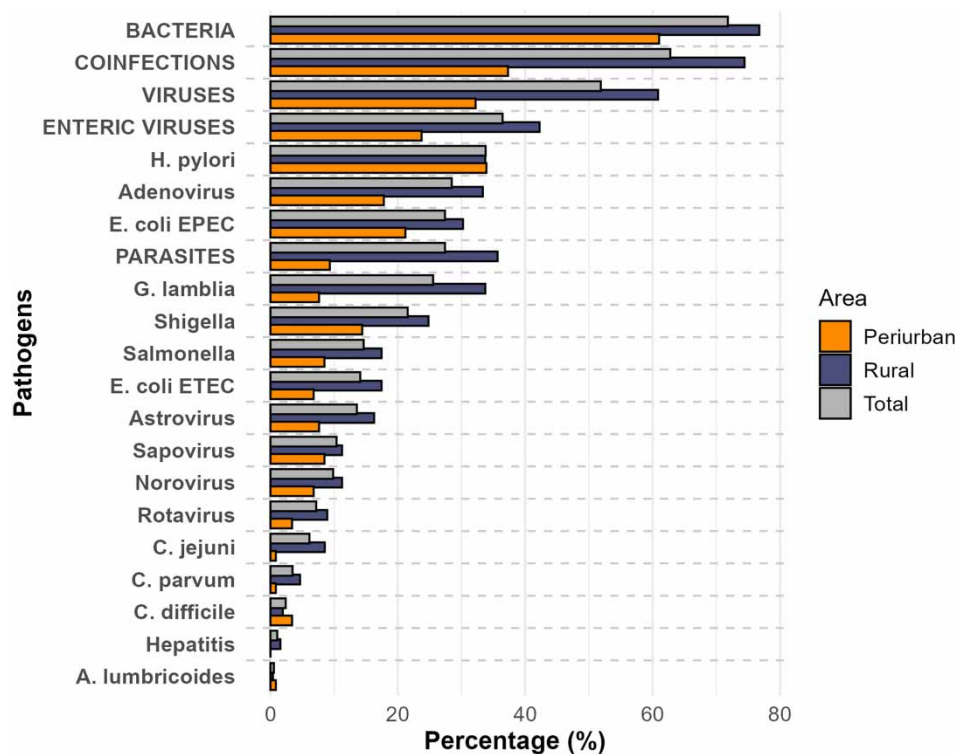
Given the high prevalence of multiple infections, coinfection analyses were conducted to evaluate associations between pathogens. Statistically significant associations were observed between norovirus and adenovirus (aOR = 2.33; 95% CI: 1.13–4.79), norovirus and *Campylobacter jejuni* (aOR = 6.93; 95% CI: 2.44–19.33), sapovirus and *Salmonella* (aOR = 2.88; 95% CI: 1.21–6.52), adenovirus and *Shigella* (aOR = 1.75; 95% CI: 1.00–3.04), adenovirus and *H. pylori* (aOR = 1.79; 95% CI: 1.06–3.01). Within the *Escherichia coli*, strong associations were observed between enterotoxigenic *Escherichia coli* (ETEC) toxin genes (*estA* and *eltB*, aOR = 29.15; 95% CI: 11.55–81.56), as well as between pathotypes, including ETEC (*estA*) and EPEC (*eae*; aOR = 2.64; 95% CI: 1.15–6.05). These associations are illustrated in Figure 4, with detailed statistics provided in Supplementary Table S4.

Pathogen prevalence was generally higher in rural than in peri-urban settings. Compared with the peri-urban participants, individuals living in rural areas had significantly higher odds of infection with viruses, bacteria, parasites, and overall coinfections, with particularly elevated odds for *G. lamblia* (Table 2). In the lower rural basin, infections with diarrheagenic *Escherichia coli* (DEC) were more frequent (aOR = 2.55; 95% CI: 1.31–4.95), including ETEC (*estA*, *eltB*), as well as *Salmonella* (aOR = 4.08; 95% CI: 1.68–9.94). In contrast, the upper basin, showed a higher burden of viral infections with significantly increased odds for astrovirus (aOR = 6.21; 95% CI: 2.78–13.87), adenovirus (aOR = 2.83; 95% CI: 1.48–5.39), enteric viruses overall (aOR = 2.83; 95% CI: 1.57–5.11), and other viruses (aOR = 4.69; 95% CI: 2.59–8.50) (Table 2).

Pathogen load analyses also varied by geographical setting. Adenovirus gene copy numbers per gram of feces were significantly lower in the upper rural basin than in peri-urban areas ( $\beta = -0.85$ ; SE = 0.33;  $p = 0.023$ ) (Supplementary Figure S1a).

### Mother-child differences and concordance in pathogen carriage

Patterns of pathogen carriage differed between mothers and children (Table 3). Children were more likely to carry viral infections overall (aOR = 2.52; 95% CI: 1.62–3.93), including enteric viruses (aOR = 1.80; 95% CI: 1.15–2.81), as well as parasitic infections (aOR = 3.87; 95% CI: 2.25–6.65), particularly sapovirus, adenovirus, and *G. lamblia*. In contrast, mothers were more likely to harbor bacterial pathogens, notably *Salmonella* and *H. pylori* (Table 3).



**Figure 3** | Distribution of pathogens by geographical area. Percentages of individuals with detected pathogens stratified by geographical area: peri-urban and rural areas (lower and upper basin). Percentages represent the proportion of individuals in each area with at least one detected pathogen belonging to each pathogen group. Pathogen abbreviations: *A. lumbricoides*, *Ascaris lumbricoides*; *C. difficile*, *Clostridium difficile*; *C. parvum*, *Cryptosporidium parvum*; Group A rotavirus; Norovirus of genogroups GI and GII; *G. lamblia*, *Giardia lamblia*; *H. pylori*, *Helicobacter pylori*; *C. jejuni*, *Campylobacter jejuni*; *E. coli* ETEC (*estA*, heat-stable toxin gene) and (*eltB*, heat-labile toxin gene) enterotoxigenic *Escherichia coli*; *E. coli* EPEC (*eae*, intimin adherence gene) and (*bfpA*, bundle-forming pilus gene) enteropathogenic *Escherichia coli*. Enteric viruses include one or more of the following pathogens: rotavirus, norovirus (GI and GII), astrovirus, sapovirus, and hepatitis A virus. Viruses include one or more of the following pathogens: rotavirus, norovirus (GI and GII), astrovirus, sapovirus, adenovirus (any detectable adenovirus), and hepatitis A virus. Bacteria include one or more of the following pathogens: *H. pylori*, *Escherichia coli* EPEC (*eae*, *bfpA*), *Escherichia coli* ETEC (*estA*, *eltB*), *Shigella*, *Salmonella*, *C. jejuni*, and *C. difficile*. Parasites include one or more of the following pathogens: *G. lamblia*, *C. parvum*, and *A. lumbricoides*.

Quantitative analyses indicated that children carried significantly higher viral loads than mothers for adenovirus ( $\beta = 0.76$ ; SE: 0.26;  $p = 0.016$ ) and astrovirus ( $\beta = 1.51$ ; SE: 0.50;  $p = 0.026$ ) (Supplementary Figure S1b).

To assess whether these differences translated into shared infections within households, mother-child pathogen concordance was evaluated using Cohen's kappa coefficient, and co-occurrence patterns were further explored using network analysis based on betweenness centrality. Of the 14 pathogens detected in both groups, six showed statistically significant concordance, exceeding the level expected by chance. The highest agreement was observed for astrovirus ( $\kappa = 0.55$ ), followed by rotavirus ( $\kappa = 0.34$ ). Moderate concordance was also identified for *C. jejuni* ( $\kappa = 0.28$ ), *H. pylori* ( $\kappa = 0.26$ ), ETEC *eltB* ( $\kappa = 0.25$ ), and *G. lamblia* ( $\kappa = 0.19$ ) (Supplementary Table S5).

Network analysis identified *H. pylori* as the central hub within household coinfection networks, exhibiting the highest betweenness centrality (0.43) and 28 connections, followed by adenovirus (0.27), with 15 connections. *G. lamblia* and astrovirus showed moderate centrality values (0.16 and 0.14, respectively), forming 12 and 13 connections each (Figure 5 and Supplementary Table S5).

## Environmental determinants of enteric infections

### Associations between drinking water source and pathogen carriage

The source of drinking water was associated with enteric pathogen carriage (Table 4). Overall, the consumption of cistern and spring water was associated with a greater probability of ETEC *eltB* carriage than was the consumption of potable water. In

**Table 2** | Enteric pathogen infection by geographical setting: odds ratios (ORs) and adjusted odds ratios (aORs)

Enteric pathogens	Peri-urban ( <i>n</i> = 118; 31.38%), ref.	Upper Rural Basin ( <i>n</i> = 95; 25.27%) vs ref.		Lower Rural Basin ( <i>n</i> = 163; 43.35%) vs ref.		Total ( <i>n</i> = 376) <i>n</i> (%)
	<i>n</i> (%)	<i>n</i> (%)	OR (CI 95%)/aOR (CI 95%)	<i>n</i> (%)	OR (CI 95%)/aOR (CI 95%)	
Rotavirus	4 (3.38)	3 (3.16)	n.s.	20 (12.27)	3.99 [1.32–11.99]*/ <b>2.13 [0.51–8.88]</b>	27 (7.18)
Astrovirus	9 (7.63)	32 (33.68)	6.15 [2.76–13.72]***/ <b>6.21 [2.78–13.87]***</b>	10 (6.13)	n.s.	51 (13.56)
Adenovirus	21 (17.80)	35 (36.84)	2.69 [1.44–5.06]**/ <b>2.83 [1.48–5.39]**</b>	51 (31.29)	2.10 [1.18–3.74]*/ <b>1.98 [0.93–4.21]</b>	107 (28.46)
Enteric viruses <sup>a</sup>	28 (23.73)	44 (46.32)	2.77 [1.54–4.98]**/ <b>2.83 [1.57–5.11]**</b>	65 (39.88)	2.13 [1.26–3.61]*/ <b>1.36 [0.66–2.77]</b>	134 (35.64)
Viruses <sup>b</sup>	38 (32.20)	64 (67.36)	4.35 [2.44–7.74]***/ <b>4.69 [2.59–8.50]***</b>	93 (57.06)	2.80 [1.70–4.59]***/ <b>1.92 [0.99–3.73]</b>	195 (51.86)
<i>Salmonella</i>	10 (8.47)	12 (12.63)	n.s.	33 (20.24)	2.74 [1.29–5.82]*/ <b>4.08 [1.68–9.94]**</b>	55 (14.63)
<i>Shigella</i>	17 (14.41)	19 (20.00)	n.s.	45 (27.61)	2.27 [1.22–4.20]*/ <b>2.14 [0.98–4.70]</b>	81 (21.54)
<i>E. coli</i> ETEC <i>estA</i>	3 (2.54)	5 (5.26)	n.s.	18 (11.04)	4.76 [1.37–16.55]*/ <b>7.18 [1.86–27.69]**</b>	26 (6.91)
<i>E. coli</i> ETEC <i>eltB</i>	8 (6.78)	10 (10.53)	n.s.	28 (17.18)	2.85 [1.25–6.51]*/ <b>5.83 [2.34–14.57]***</b>	46 (12.23)
<i>E. coli</i> EPEC <i>eae</i>	24 (20.34)	22 (23.16)	n.s.	55 (33.74)	1.99 [1.15–3.47]*/ <b>1.55 [0.74–3.24]</b>	101 (26.86)
Diarrheagenic <i>E. coli</i> (DEC) <sup>c</sup>	31 (26.27)	29 (30.53)	n.s.	75 (46.01)	2.39 [1.43–3.99]**/ <b>2.55 [1.31–4.95]**</b>	135 (35.90)
<i>Helicobacter pylori</i>	40 (33.90)	43 (45.26)	n.s.	44 (26.99)	0.72 [0.43–1.21]/ <b>0.35 [0.15–0.81]*</b>	127 (33.78)
<i>Campylobacter jejuni</i>	1 (0.85)	13 (13.68)	18.55 [2.38–144.58]*/ <b>18.77 [2.40–146.59]*</b>	9 (5.52)	n.s.	23 (6.12)
Bacteria <sup>d</sup>	72 (61.02)	74 (77.89)	2.25 [1.22–4.14]**/ <b>2.30 [1.24–4.26]*</b>	124 (76.07)	2.03 [1.21–3.40]*/ <b>1.84 [0.91–3.73]</b>	270 (71.81)
<i>Giardia lamblia</i>	9 (7.63)	24 (25.26)	4.09 [1.80–9.32]***/ <b>4.37 [1.89–10.12]***</b>	63 (38.65)	7.63 [3.61–16.14]***/ <b>12.43 [5.12–30.16]***</b>	96 (25.53)
Parasites <sup>e</sup>	11 (9.32)	26 (27.37)	3.67 [1.70–7.89]***/ <b>3.92 [1.79–8.61]**</b>	66 (40.49)	6.62 [3.30–13.26]***/ <b>9.91 [4.28–22.98]***</b>	103 (27.39)
Coinfections	44 (37.29)	71 (74.74)	4.98 [2.75–9.02]***/ <b>5.02 [2.76–9.11]***</b>	121 (74.23)	4.85 [2.90–8.09]***/ <b>5.18 [2.54–10.54]***</b>	236 (62.77)
Any pathogen	89 (75.42)	83 (87.37)	n.s.	149 (91.41)	3.47 [1.74–6.91]**/ <b>2.33 [0.95–5.70]</b>	321 (85.37)
≥ 3 pathogens	22 (18.64)	48 (50.53)	4.46 [2.41–8.23]***/ <b>4.46 [2.42–8.24]***</b>	78 (47.85)	4 [2.30–6.98]***/ <b>4.84 [2.41–9.72]***</b>	148 (39.36)
Average number of pathogens	1.42 ± 1.29	2.49 ± 1.59 ***		2.59 ± 1.60 ***		2.20 ± 1.59

OR, odds ratio; aOR, adjusted odds ratio for drinking water source and mother-child status (bold values indicate aOR); 95% CI, 95% confidence interval. The peri-urban group is the reference (ref.). Significance *p* value, \**p* < 0.05, \*\**p* < 0.01, \*\*\**p* < 0.001; n.s., not significant; *n*, number of individuals. Average ± indicates the standard deviation (SD); the differences in the total number of pathogens detected among the different categories were evaluated via the Kruskal-Wallis test to detect overall differences between groups and a Dunn post hoc test with a Bonferroni adjustment.

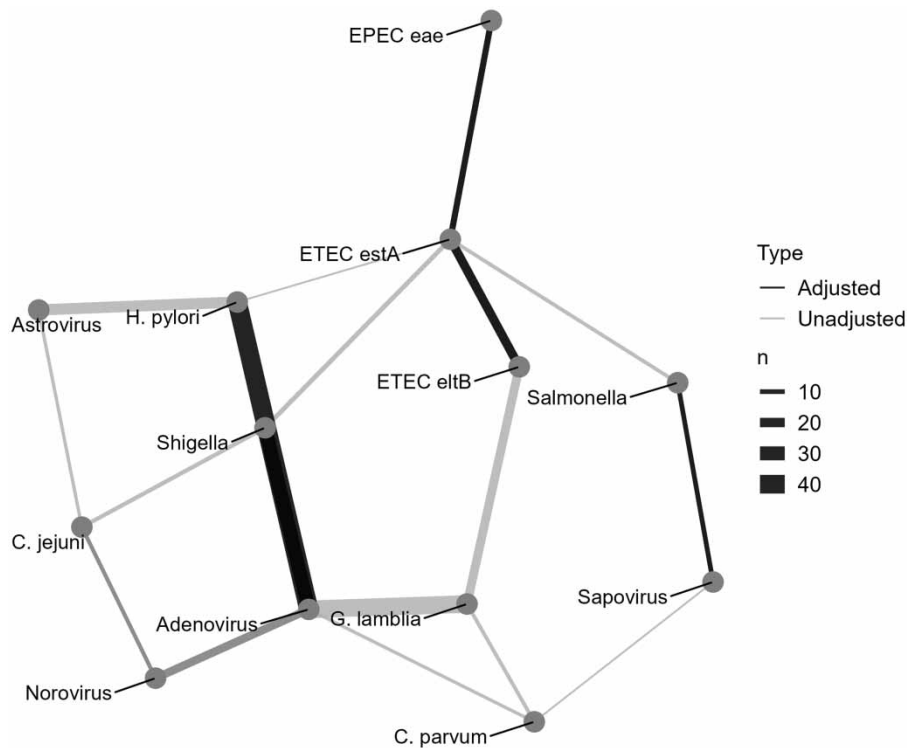
<sup>a</sup>Enteric viruses include one or more of the following pathogens: rotavirus, norovirus (GI and GII), astrovirus, sapovirus, and hepatitis A virus.

<sup>b</sup>Viruses include one or more of the following pathogens: rotavirus, norovirus (GI and GII), astrovirus, sapovirus, adenovirus (any detectable adenovirus), and hepatitis A virus.

<sup>c</sup>Diarrheagenic *Escherichia coli* (DEC) includes one or more of the following pathogens: *E. coli* ETEC (*estA*, heat-stable toxin gene) enterotoxigenic, *E. coli* ETEC (*eltB*, heat-labile toxin gene) enterotoxigenic, *E. coli* EPEC (*eae*, intimin adherence gene), enteropathogenic, and EPEC (*bfpA*, bundle-forming pilus gene) enteropathogenic.

<sup>d</sup>Bacteria include one or more of the following pathogens: *H. pylori*, *Escherichia coli* EPEC (*eae*, *bfpA*), *Escherichia coli* ETEC (*estA*, *eltB*), *Shigella*, *Salmonella*, *C. jejuni*, and *C. difficile*.

<sup>e</sup>Parasites include one or more of the following pathogens: *G. lamblia*, *C. parvum*, and *A. lumbricoides*.



**Figure 4** | Coinfection networks per individual, unadjusted and adjusted for mother-child status and geographic settings. Circular nodes represent individual participants, and gray edges indicate the presence of pathogens in coinfections. Networks highlight statistically significant associations ( $p < 0.05$ ).  $n$  denotes the number of individuals included.

**Table 3** | Odds ratios (ORs) and adjusted odds ratios (aORs) for pathogens in mother-child pairs

Enteric pathogens	Mothers ( $n = 164$ ; 43.62%), ref. $n$ (%)	Children ( $n = 212$ ; 56.38%) vs ref.	
		$n$ (%)	OR (CI 95%)/aOR (CI 95%)
Sapovirus	9 (5.49)	30 (14.15)	2.84 [1.31–6.16]*/ <b>2.85 [1.31–6.21]*</b>
Adenovirus	29 (17.68)	78 (36.79)	2.71 [1.66–4.42]***/ <b>2.85 [1.72–4.71]***</b>
Viruses <sup>a</sup>	66 (40.24)	129 (60.85)	2.31 [1.52–3.50]***/ <b>2.52 [1.62–3.93]***</b>
Enteric viruses <sup>b</sup>	48 (29.27)	89 (41.98)	1.75 [1.13–2.70]*/ <b>1.80 [1.15–2.81]*</b>
<i>Salmonella</i>	34 (20.73)	21 (9.90)	0.42 [0.23–0.76]*/ <b>0.40 [0.22–0.73]**</b>
<i>Helicobacter pylori</i>	77 (46.95)	50 (23.58)	0.35 [0.22–0.54]***/ <b>0.33 [0.21–0.53]***</b>
Bacteria <sup>c</sup>	130 (79.27)	140 (66.04)	0.51 [0.32–0.82]*/ <b>0.49 [0.30–0.79]*</b>
<i>Giardia lamblia</i>	22 (13.42)	74 (34.91)	3.46 [2.04–5.88]***/ <b>3.9 [2.22–6.82]***</b>
Parasites <sup>d</sup>	24 (14.63)	79 (37.26)	3.46 [2.07–5.80]***/ <b>3.87 [2.25–6.65]***</b>
Coinfections	97 (59.15)	139 (65.57)	n.s.
Average number of pathogens	2.08 ± 1.50	2.29 ± 1.65	

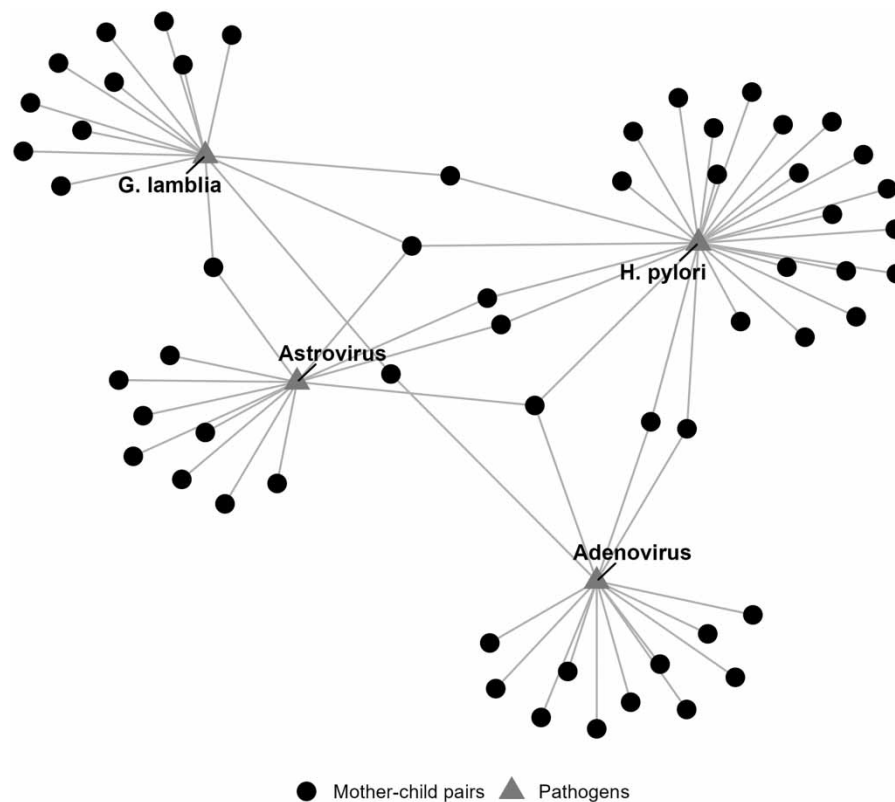
OR, odds ratio; aOR, adjusted odds ratio for geographical setting and drinking water source (bold values indicate aOR); 95% CI, 95% confidence interval. The mothers' group is the reference (ref.). Significance  $p$  value, \* $p < 0.05$ , \*\* $p < 0.01$ , \*\*\* $p < 0.001$ ; n.s., not significant;  $n$ , number of individuals. Average ± indicates the standard deviation (SD); comparisons between mothers and children were performed via the Mann-Whitney  $U$  test (Wilcoxon rank-sum test).

<sup>a</sup>Viruses include one or more of the following pathogens: rotavirus, norovirus (GI and GII), astrovirus, sapovirus, adenovirus (any detectable adenovirus), and hepatitis A virus.

<sup>b</sup>Enteric viruses include one or more of the following pathogens: rotavirus, norovirus (GI and GII), astrovirus, sapovirus, and hepatitis A virus.

<sup>c</sup>Bacteria include one or more of the following pathogens: *H. pylori*, *E. coli* EPEC (*eae*, *bfpA*), *E. coli* ETEC (*estA*, *eltB*), *Shigella*, *Salmonella*, *C. jejuni*, and *C. difficile*.

<sup>d</sup>Parasites include one or more of the following pathogens: *G. lamblia*, *C. parvum*, and *A. lumbricoides*.



**Figure 5** | Network of pathogens between mothers and children. Circular nodes represent families in the study population, and triangular nodes represent pathogens. The gray edges indicate the presence of a pathogen in mother-child coinfections. Pathogens exhibiting a greater number of connections with other pathogens act as hubs within family coinfections. *E. coli* ETEC (*estA*, heat-stable toxin gene) is enterotoxigenic; *E. coli* ETEC (*eltB*, heat-labile toxin gene) is enterotoxigenic; *E. coli* EPEC (*eae*, intimin adherence gene) is enteropathogenic; *H. pylori*, *Helicobacter pylori*; *G. lamblia*, *Giardia lamblia*; *C. jejuni*, *Campylobacter jejuni*; and *C. parvum*, *Cryptosporidium parvum*.

particular, individuals using cistern water had significantly greater odds of infection with adenovirus (aOR = 4.25; 95% CI: 1.68–10.79), *Shigella* (aOR = 5.65; 95% CI: 2.21–14.43), and DEC (aOR = 3.18; 95% CI: 1.30–7.80) (Table 4).

Pathogen loads analyses further showed that *G. lamblia* gene copy numbers were higher among individuals consuming cistern ( $\beta = 0.99$ ; SE: 0.43;  $p = 0.047$ ) or spring water ( $\beta = 0.84$ ; SE: 0.34;  $p = 0.047$ ) compared with those consuming potable drinking water (Supplementary Figure S1c).

### Water quality parameters and their associations with enteric infections and diarrhea

Most physicochemical and microbiological parameters of the analyzed water samples complied with drinking water standards, with the exception of biochemical oxygen demand (BOD), chemical oxygen demand (COD), electrical conductivity, and total coliforms, which exceeded the World Health Organization (WHO) guidelines in most reservoirs (Supplementary Table S6). Correlation analysis (Figure 6) revealed that elevated electrical conductivity was associated with frequent episodes of diarrhea in children, the presence of enteric bacteria (ETEC and *Shigella*), and defecation in open fields or rivers. Additionally, total coliforms were positively correlated with the reported occurrence of diarrhea in children during the previous week (Figure 6).

### WASH, demographics, and health-related factors associated with enteric pathogen carriage

Associations between demographic characteristics, health indicators, and WASH conditions and enteric pathogen carriage were evaluated using logistic regression models and correlation analyses.

With respect to health and demographic factors, frequent episodes of diarrhea in children were strongly associated with *Shigella* carriage (aOR = 77.29, 95% CI: 8.63–692.23). In contrast, higher housing quality, assessed based on roof, floor, and wall materials, was associated with a lower likelihood of adenovirus carriage. Agricultural occupation was also linked

**Table 4** | Odds ratios (ORs) and adjusted odds ratios (aORs) for pathogen infections according to drinking water source

Enteric pathogens	Potable (n = 77; 20.48%), ref n (%)	Cistern (n = 29; 7.71%) vs ref.		Spring (n = 270; 71.81%) vs ref.	
		n (%)	OR (CI 95%)/aOR (CI 95%)	n (%)	OR (CI 95%)/aOR (CI 95%)
Rotavirus	11 (14.28)	5 (17.24)	n.s.	11 (4.07)	0.25 [0.11–0.61]* /0.44 [0.13–1.48]
Adenovirus	18 (23.38)	16 (55.17)	4.03 [1.64–9.95]**/4.25 [1.68–10.79]**	73 (27.04)	n.s.
<i>Shigella</i>	14 (18.19)	16 (55.17)	5.54 [2.18–14.08]**/5.65 [2.21–14.43]**	51 (18.89)	n.s.
<i>E. coli</i> ETEC <i>eltB</i>	4 (5.19)	7 (24.14)	5.81 [1.55–21.69]*/5.79 [1.55–21.62]*	35 (12.96)	2.72 [0.93–7.90]/7.74 [2.44–24.60]**
Diarrheagenic <i>E. coli</i> DEC <sup>a</sup>	29 (37.66)	19 (65.52)	3.14 [1.29–7.69]*/3.18 [1.30–7.8]*	87 (32.22)	n.s.
Bacteria <sup>b</sup>	54 (70.13)	28 (96.55)	11.93 [1.53–92.85]*/12.53 [1.60–98.06]*	188 (69.63)	n.s.
Coinfection	52 (67.53)	26 (89.66)	4.17 [1.15–15.09]*/4.15 [1.14–15.06]	158 (58.52)	n.s.
≥3 pathogens	25 (32.47)	23 (79.31)	7.97 [2.88–22.05]***/7.96 [2.88–22.02]***	100 (37.04)	1.22 [0.72–2.09]/2.31 [1.14–4.67]*
Average number of pathogens	2.14 ± 1.33	3.86 ± 1.77***		2.04 ± 1.54	

OR, odds ratio; aOR, adjusted odds ratio for geographical settings, and mother-child status (bold values indicate aOR); 95% CI, 95% confidence interval. The drinking water (potable) group was used as a reference (ref.). Significance *p* value, \**p* < 0.05, \*\**p* < 0.01, \*\*\**p* < 0.001; n.s., not significant; n, number of individuals. Average ± indicates the standard deviation (SD); the differences in the total number of pathogens detected among the different categories were evaluated via the Kruskal-Wallis test to detect overall differences between groups and a Dunn post hoc test with a Bonferroni adjustment.

<sup>a</sup>Diarrheagenic *Escherichia coli* (DEC) includes one or more of the following pathogens: *E. coli* ETEC (*estA*, heat-stable toxin gene) enterotoxigenic, *E. coli* ETEC (*eltB*, heat-labile toxin gene) enterotoxigenic, *E. coli* EPEC (*eae*, intimin adherence gene), enteropathogenic, and EPEC (*bfpA*, bundle-forming pilus gene) enteropathogenic.

<sup>b</sup>Bacteria include one or more of the following pathogens: *H. pylori*, *E. coli* EPEC (*eae*, *bfpA*), *E. coli* ETEC (*estA*, *eltB*), *Shigella*, *Salmonella*, *C. jejuni*, and *C. difficile*.

to increased bacterial carriage (aOR = 17.59, 95% CI: 2.86–108.03) (Supplementary Table S7). Similar trends were observed in correlation analyses, which additionally identified associations with other pathogens (Supplementary Figure S2).

Regarding water-handling practices, the use of containers without handles to extract stored water was associated with a higher likelihood of ETEC (*eltB*) carriage (aOR = 9.83, 95% CI: 2.38–40.59), whereas consumption of boiled drinking water was associated with a markedly lower likelihood (aOR = 0.01, 95% CI: 0.00–0.10) (Supplementary Table S7). Correlation analyses further linked ETEC, *Salmonella*, and *G. lamblia* with the use of handleless containers and water boiling practices (Figure 7).

In terms of sanitation, open defecation in fields or rivers was associated with a higher likelihood of ETEC *eltB* carriage (aOR = 9.79, 95% CI: 2.63–36.47) (Supplementary Table S7), as well as with *Salmonella*, *G. lamblia*, and overall coinfections (Supplementary Figure S2). Notably, both open-field defecation and the use of handleless containers were also associated with agricultural occupation (Supplementary Figure S2).

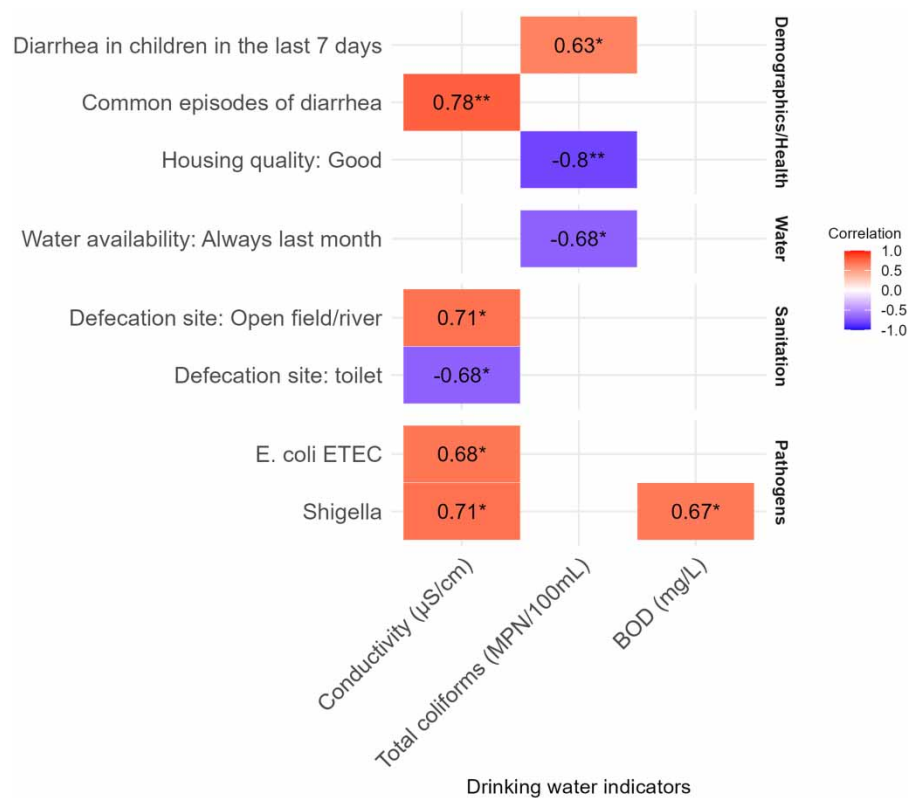
Finally, hygiene practices were associated with differences in pathogen carriage. Washing hands after contact with animal feces was associated with a lower likelihood of ETEC *estA* carriage (Supplementary Table S7), whereas not washing hands after touching animals correlated with other inadequate hygiene behaviors, including not washing hands after diaper handling or contact with latrines (Figure 7).

## DISCUSSION

This study provides a comprehensive assessment of enteric pathogen carriage in high-risk peri-urban and rural communities of the La Paz River Basin, Bolivia. We report an alarmingly high overall prevalence (85%) of viral, bacterial, and parasitic infections; frequent coinfections (63%); and marked heterogeneity in pathogen distribution shaped by geographic setting, age, and specific modifiable socioeconomic and WASH-related factors.

### Prevalent viral, bacterial, and parasitic pathogens

A particularly notable finding was the high prevalence (28%) of adenoviruses detected using a broad human adenovirus qPCR assay (pan-HAV), accounting for more than half (55%) of all viral infections and exceeding the combined prevalence of

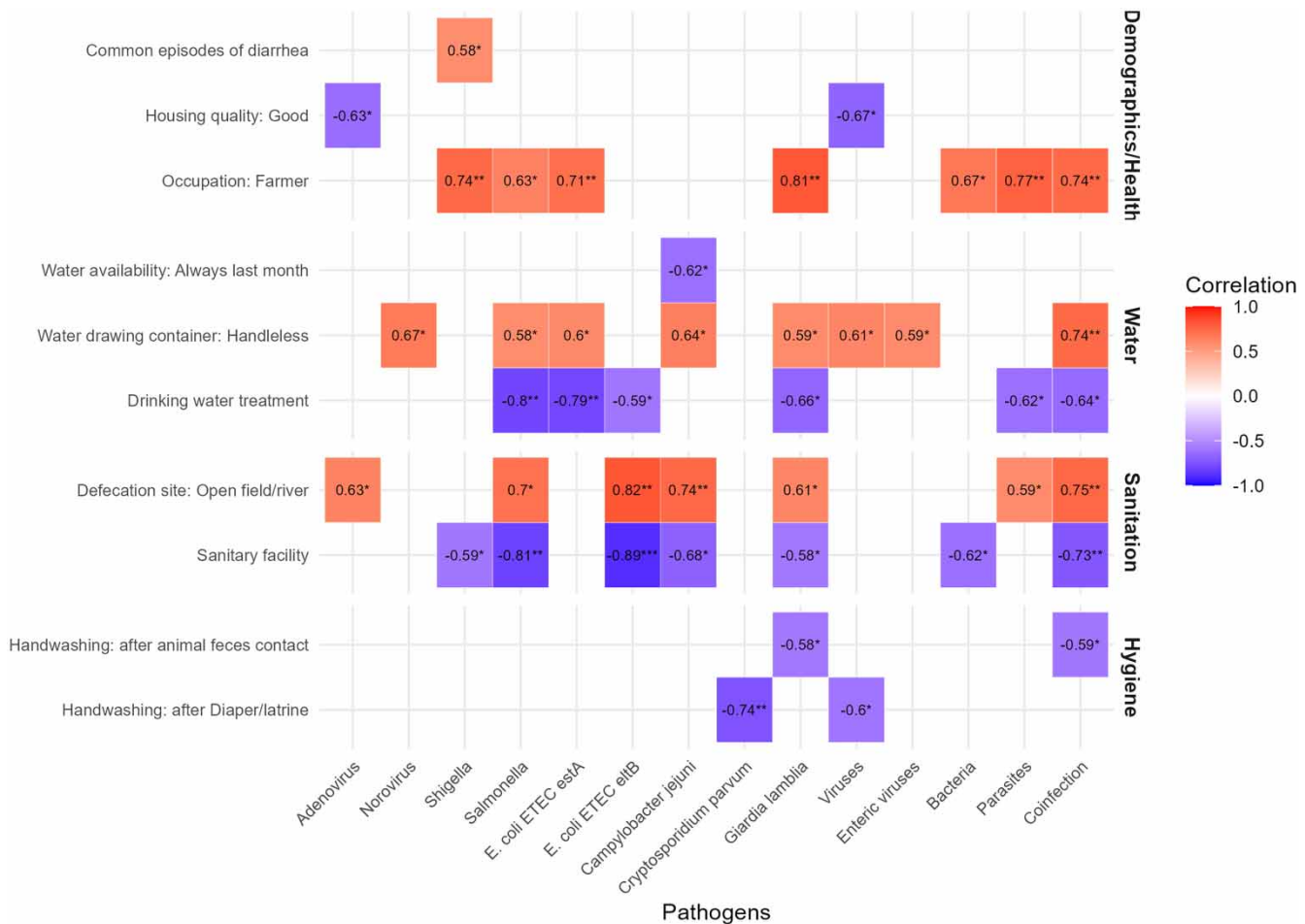


**Figure 6** | Spearman correlations among drinking water physicochemical and microbiological parameters, demographic characteristics, WASH, and pathogens. Colored boxes indicate statistically significant positive (red) and negative (blue) correlations; significance  $p$  value, \* $p < 0.05$ , \*\* $p < 0.01$ , \*\*\* $p < 0.001$ . *E. coli* ETEC: (*estA*, heat-stable toxin gene) and (*eltB*, heat-labile toxin gene), enterotoxigenic *Escherichia coli*.

classic enteric viruses, including rotavirus, norovirus, astrovirus, sapovirus, and hepatitis viruses. As no samples were positive for the classical enteric adenovirus types 40 (HAdV-F40) and 41 (HAdV-F41) belonging to human adenovirus species F (HAdV-F), the detected viruses were likely non-enteric adenovirus types, which constitute the majority of the more than 100 human adenovirus genotypes described to date (HAdV Working Group no date). Although non-enteric adenoviruses are most commonly associated with respiratory or latent infections, they can replicate in the intestinal tract, be shed in feces (Kosulin *et al.* 2016), and have been implicated in diarrheal disease (Kumthip *et al.* 2019; De Francesco *et al.* 2021).

Their strong association with open-field defecation and inverse association with housing quality underscore their well-established role as biomarkers of human fecal contamination (Hundesu *et al.* 2006; Li *et al.* 2021). The high prevalence observed here, suggests broad environmental circulation, multiple exposure routes, and extensive person-to-person transmission (La Rosa *et al.* 2013; Owliaee *et al.* 2024). As adenoviruses are among the most frequently detected viruses in sewage worldwide (Shaheen *et al.* 2024), their dominance may also reflect persistent, year-round shedding in this population, in contrast with the sharp seasonal peaks typical of other enteric viruses (Kumthip *et al.* 2019; Price *et al.* 2019; Guga *et al.* 2022; Keita *et al.* 2023).

Beyond adenoviruses, *H. pylori*, atypical EPEC, *Giardia*, and *Shigella* were highly prevalent and frequently co-occurred, suggesting endemic circulation in the region, similar to other comparable settings (Glynn *et al.* 2002; Rodas *et al.* 2005; Gonzales *et al.* 2013; Camacho-Alvarez *et al.* 2021; Apaza *et al.* 2023). Network analyses identified *Shigella*, *H. pylori*, and adenovirus as central nodes in coinfection networks, reinforcing their role in driving mixed infections. Repeated exposure and prolonged asymptomatic carriage likely contribute to the sustained presence of these pathogens, as documented in previous studies (Ochoa *et al.* 2008; Levine & Robins-Browne 2012; Waldram *et al.* 2017; Stefano *et al.* 2018; Ibrahim *et al.* 2019; McMurry *et al.* 2021; Kralicek *et al.* 2022). Consistent with this interpretation, maternal reports of frequent diarrheal episodes in children associated with *Shigella* carriage further support its role in recurrent or persistent infections.



**Figure 7** | Spearman correlations between demographic characteristics, WASH indicators, and enteric pathogens. Colored boxes indicate statistically significant positive (red) and negative (blue) correlations; significance p value, \* $p < 0.05$ , \*\* $p < 0.01$ , \*\*\* $p < 0.001$ . *E. coli* ETEC: (*estA*, heat-stable toxin gene) and (*eltB*, heat-labile toxin gene), enterotoxigenic *Escherichia coli*.

The high prevalence of *H. pylori* and *Shigella* is particularly concerning since both pathogens can establish colonization from early childhood (Kienesberger *et al.* 2018; Bagamian *et al.* 2023) and are associated with iron deficiency, anemia, and impaired growth (Queiroz *et al.* 2013; Rogawski *et al.* 2017; Lambrecht *et al.* 2022; McQuade *et al.* 2022; Nasrin *et al.* 2022; Sandoval-Ramírez *et al.* 2023). These pathogens are also widely reported in both symptomatic and asymptomatic carriers, particularly in rural settings (Albert *et al.* 1999; Estrada-Garcia *et al.* 2009; Praharaaj *et al.* 2018; Bryan *et al.* 2021; Jesser *et al.* 2025). In the context of widespread childhood undernutrition in rural Bolivia (Cordero *et al.* 2019; Miranda *et al.* 2020), these findings highlight the public health relevance of these pathogens, which may substantially contribute to chronic morbidity and environmental enteric dysfunction.

### Pathogen prevalence by geographic setting

The significantly higher odds of enteric infection observed in rural than in peri-urban communities highlight persistent inequities in access to safe water, sanitation, and hygiene services. These findings reflect structural vulnerabilities that sustain fecal-oral transmission across the peri-urban and rural landscape and are consistent with observations from other low-resource settings (Acosta *et al.* 2016; Pelkonen *et al.* 2018; Fan *et al.* 2019; Chard *et al.* 2020; Troeger *et al.* 2020; Gizaw *et al.* 2023; Jesser *et al.* 2025; Kyu *et al.* 2025).

A pronounced spatial disparity in pathogen distribution was evident, with viral infections, particularly astrovirus and adenovirus, more frequently detected in the upper basin, whereas bacterial pathogens, such as diarrheagenic *E. coli* and *Salmonella*, predominated downstream. This pattern may be consistent with differences in environmental, altitudinal, and

climatic conditions between the two regions. Warmer temperatures in the lower basin may favor the persistence and transmission of enteric bacteria (Carlton *et al.* 2016; Chao *et al.* 2019), while the colder conditions of the higher-altitude upper basin, estimated to be on average approximately 7–9 °C lower, may support the environmental stability of non-enveloped enteric viruses. Astrovirus and adenovirus are known to persist in water, on fomites, and on household surfaces and to exhibit greater resistance to environmental inactivation than many bacteria and enveloped viruses (Abad *et al.* 2001; Moser & Schultz-Cherry 2008; Vasickova *et al.* 2010; Bosch *et al.* 2014; Kotwal & Cannon 2014). In addition, close contact within overcrowded households may facilitate person-to-person transmission consistent with reports of high levels of viral shedding of astrovirus in stool and the ubiquitous circulation of adenoviruses (Fabiana *et al.* 2007; Bosch *et al.* 2014; Parrón *et al.* 2021; Qiu *et al.* 2023).

Furthermore, the downstream predominance of bacterial pathogens may also reflect the influence of the La Paz River, which traverses the lower basin region, acting as a conduit for untreated urban wastewater. This interpretation is consistent with previous reports documenting high levels of fecal contamination, the presence of diarrheagenic *Escherichia coli*, and antimicrobial resistance in river waters (Ohno *et al.* 1997; Poma *et al.* 2016; Guzman-Otazo *et al.* 2019, 2022; Ginn *et al.* 2021; Calderón *et al.* 2023).

### Pathogen profiles between mothers and children

Distinct differences in pathogen carriage were observed between mothers and children. Children carried a higher burden of viral and parasitic infections, consistent with greater environmental exposure and immature immune defenses (Teran *et al.* 2011; Simon *et al.* 2015), whereas mothers more frequently harbored bacterial pathogens, suggesting chronic or recurrent colonization (Monack *et al.* 2004; Opintan *et al.* 2010). Previous studies indicate that caregivers may act as asymptomatic reservoirs of enteric bacteria, providing a sustained source of exposure and potential transmission to children (Odetoyin *et al.* 2016; Belina *et al.* 2023). The significant mother–child cooccurrence observed for astrovirus, adenovirus, *C. jejuni* and *H. pylori* supports within-household transmission.

Network analyses further highlighted distinct household transmission dynamics. Children appeared to be key drivers of viral and parasitic spread, in line with their higher astrovirus and adenovirus loads and greater prevalence of *G. lamblia*, whereas *H. pylori* occupied a more central, mother-associated position within the network, suggesting a potential role for maternal or intrafamilial transmission pathways (Escobar & Kawakami 2004; Konno *et al.* 2005; Kouitcheu Mabeku *et al.* 2025).

### Modifiable WASH factors and infection risks

Despite partial compliance with physicochemical drinking water standards, widespread microbiological contamination was evident. Drinking water source emerged as a key determinant of infection risk. Households relying on cistern water exhibited the highest pathogen burdens, frequent coinfections, and elevated parasite loads, consistent with high levels of microbial contamination, followed by users of spring water. Elevated electrical conductivity, a proxy for organic and fecal pollution, was associated with *Shigella* and ETEC infections, while increased coliform concentrations were linked to pediatric diarrhea. The pronounced vulnerability of cistern water to environmental contamination and infrequent maintenance (Ben Ayed *et al.* 2020; Rao *et al.* 2022; Murdock *et al.* 2024) identifies these systems as critical targets for intervention. This pattern of source-dependent contamination, pathogen infection, and disease mirrors findings from other low-resource settings, where fecal contamination of non-piped water sources has been repeatedly linked to enteric pathogen infections and diarrheal disease (Taulo *et al.* 2012; Singh *et al.* 2019; Olalemi *et al.* 2021; Nowicki *et al.* 2022; Santos *et al.* 2023; Falcone *et al.* 2024; Mogane & Momba 2025).

Notably, among all pathogens assessed, ETEC displayed a distinct epidemiological profile, characterized by strong associations with unsafe drinking water sources and household water management practices. This pattern reinforces its well-established role as a predominantly waterborne pathogen in low-resource settings (Qadri *et al.* 2005; Lothigius *et al.* 2008; Gonzales-Siles & Sjöling 2016; Poma *et al.* 2016; Guzman-Otazo *et al.* 2019), and highlights its utility as a sentinel indicator of water-related transmission risk in these communities.

Agricultural occupation was also associated with a markedly higher likelihood of bacterial carriage, likely reflecting repeated exposure to pathogen-contaminated river water and soil (Trang *et al.* 2007; Poma *et al.* 2016; Guzman-Otazo *et al.* 2019). This observation underscores the river environment as a potential driver of enteric infections in the lower

basin, where a substantial proportion of the population is engaged in agricultural activities and relies on river water for irrigation.

Beyond water quality source, unsafe sanitation practices and household behaviors further amplified infection risk. Open-field defecation and inadequate water handling were associated with increased pathogen carriage. Although boiling drinking water was protective, this benefit may be undermined by post-treatment recontamination during unsafe storage, particularly in open or handle-less containers. Inadequate hand hygiene after contact with animals or feces further increased infection risk, consistent with evidence identifying animal feces as a major household contamination and food contamination sources (Pickering *et al.* 2011; Ercumen *et al.* 2017; Delahoy *et al.* 2018).

Collectively, these findings indicate that enteric infection risk arises from an interconnected chain of exposure, from contaminated environmental sources to domestic practices, underscoring the need for coordinated approaches that address both environmental contamination and household behaviors.

Limitations: This study provides one of the first comprehensive assessments in Bolivia of a wide spectrum of enteric pathogens (viruses, bacteria, and parasites) using sensitive molecular methods in asymptomatic mothers and children from rural and peri-urban communities. Its integration of microbial, environmental, and socio-behavioral data, complemented by network analyses, offers valuable insights into concurrent infections and potential overlapping transmission pathways. Nonetheless, some limitations should be considered. First, the relatively small population size limits statistical power and constrains the ability to fully evaluate potential confounders and complex interactions among WASH indicators, socioeconomic factors, and environmental exposures. Second, the cross-sectional design precludes causal inference and prevents assessment of temporal dynamics or seasonal variation in pathogen transmission. Third, although stool samples were analyzed via sensitive molecular methods, these approaches cannot distinguish between active infection and prolonged asymptomatic carriage, which is common for pathogens such as *H. pylori* and *Giardia*. Fourth, the high prevalence of certain pathogens may be overestimated, as children without diarrhea at the time of sampling may have experienced symptomatic episodes in the preceding weeks, with pathogen DNA/RNA still detectable. Fifth, while self-report survey data provide valuable insights into WASH practices and health outcomes, they are subject to recall and reporting biases, and the surveys do not capture information on household income or domestic animals, such as livestock. Despite these constraints, the study contributes preliminary baseline evidence for the region and highlights the need for longitudinal, multi-scalar approaches integrating microbiological, environmental, and social dimensions to clarify the complex drivers of enteric pathogen transmission.

## CONCLUSIONS

This study documents a substantial burden of enteric pathogens in high-risk peri-urban and rural communities of the La Paz River Basin, Bolivia. We report an exceptionally high overall prevalence of viral, bacterial, and parasitic pathogens (85%), frequent coinfections (63%), and marked heterogeneity in pathogen distribution shaped by geography, age, and modifiable socioeconomic and WASH-related factors. These findings highlight the interconnected nature of environmental contamination, household behaviors, and social vulnerability in sustaining enteric pathogen transmission. Addressing this burden will require integrated public health interventions that combine improvements in water source protection and sanitation infrastructure with targeted strategies to promote safe water handling, hygiene practices, and risk reduction in agricultural settings.

## ACKNOWLEDGEMENTS

We thank the French National Research Institute for Sustainable Development (IRD) and the EVAM (European Virus Archive–Marseille) technological platform for contributing to positive controls, primers, and probes. We are deeply grateful to all the communities who participated in the study for their collaboration and trust throughout the study.

## FUNDING

This research was supported by the UMSA–SIDA Diarrheal Diseases Subprogram and the Bolivia WATCH (WASH Thinking Connected to Hydrology) program in collaboration with the Stockholm Environment Institute (SEI), both funded by the Swedish International Development Cooperation Agency (SIDA).

## AUTHORS CONTRIBUTIONS

V.I. conceptualized and designed the study. A.S. and C.L. contributed to the design of the field site and community surveys. C.C. and S.J. performed the laboratory analyses, whereas V.I., A.T., B.C., J.A., and J.M. collected samples, conducted the surveys, and contributed to specific laboratory procedures. C.C. performed the statistical analyses. C.C. and V.I. drafted the manuscript. L.I. and S.P. critically revised the manuscript and provided technical support. All the authors reviewed and approved the final version of the manuscript.

## ETHICS STATEMENT

This study was approved by the Research Ethics Committee of the National Bioethics Committee of Bolivia (CEI-CNB: 16/2017; *Pilot Evaluation of the Potential Role of Histo-Blood Group Antigens in Susceptibility to Norovirus and Rotavirus Infection*). Permission to conduct the study was sought from the respective municipal authorities. Verbal informed consent was obtained from all adult participants (the parents or legal guardians of minors) who answered the survey and provided stool samples. The ethics committee approved the use of verbal consent due to the low-risk, observational nature of the study and the cultural context of the participating communities.

## DATA AVAILABILITY STATEMENT

All relevant data are included in the paper or its Supplementary Information.

## CONFLICT OF INTEREST

The authors declare there is no conflict.

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First received 12 November 2025; accepted in revised form 12 January 2026. Available online 6 February 2026