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Authors' Contribution

AJA conceived and designed the study; AJA and AMMQ wrote and revised the paper.

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Variability of Bacteria in Human Populations: Axes, Drivers, Methods, and Implications

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Bacteria in a human population differ in three interrelated aspects. The first is community composition, or which taxa are there in which proportion. The second is strain genetics, or the lineages and mobile elements like plasmids, integrons, and phages. The third is the function of which metabolic pathways, virulence factors, and antimicrobial-resistance genes are present. A variety of factors influence the patterns seen in the development of infections. These factors include the food systems that we are subjected to in addition to our diets, exposure to antibiotics from humans and animals, the sanitation and water supplies, air quality and the built system, early life factors such as the delivery mode, breastfeeding, and host genetics such as FUT2 secretor status, vaccination and serotype replacement, health systems and infection control, urbanization and mobility, and animal-human interfaces. Comparative cross-continental studies reveal strong lifestyle gradients, such as those between rural/traditional versus urbanized cohorts. The genomic epidemiology shows vaccine-forced serotype turnover (pneumococci), hospital-adapted clonal cycles (MRSA), and pandemic lineages of enteric pathogens. Through shotgun metagenomics, isolate WGS, multi-omics, and wastewater metagenomics, we can resolve population-level surveillance. The consequences range from local resistomes, vaccine strategy, sanitation priority, and One Health to clinical empiric therapy.



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INTRODUCTION

There is an axis of dietary and lifestyle factors that exists globally (De Filippo *et al.*, 2010). Traditional or agrarian diets that are high in complex polysaccharides are associated with a gut profile rich in Prevotella (Yatsunenko *et al.*, 2012). On the other hand, highly processed and fat- and protein-rich diets favour Bacteroides and other bile-resistant taxa. Urbanization is often linked to a decrease in alpha diversity and predictable community structure shifts (De Filippo *et al.*, 2010; Yatsunenko *et al.*, 2012) (Table 1).

Different populations within the gene pool of a given species often contain different viral lineages, where the differences are SNPs and mobile elements that impact virulence, biofilm capacity, AMR, and persistence in an ecological niche. Research on antibiotic-resistant strains of bacteria shows that microbial strains in various parts of the world are undergoing evolution with time. For example, the ST 239 strain of *Staphylococcus aureus* is being replaced by the ST22/CC8 strain (Hsu *et al.*, 2015; Lawal *et al.*, 2022) (Figure 1).

Table 1. Expected contrasts: Rural agrarian vs. Urbanized populations.

Dimension	Rural agrarian (traditional)	Urbanized (Westernized)	Representative sources
Dominant gut taxa	Prevotella-rich; higher alpha diversity; plant fermenters	Bacteroides & bile-tolerant genera; often lower alpha diversity	(De Filippo <i>et al.</i> , 2010; Yatsunenko <i>et al.</i> , 2012)
Functional profile	Complex carbohydrate metabolism; SCFA production	Higher bile acid metabolism; xenobiotic handling	(Yatsunenko <i>et al.</i> , 2012)
Resistome (community)	Lower abundance of some ARGs (context-dependent)	Higher ARG abundance observed in some urban sewage surveys	(Hendriksen <i>et al.</i> , 2019)
Enteric pathogen exposure	Higher environmental exposure where WASH coverage is low	Lower exposure with robust WASH; outbreaks still occur	(Humphrey <i>et al.</i> , 2019; Luby <i>et al.</i> , 2018)

Functional potential (metabolism, resistomes)

Through shotgun metagenomics, the analysis by the researchers reveals that there are observable differences in functional gene content, which include short-chain fatty acid biosynthesis, vitamin pathways, bile-acid metabolism, and xenobiotic handling. Moreover, differences are also visible in the resistomes, which refer to the repertoire of resistance genes (Hendriksen *et al.*, 2019).

The metagenomic analysis of sewage on the community scale detects systematic regional differences in the abundance and diversity of AMR genes. Such an analysis provides a complementary population-level view that clinical

sampling alone may miss out on (Hendriksen *et al.*, 2019).

Diet and food systems

Diet is a primary determinant of gut ecology. A large study featured in Nature showed that microbiome structure varies by age and geography with data from Venezuela, rural Malawi, and the metropolitan USA (Yatsunenko *et al.*, 2012). Research comparing children in rural Burkina Faso and urban Italy connected consumption of fiber-rich plant-based diets with Prevotella enrichment and functional capabilities. Furthermore, urbanization distorted composition toward Bacteroides and bile-tolerant taxa (De Filippo *et al.*, 2010).

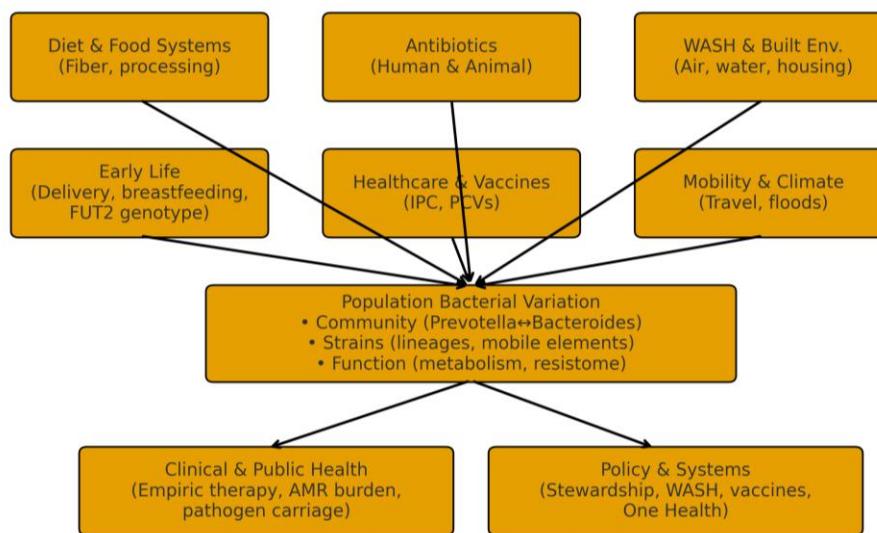


Fig. 1. Conceptual framework linking population-level drivers to bacterial community, strain, and functional variation, and to clinical/policy outcomes (schematic).

Antibiotic exposures in humans and animals

The use of antibiotics by humans is very different from one country to another and has increased in many areas over the last twenty years (Ashraf and Iqbal, 2021; Ashraf *et al.*, 2020; Klein *et al.*, 2018). The global antimicrobial use in food-animal production is substantial and likely to remain high (Iqbal and Iqbal, 2020; Iqbal and Ashraf, 2023). As a result, it has implications for shared resistomes across the human-animal interface. The pressures in an environment differ because of differences in stewardship which selects for unique community resistomes and pathogen clones (Van Boekel *et al.*, 2015; Van Boekel *et al.*, 2019).

Water, sanitation, and hygiene (WASH) and the built environment

Access to sanitation, treatment of wastewater, and crowding affect exposure to enteric pathogens. Two major cluster-randomized trials in Bangladesh and Zimbabwe (WASH Benefits; SHINE) found mixed effects on diarrhoea and growth outcomes but did find reductions in some enteropathogen burdens and changes in some biomarkers. These findings highlight the strong effect of coverage, intensity, and context on

bacterial incidence in the environment (Humphrey *et al.*, 2019; Khalid *et al.*, 2016; Luby *et al.*, 2018; Pickering *et al.*, 2019; Yunus *et al.*, 2016). Wastewater metagenomics gives a snapshot of AMR in the population, which can work well with clinical surveillance (Hendriksen *et al.*, 2019).

Air quality and pollution

More and more evidence shows that outdoor and indoor air pollution may disturb microbiomes in the airway and gut. Intervention work is linking cleaner indoor air to respiratory improvements and microbiome shifts. Different populations have differences in how much fuel they use, the cooking practices they follow, and so on. After all, one practice can change the microbial ecology of a population strongly. Thus, they can become different from each other (Alderete *et al.*, 2018; Mutlu *et al.*, 2018).

Early-life seeding: delivery mode, breastfeeding, host genetics

The initial colonization phase of the gut microbiota is influenced by the birth of an individual (Turroni *et al.*, 2022). A-mode of birth is associated with the differences in the early-life

gut microbiomes of babies that are delivered through C-section as compared to their vaginally delivered counterparts. According to research that involved tracking the source of bacteria, breast milk directly seeds the infant's gut. Their breast milk organs are basically an ilk strain of drugs. Thus, this shows that a considerable fraction of the early infant gut originates from breast milk and areolar skin (Pannaraj *et al.*, 2017). The genetics of the host is also critical: FUT2 (secretor) genotype is correlated with the adult gut community structure and infant colonization patterns (Wacklin *et al.*, 2011; Wacklin *et al.*, 2014).

Vaccination and immune landscapes

Vaccination changes circulating bacterial lineages and serotype distributions. Since the introduction of pneumococcal conjugate vaccines (PCV10/PCV13) for children, disease due to vaccine-type strains has declined. However, pneumococcal serotype replacement may differ by setting. In light of the switch from PCV13 to PCV10 at the national level, 19A rebounded. PCVs of higher valency will tackle this residual disease (Anglemyer *et al.*, 2024; Desmet *et al.*, 2021).

Healthcare ecosystems and infection control

Hospital networks, device use, antimicrobial stewardship, and infection-prevention policies select for (and against) particular nosocomial lineages. The interplay of these factors explains regional differences and temporal turnover in predominant MRSA clones (Hsu *et al.*, 2015; Lawal *et al.*, 2022).

Mobility, urbanization, and climate

Travel, migration, city life, and climate put pressure on bacteria. According to genomic analyses, Africa has a history of long-term regional waves of seventh-pandemic *Vibrio cholerae* El Tor lineage. Furthermore, recent cholera outbreaks have been shown to result from the interaction of 'hydrology and infrastructure' with pathogen lineages (Chaguza *et al.*, 2024; Weill *et al.*, 2017).

Case studies

Lifestyle gradients in the gut microbiome

Groups that live in rural areas or eat traditional diets have different gut microbes from those who live in cities. The former has more diverse microbes that are rich in Prevotella, while urban groups have mostly *Bacteroides* and bile-resistant microbes. This is due to the high levels of fiber found in traditional diets, which can be fermented, while *Bacteroides* can withstand bile acids (De Filippo *et al.*, 2010; Yatsunenko *et al.*, 2012). These differences are in relation to shifting fermentative pathways, short-chain fatty acid profiles, which may affect immune tone and metabolic phenotypes (Yatsunenko *et al.*, 2012).

Vaccine-shaped pneumococcal populations

After PCV introduction, cases of the disease caused by the vaccine strain drop, but shifts depend on the product and policy. In sites that switched from vaccinating with PCV13 to PCV10, serotype 19A generally rebounded. Multi-country analyses showed different replacement kinetics and suggested potential benefits of higher-valency PCVs (Anglemyer *et al.*, 2024; Desmet *et al.*, 2021).

Clonal waves in MRSA

Hospital-adapted lineages such as ST239 dominated for years in parts of Asia and elsewhere, but several regions now report declines and replacement by other clones (e.g., ST22, ST5, ST59), driven by antibiotic pressures and prevention practices (Hsu *et al.*, 2015; Lawal *et al.*, 2022). Such clonal turnovers force regular recalibration of empiric therapy and decolonization strategies.

Pandemic lineages: *Vibrio cholerae*

Evidence collected on a global scale indicates that cholera epidemics found in Africa resulted from repeated introductions of the seventh pandemic El Tor lineage and that the subsequent waves were connected to the regions where these epidemics originated. Recent genomes from southern Africa highlight

the resurgence of these epidemics in connection to climate change as well as linkage with other regions of Africa (Chaguza *et al.*, 2024; Weill *et al.*, 2017).

Detecting population differences: methods and study designs

From community profiling to strain-resolved genomics

Studies of the 16S rRNA gene permit wide-range analyses but not resolution of strains or functions. Metagenomics reveals taxonomic diversity and potential functionality of genes in environmental microbiomes. MLST/cgMLST/SNP phylogenies WGS plus typing is essential for pathogens (e.g., MRSA sequence types; pneumococcal serotypes/sequence types). The Multi-omics relate microbiome community function to host response. For example, the design of the NIH Integrative Human Microbiome Project (iHMP) (Lloyd-Price *et al.*, 2019).

Community-scale environmental sampling

The use of wastewater or sewage metagenomics to understand the population-level resistomes and pathogen signals can offer a clear regional structure, and also provides a low-cost means to complement clinical AMR surveillance (Hendriksen *et al.*, 2019).

Epidemiological frameworks

Research using cross-sectional and cohort approaches can be implemented across urbanization or dietary gradients. Similarly, quasi-experimental sanitation upgrades with pre/post sampling (as utilized in WASH trials) may also be conducted (Humphrey *et al.*, 2019; Luby *et al.*, 2018). It is also feasible to harness integrated clinical surveillance systems (e.g., WHO GLASS) for AMR trends (Organization, 2022).

A simple synthesis

To summarize all the different causes of bacterial adaptation to human hosts, we came

up with the following concatenated formula that covers most potential human-bacterial adaptation causes: (Diet Early life) (Antibiotic exposures human, animal) (WASH (water, sanitation and hygiene) + Built environment + Air quality) (Healthcare system vaccines) (Host genetics) (Mobility/Urbanization/Climate). These factors will be subsequently filtered by local ecology and history. For instance, the two populations will differ with respect to both their patterns of commensal microbiome structure and pathogen lineages/resistomes if one has high C-section rates, little breastfeeding, a lot of macrolide/fluoroquinolone use in outpatients, little access to sanitation, and frequent exposure to hospitals (De Filippo *et al.*, 2010; Humphrey *et al.*, 2019; Klein *et al.*, 2018; Pannaraj *et al.*, 2017; Wacklin *et al.*, 2011; Yatsunenko *et al.*, 2012).

Practical implications

Clinical care and empiric therapy

Local antibiograms matter. Different regions should have different first-line choices for the same syndrome. This has different reasons, but integration of rapid diagnostics with stewardship and local resistance data could improve outcomes (Organization, 2022) (Table 2).

Vaccine policy

Serotype replacement is setting-specific. PCV product choices and schedules should reflect local serotype surveillance, with periodic updates as replacement patterns evolve (Anglemyer *et al.*, 2024; Desmet *et al.*, 2021).

WASH and environmental policy

Investing in sanitation and safe water can help reduce the transmission of pathogens. But having higher coverage and quality is key to generating significant growth effects. Wastewater-based AMR surveillance can generate early warning and community-level measurements (Hendriksen *et al.*, 2019; Humphrey *et al.*, 2019; Luby *et al.*, 2018).

Table 2. Population-tailored implications for practice and policy.

Area	Implications	Notes / Examples
Empiric therapy & stewardship	Use local antibiograms; prioritize rapid diagnostics; de-escalate based on results	Regional heterogeneity apparent in GLASS reporting
Vaccination policy (pneumococci)	Monitor serotype replacement; consider higher-valency PCVs as needed	19A rebounds after PCV13→PCV10 switches in some settings
WASH investment	Aim for high-quality, high-coverage sanitation/water with sustained O&M	Effects vary with coverage and context (Bangladesh, Zimbabwe trials)
Air quality interventions	Reduce PM/NO ₂ exposures; anticipate respiratory and microbiome co-benefits	Intervention and observational evidence emerging
One Health AMR surveillance	Pair clinical data with wastewater metagenomics; include animal/agriculture sectors.	Global sewage resistome catalogs; national action plans

Air-quality action

Clean indoor air is associated with better respiratory health and microbiome changes. These are co-benefits of air-quality policy in rapidly urbanizing settings (Alderete *et al.*, 2018; Mutlu *et al.*, 2018).

One Health and mobility

Agricultural antibiotic stewardship, management of animal–human interfaces, climate resilience, and cross-border genomic surveillance are essential to track and manage population-specific lineages and resistomes (Hendriksen *et al.*, 2019; Van Boekel *et al.*, 2015; Van Boekel *et al.*, 2019; Weill *et al.*, 2017).

Outlook

Priorities include: filling geographical blind spots with balanced sampling; integrated One Health surveillance linking clinical, environmental, and animal reservoirs; causal evaluation of policy levers (diet shifts, vaccine switches, sanitation upgrades, air-quality interventions) via natural experiments and stepped-wedge designs; and agile vaccine/therapeutic development in response to lineage and serotype turnover (Hendriksen *et al.*, 2019; Lloyd-Price *et al.*, 2019; Organization, 2022; Yatsunenko *et al.*, 2012).

CONFLICT OF INTEREST

Author of this article wish to declare that there is no potential conflict of interest.

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