REVIEW

Bacteroides: From a Fecal Pollutant to a Useful Tool in Solving Water Pollution

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ABSTRACT

Bacteroides spp. are Gram-negative bacilli, non-endospore-forming and obligate anaerobes, belonging to Phylum Bacteroidetes, Class Bacteroidia, Order Bacteroidales, Family *Bacteroidaceae*, with 40 taxonomically recognized species. They are anaerobes, and hence, commonly found in warm-blooded animals' guts and fecal microbiome, where they are the most dominant bacteria, having either mutually or commensally co-evolved with their host. However, they are also disease-causing and carriers of antibiotic resistance genes. Hence, release of *Bacteroides*-dominated feces by hosts causes fecal pollution, especially in water bodies. Despite being anaerobes, *Bacteroides* have a short lifespan. They leave their genetic materials behind as environmental DNA, which remain viable for PCR. DNA isolation can determine the feces' source—a technique known as microbial source tracking (MST). There are two types of MST: library-dependent (LDM) and -independent (LIM). *Bacteroides* use falls under LIM, wherein animal associated *Bacteroides* markers determine the fecal contamination's source. Due to extensive co-evolution between *Bacteroides* and hosts, most LIM-MST biomarkers are *Bacteroides*-based [*PigBac* (pigs), *CowBac* (cows), *ChickenBac* (chicken)] and human-based (*HF183, HumBac*), etc. MST also effectively determines fecal pollution extent from anthropogenic and agricultural sources. Therefore, MST can directly determine a definitive fecal pollutant source. The main limitation of LIM-MST is the lack of markers for other animals. Most available MST markers are directed toward domesticated animals (chickens, cows, pigs). Moreover, even existing markers are affected by geography and animal diet. These limitations warrant continued efforts to fill the gaps by designing more specific and sensitive MST animal markers. This review aims to initiate interest in the use of *Bacteroides* for efficient water quality monitoring.

INTRODUCTION

The gut contains a rich microbial ecosystem that plays a key role in animal health (Turroni et al. 2020; Zafar and Saier 2021). The human intestine alone contains approximately 10^{11} to 10^{12} bacteria per gram of colonic content (Eckburg et al. 2005).

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Email Address: wlrivera@science.upd.edu.ph
Date received: September 24, 2023
Date revised: November 6, 2023
Date accepted: November 21, 2023

KEYWORDS

Bacteroides, fecal pollution, microbial source tracking (MST), library-independent MST, MST markers

Numerically, the most dominant group of bacteria in the human intestine and other warm-blooded animals belongs to the Order Bacteroidales (Kabiri et al. 2013; Coyne et al. 2014; Tamana et al. 2021; Zafar and Saier 2021). *Bacteroides* exclusively live and grow in their animal host's gut, suggesting a strong evolutionary adaptation to the gastrointestinal tract (GIT) environment (Wexler and Goodman 2017). *Bacteroides* are introduced into its human host via vaginal or cesarian delivery and skin contact with lactating mother (Wang et al. 2015; Milani et al. 2017). *B. thetaiotamicron* is commonly found to be the prevalent *Bacteroides* during the lactating months of a human baby since this *Bacteroides* species can highly degrade glycan from human milk (Fouhy et al. 2012; Milani et al. 2017). As more solid foods are introduced, more *Bacteroides* species inhabit the niches in the gut since they are highly specialized in the degradation of several kinds of glycan. As humans grow and consume more food groups, particularly during childhood, *Bacteroides* species shift dominance to other species such as *B. ovatus* and *B. xylanisolvens* (Zhong et al. 2019). Differences in diets among adults show differences in dominant *Bacteroides* species. Among omnivorous adult humans, *B. salanitronis* and *B. coprocola* co-dominate in the gut. Conversely, for vegetarian adults, *B. vulgatus* is dominant while *B. salyersiae* is prevalent in vegans (Ferrocino et al. 2015). However, *B. thetaiotamicron* and *B. fragilis* are generally found in high concentrations in all stages of life (Zafar and Saier 2021).

Bacteroides in the gut play beneficial roles in their warm-blooded animal hosts, although *Bacteroides* have already been isolated from cold-blooded animals such as fishes and frogs (Kabiri et al. 2013; Gibb et al. 2017). They have been recognized either as mutualists or commensals by providing nutritional and immunological benefits, thus establishing stable long-term beneficial relationships with their hosts. Thus, *Bacteroides* are considered clinically important anaerobes that are directly related to intestinal well-being (Hong et al. 2008). They are so extensive and highly adapted to life and survival in the gut that they have evolutionarily become an essential species in the gut microbial food web (Wexler and Goodman 2017). However, they can also cause harm like abscesses to infected organs and bacteremia when they break out of the gut. Moreover, *Bacteroides* undergo extensive horizontal gene transfer (HGT) that include virulence genes and antimicrobial resistomes. Resistomes are well characterized collection of antibiotic resistance genes (ARGs) from a variety of environments (Ma et al. 2021). Some of the ARGs are transferred to other *Bacteroides* spp. or other transient bacteria of the gut, and thus, when these *Bacteroides* or the transient bacteria are expelled with the feces, they have with them the antibiotic resistance phenotype (Huddleston 2014). *Bacteroides* constitute 30%–50% of the total fecal bacteria, with concentrations of 10^{11} cells per gram of feces (Paruch et al. 2019). Although only a small portion of the gut microbial population is culturable, 14%–40% of cultivable microorganisms in the fecal microbiota are *Bacteroides* (Hong et al. 2008). Due to the dominance of *Bacteroides* in both the gut and fecal microbiome and its strong evolutionary ties to its host, it has been used as an alternative fecal bacterium for monitoring water pollution, instead of the traditional fecal indicator bacteria (FIB) such as the fecal coliforms (*Escherichia coli* and *Enterococcus faecalis*). Hence, this review discusses *Bacteroides* as a fecal pollutant that contributes to the degradation of water quality and causes illnesses, to a more positive role of being part of the solution by identifying the fecal origin – a step forward for developing better governmental policies in addressing the problem of water pollution.

Taxonomy and biology of *Bacteroides*

Taxonomically, *Bacteroides* sp. belongs to Phylum Bacteroidetes, Class Bacteroidia, Order Bacteroidales, and Family *Bacteroidaceae*. In a review by Wexler (2007), there were 21 taxonomically known species of *Bacteroides*. Those were *B. acidafaciens, B. caccae, B. coprocola, B. coprosuis, B. eggerthii, B. finegoldii, B. fragilis, B. helcogenes, B. intestinalis, B. massiliensis, B. nordii, B. ovatus, B. thetaiotamicron, B. vulgatus, B. plebius, B. uniformis, B. salyersae, B. pyogenes, B. goldstenii, B. dorei,* and *B. johnsonii*. Through the succeeding years, the number of *Bacteroides* species reached 136 (https://lpsn.dsmz.de/). However, further research on each *Bacteroides* shows that out of 136, only 40 are taxonomically legitimate as enumerated in Table 1. The remaining 96 "*Bacteroides*" were either taxonomically transferred to a different genus and have simply become a taxonomic synonym or were not validly published. For example, *B. massiliensis* has been changed to *Phocaeicola massiliensis, B. goldsteineii* to *Parabacteroides goldsteinii,* and *B. dorei* to *Phocaeicola dorei*. Moreover, some that were identified as "*Bacteroides"* are not considered taxonomically legitimate, yet they were not validly published. This includes *B. congoensis, B. cutis,* and *B. sediment,* etc.

Although *Bacteroides* is the most predominant bacterial group in the gut, there are only 40 taxonomically legitimate known species compared with other bacteria. This may be because *Bacteroides* are anaerobes, and anaerobic conditions are one of the most challenging conditions to be able to obtain an enriched or pure culture (Mori and Kamagata 2014).

Table 1: List of 40 *Bacteroides* valid species

	Bacteroides species	GenBank Accession Number	Source	Reference
1.	*B. acidifaciens*	AB510696	Mice cecum	Miyamoto and Itoh 2000
2.	*B. caccae*	X83951	Human feces	Johnson et al. 1986
3.	*B. caecicola*	AB910337	Chicken cecum	Irisawa et al. 2016
4.	*B. caecigallinarum*	AB861981	Chicken cecum	Saputra et al. 2015
5.	*B. caecimuris*	KR364741	Mice intestine	Lagkouvardos et al. 2016
6.	*B. cellulosilyticus*	AJ583243	Human gut	Robert et al. 2007
7.	*B. clarus*	AB490801	Human feces	Watanabe et al. 2010
8.	*B. coprosuis*	AB510699	Pig manure	Whitehead et al. 2005
9.	*B. eggerthii*	AB050107	Human feces	Holdeman and Moore 1974 (Approved Lists 1980)

10.	*B. faecalis*	MK207058	Human feces	Yu et al. 2019
11.	*B. faecichinchillae*	AB574480	Chinchilla feces	Kitahara et al. 2012
12.	*B. faecis*	AB547640	Human feces	Kim et al. 2010
13.	*B. finegoldii*	AB222699	Human feces	Bakir et al. 2006a
14.	*B. fluxus*	AB490802	Human feces	Watanabe et al. 2010
15.	*B. fragilis*	AB050106	Human intestine	Castellani and Chalmers 1919 (Approved Lists 1980)
16.	*B. galacturonicus*	DQ497994	Human intestine	Jensen and Canale-Parola 1986
17.	*B. gallinaceum*	AB910339	Chicken cecum	Irisawa et al. 2016
18.	*B. gallinarum*	AB253732	Chicken cecum	Lan et al. 2006
19.	*B. graminisolvens*	AB363973	Cow waste	Nishiyama et al. 2009
20.	*B. helcogenes*	AB200227	Pig feces	Benno et al. 1983
21.	*B. intestinalis*	AB214328	Human feces	Bakir et al. 2006b
22.	*B. koreensis*	KX025133	Human feces	Shin et al. 2017
23.	*B. kribbi*	KX025134	Human feces	Shin et al. 2017
24.	*B. luhongzhouii*	MK584158	Human feces	Ge et al. 2021
25.	*B. luti*	AB787271	Anaerobic treatment sludge/ facility	Hatamoto et al. 2014
26.	*B. nordii*	AB510704	Human intestine	Song et al. 2004
27.	*B. oleiciplenus*	AB490803	Human feces	Watanabe et al. 2010
28.	*B. ovatus*	X83952	Human feces	Eggerth and Gagnon 1932 (Approved Lists 1980)
29.	*B. pectinophilus*	ABVQ01000036	Human intestine	Jensen and Canale-Parola 1986
30.	*B. propionicifaciens*	AB264625	Cow feces	Ueki et al. 2008
31.	*B. pyogenes*	AB200229	Pig feces	Benno et al. 1983
32.	*B. reticulotermitis*	AB692943	Termite gut	Sakamoto and Ohkuma 2013
33.	*B. rodentium*	AB547646	Chinchilla feces	Kitahara et al. 2011
34.	*B. salyersiae*	AB510707	Human intestine	Song et al. 2004
35.	*B. stercorirosoris*	AB574481	Chinchilla feces	Kitahara et al. 2012
36.	*B. stercoris*	X83953	Human feces	Johnson et al. 1986
37.	*B. thetaiotaomicron*	AB050109	Human gut	Castellani and Chalmers 1919 (Approved Lists 1980)
38.	*B. uniformis*	AB050110	Human feces	Eggerth and Gagnon 1932 (Approved Lists 1980)
39.	*B. xylanisolvens*	AB510713	Human feces	Chassard et al. 2008
40.	*B. zhangwenhongii*	CP059856	Human feces	Ge et al. 2021

Morphologically, *Bacteroides* are Gram-negative, non-motile, rod-shaped, and non-spore-forming bacteria, as consistently shown in all references enumerated in Table 1. Based on these references, most pure culture isolations were performed using Eggerth-Gagnon (EG) Agar supplemented with 5% blood. However, several recent publications on *Bacteroides* isolation use *Bacteroides* Bile Esculin (BBE) agar (Niestepski et al. 2019; Zamani et al. 2020; Dela Rosa and Rivera 2021). Interestingly, the colonial morphology is circular, entire, raised convex, smooth, and grayish to off-white for both EG and BBE agars. In all instances, the culture condition is at 37°C for 48–72 h in an anaerobic condition to simulate the submicromolar range of oxygen levels in the large intestine. Besides its anaerobic physiology, due to the challenging environment of the large intestine, where most of the gut microorganisms' live, *Bacteroides* have developed other adaptive mechanisms for their survival in the adverse environment of the large intestine. For example, many species of *Bacteroides* contain cytochrome *bd* oxidase that uses oxygen as a terminal electron acceptor, thus, lowering oxygen levels in the gut. Interestingly, some *Bacteroides* contain the gene *nrdA,* which codes for an enzyme used only in aerobic respiration. Through these, *Bacteroides* can tolerate oxygen and allow their spread to new hosts. (Smalley et al. 2002; Wexler and Goodman 2017).

Bacteroides and the vertebrate gut

Bacteroides as mutualist and commensal

Intestinal *Bacteroides* have co-evolved intricate symbiotic relationships with their specific animal hosts (Bäckhed et al. 2005). The interaction is characterized by *Bacteroides* producing secondary metabolites essential to its host, and in return, the animal host providing stable gut microbial ecosystem (Groussin et al. 2021). Moreover, to a limited extent, *Bacteroides* are also involved in developing the host's immune system (Troy and Kasper 2010). In comparing the fecal microbiota of different host vertebrates using 16S rRNA gene, it showed that *Bacteroides* spp. co-evolve with their hosts, and co-diversified with them (Ley et al. 2008). Symbiosis is so strong that there is a development of host-microbiome fidelity and cohesive association (Groussin et al. 2017).

One of the well-researched symbiotic relationships between *Bacteroides* and its human host is glycans – simple and complex carbohydrates that play metabolic, structural, and physical role in biological systems (Comstock 2009; Varki 2017). The mammalian host lacks the enzymatic capacity to degrade glycans, however, *B. thetaiotamicron*, a glycophile, can break down various dietary glycans. It has 88 polysaccharide utilization loci for degrading various glycans, including plant glycans/polysaccharides (Guo et al. 2020). This capability is not exclusive to *B. thetaiotamicron.* The collective *Bacteroides* population poses an enormous, combined polysaccharide degradative ability capable of metabolizing more than a dozen different kinds of plant and host-derived polysaccharides (Comstock 2009; Wexler and Goodman 2017).

More recently, *B. thetaiotamicron* was proven to restrict the growth of *Clostridioides difficile* colonization in the gut. There is a direct association that *B. thetaiotamicron* increases the concentration of several acids (α-muricholic, β-muricholic, ketolithocholic, and deoxycholic) known to inhibit *C. difficile* and reduces the taurocholic acid production that promotes *C. difficile* germination (Li et al. 2021b).

On the other hand, *B. fragilis*, conversely, exerts a beneficial immunologic effect. In an experiment conducted on germ-free gut mice, it was discovered that the mice have smaller Payer's patches, fewer germinal centers, reduced IgA-producing plasma cells, decreased $CD4^+$ T cells in the intestinal lamina propria, and structural defects of the splenic and lymphoid nodes. However, after orally introducing *B. fragilis,* it was adequate to correct the abnormalities (Troy and Kasper 2010). Additionally, a *B. fragilis* strain isolated from a baby's feces was shown to have the capability to improve phagocytosis, improve IL-10 production, and increase CD80 and CD86 of M1 macrophage cell surface expression (Deng et al. 2016; Landuyt et al. 2021). There are proposals of developing *B. fragilis* as a probiotic because of its beneficial effect on its host (Deng et al. 2016). Other beneficial effects of other *Bacteroides* species are from *B. dorei, B. xylanisolvens, B. acidafaciens, B. ovatus,* and *B. uniformis.* These *Bacteroides* species have been proposed as live biotherapeutic products (LBP) or are also called next-generation probiotics (NGP). Generally, LBP/NGP is still under study and has no history yet of being used as a probiotic, unlike traditional probiotics (*Lactobacillus* and *Bifidobacterium*) with long and successful industrial use. Moreover, traditional probiotics are commonly used as food and supplements, but LBP/NGP is still being studied for a possible preclinical mode of action, pharmacokinetics, and pharmacodynamics (O'Toole et al. 2017).

Another example is *B. xylanisolvens* which was reported to possess immunomodulatory properties and produce short fatty acids (propionate and succinate) in the gut (Ulsemer et al. 2012). The research has shown that pasteurized *B. xylanisolvens* increases the level of TNFα-specific IgM antibodies and promotes a robust response to cancer treatment.

Another beneficial relationship between mammalian host and *Bacteroides* that is well documented is *B. acidafaciens* which increases the production of IgA in the large intestine by increasing IgA^+ B cells (Yanagibashi et al. 2013). *B. uniformis,* on the other hand, when administered to obese mice, was shown to have beneficial effects in preventing obesity by significantly modifying total body weight. Further experiments have shown that the continuous administration of *B. uniformis* substantially reduces fat micelles in enterocytes and reduces leptin levels, serum cholesterol and triglyceride levels, which indicates that *B. uniformis* has a positive effect on the hepatic steatosis. Lastly, mice fed with the recombinant strain of *B. ovatus* that produces TGF-β1 can prevent or treat acute colitis (Gauffin Cano et al. 2012).

In another study, *B. fragilis* was shown to produce a capsular polysaccharide that helps protect a person from nerve demyelination (Ochoa-Reparaz et al. 2010). Furthermore, pediatricians analyzed the guts of 405 infants and found that those infants with *Bacteroides*-dominant microbiota were positively correlated with higher cognitive and language performance (Tamana et al. 2021). *B. fragilis* was even shown to produce large quantities of γ-aminobutyric acid (GABA), a neurotransmitter that influences behavior and response to stress (Strandwitz et al. 2019).

Bacteroides as a disease-causing organism

Although *Bacteroides* is known to be a mutualist or commensal when in the gut, it is equally known to be pathogenic when it escapes the gut due to a breached or compromised mucosal wall of the intestine. This implies that location is pivotal. It has caused abscesses in the liver, abdominal cavity, brain, pelvis, lungs, perirectal area, gangrenous appendicitis, diverticulitis, inflammatory bowel disease, and bacteremia. There was even a study with 365,490 healthcare-related infections, which revealed that *Bacteroides* spp. is on the top 15 most common pathogen that causes nosocomial infections (Wexler 2007; Brook 2016; Weiner et al. 2016). Among the *Bacteroides* species, *B. fragilis* is identified to be the most virulent, with *B. ovatus, B. thetaiotamicron,* and *B. vulgatus* to be clinically important species (Majewksa et al. 2021). It is interesting because *B. fragilis* and *B. thetaiotamicron* are considered beneficial and at the same time, pathogenic (Mazmanian and Kasper 2006). The beneficial effects of *B. fragilis* are strain dependent. There are other strains of *B. fragilis* that produce fragilysin toxin associated with colorectal cancer (Cheng et al. 2020). Additionally, *B. fragilis* has been isolated from 63%–80% of *Bacteroides*-related infections. Conversely, *B. thetaiotamicron* accounts for 13%–17% of *Bacteroides* infection cases (Cerdeño-Tárraga et al. 2005). Moreover, some strains of *B. fragilis* and *B. thetaiotamicron* were found to have genes that encode C10 proteases. These *Bacteroides* C10 proteases were identified to be homologous to the C10 cysteine protease of *Streptococcus pyogenes* (Thornton et al. 2012). A genetic exchange may have caused such homology via HGT between the two bacteria. There are recent documentation of other *Bacteroides* species associated with infection such as *B. dorei* and *B. pyogenes*. An invasive strain of *B. dorei* was isolated from a patient and shown to have contributed to the patient's mycotic aortic aneurysm. This report suggests caution in using *B. dorei* for biotherapeutic purposes, as some have already proposed (O'Toole et al. 2017; Matsuoka et al. 2021). This is very interesting because *B. dorei* was considered to play a probiotic role in the gut (Zafar and Saier 2018). *B. pyogenes* can cause bacteremia secondary to cat and dog bites, prosthetic joint, and amputation infections (Majewksa et al. 2021). Moreover, *B. vulgatus* and *B. ovatus*

were associated with possible increased incidence of Crohn's and Coeliac diseases (Zafar and Saier 2018).

A very important characteristic of *Bacteroides* is their extensive ability for HGT. A study has shown that *Bacteroides* species engage more frequently in HGT than other bacterial species in the gut. *Bacteroides* displayed an average HGT frequency range of 0.85%–2.3% for 10-kb+ HGT and 6.0%–10.1% for 500-bp+ HGT. Additionally, two other gut bacteria: *Bifidobacterium longum* and *Akkermansia muciniphila* have a HGT frequency of 0.04% and 0.06% for 10-kb+ HGT and 0.81% and 1.64% for 500-bp+ HGT, respectively (Groussin et al. 2021). *Bacteroides* HGT is so extensive that it was reported to have performed interspecies and even interfamily HGTs – the most likely mechanism that *Bacteroides* gets other bacteria to acquire antibiotic resistance (Coyne et al. 2014). In the gut, *Bacteroides* serves as an antibiotic resistance gene reservoir that transfers those resistance genes to transient bacteria – those that just pass through or do not colonize the gut (Huddleston 2014).

Quick genetic exchanges happen by conjugation as the favored mechanism of HGT due to the protection it provides to the DNA during transfer (Arber 2014). In another study, *B. fragilis* was shown to have a novel HGT mechanism that allows them to immediately insert very large segments of *Bacteroides* chromosomal DNA. Since large segments are transferred instead of multiple small segments, it allows *Bacteroides* to rapidly adapt to changing host GIT environment (Husain et al. 2017). It was also observed that most genes that contribute to strain diversity are in regions more likely to be acquired by HGT and spread out in multiple elements such as from phage, conjugative plasmids, and conjugative transposons (Coyne et al. 2014).

Fecal water pollution

Bodies of water are one of the primary components of our ecosystem that play a fundamental role in the existence of all biological systems. For humans, water plays an important role in the fields of agriculture, livestock, forestry, industry, fisheries, aquaculture, energy production, recreation, and others (Effendi 2016; Ogunkunle et al. 2016). But for the simple yet vital part of it, water is an essential component of cellular homeostasis of the human body (Popkin et al. 2010). Unfortunately, there are reports of massive water pollution/contamination globally (Yan et al. 2015; Maceda-Veiga et al. 2017; Noorhosseini et al. 2017; Ruzol et al. 2017). Water pollution is defined as the direct/indirect and sudden or gradual negative alteration of water's physico-chemical and biological properties, which deteriorates water quality. Consequently, it becomes a hazard to the health of any organism and makes it unfit to its other assigned uses, incurring economic loss and social instability. Pollutants can be natural contaminants, such as those due to weathering and soil leaching which are gradual processes rather than anthropogenic sources that are rapid and usually on the rise and associated with industrial, agricultural, and domestic effluents (Ogunkunle et al. 2016). There are two types of water pollutant that affect water quality. These are the non-point sources (NPS) and point sources (PS). In NPS, pollutants enter the water system from unidentified diffuse sources and are difficult to control, like stormwater runoff and domestic and wild animal defecation. Alternatively, PS are impurities that enter the water system from an easily identifiable location via a direct route like effluents from sewage treatment plants, industrial effluents, and municipal wastes (Ahmed et al. 2005; Jamwal et al. 2011). An increasingly concerning water contaminant that threatens freshwater systems is fecal pollution, as it may cause the spread of microbial pathogens and increase the nutrient load of water (Fan et al. 2017). Contaminated feces from infected animal sources may contain various pathogenic microorganisms like *Escherichia coli, Campylobacter, Salmonella, Shigella, Yersinia, Pasteurella, Francisella, Vibrio, Entamoeba histolytica, Blastocystis, Giardia,* and various viruses, such as adenoviruses, enteroviruses, and rotaviruses. Their release in freshwater bodies leads to waterborne diseases (Savichtcheva and Okabe 2006; Woodall 2009; Hampson et al. 2010; Efstratiou et al. 2017).

A major source of fecal pollution is from anthropogenic activities. It comes from agricultural, industrial, municipal, and household wastes (Li et al. 2021a). Poor fecal waste management in farms, inefficient discharge of water from treatment plants (Diaz-Gavidia et al. 2022), and reuse of municipal and domestic wastewater in agricultural irrigations (Al Hamedi et al. 2023) are the causes of widespread fecal pollution. However, efforts have been made to solve this challenge. Yet, the situation of fecal pollution lingers because of our inability to pinpoint the sources of the pollutant – a key step in mitigating the fecal pollution problem (Xue et al. 2018). If the point of origin of fecal contamination and pathogens is precisely and accurately known whether human or animal, then the proper government policy, management, minimization of public health risks associated with fecal contamination, and remediation efforts can be apportioned more efficiently and effectively (Ahmed et al. 2005; Savichtcheva and Okabe 2006). Thus, a relatively new technique that answers the question of reliably pinpointing the source of the fecal contamination by using fecal bacteria and determining how much of each source contributes to the contamination is called microbial source tracking (MST) (Harwood et al. 2014).

Microbial source tracking

MST, the same as fecal source tracking and bacterial source tracking, is based on fecal microorganisms being strongly associated with their host species. Moreover, it supports the idea that some identified attributes or patterns (i.e., antibiotic resistance patterns, 16S rRNA gene sequences) of the host-associated microorganisms can be used as markers for tracing the fecal contamination back to its host (Harwood et al. 2014). It is a relatively new approach to discriminate, pinpoint, and quantify human and other fecal contamination that may exist in the environment and is usually applied in aquatic environments (Odagiri et al. 2015; Mattioli et al. 2017). In short, MST is about identifying the specific animal source of a given fecal contaminant. This contrasts with the traditional culture-based method that is limited to determining the presence of a fecal contaminant (Rivera and Rock 2011).

Globally, different MST methods have been used to accomplish the goal of MST, which is to determine fecal pollution sources so that the needed socio-political and environmental actions can be undertaken. Some MST research was conducted in Virginia, USA, in which antibiotic resistance patterns and carbon utilization profiles were used to find out whether there was fecal pollution in their waters and to trace its specific sources (Wiggins 1996; Hagedorn et al. 2003). The biochemical fingerprinting MST method was used in Queensland, Australia, to identify the sources of *E. coli* and *Enterococci* in Eudio, Creek (Ahmed et al. 2005). The human specific *HF183 Bacteroides* MST marker was used to assess the extent of human fecal pollution in two freshwater canals in Ghent, Belgium. Conversely, a similar assessment but on pig fecal pollution was done in Britanny, France (Mieszkin et al. 2009). Fatty acid methyl ester (FAME) profiling analysis was used in Pasadena, USA, to source-track the fecal coliforms (Duran et al. 2006). In Michigan, USA, MST method using the β-glucuronidase gene was used to know whether household pets have a significant input in the fecal pollution in the surrounding surface waters (Ram et al. 2007). In France, two library-independent MST methods were used (Bacteroidales 16S rRNA gene marker detection and F-specific RNA bacteriophage genotyping) to source track the fecal pollution in a French estuary (Gourmelon

et al. 2007). MST was also used in Florida, USA, to evaluate the effect of stormwater concerning water quality using BOX-PCR (Brownell et al. 2007). In Nicoya, Costa Rica, MST was used to determine the water quality of shellfish harvesting waters using both viral and bacterial based MST markers (Symonds et al. 2017). Other MST research was conducted in Korea, using F+ RNA coliphages to source track fecal pollution in Metropolitan Seoul and Gyeonggi province (Lee et al. 2011), Lake Taihu in China (Hagedorn and Xinqiang 2011; Vadde et al. 2019), and Dargle River and its tributaries in Dublin, Ireland (Ballesté et al. 2020). Interestingly, MST was even used to test for fecal contamination in fresh produce like tomatoes, jalapeño peppers, and cantaloupe and to even determine the sources of the fecal contaminant (Lee and Lee 2012; Ravaliya et al. 2014). This showed that MST could also be used in other aspects of research outside its usual or traditional context, which is for assessing environmental water fecal pollution. These studies conducted globally show the scale at which MST has been successfully used to monitor fecal pollution, particularly in developed nations. Unfortunately, its application in many developing countries is still limited (Somnark et al. 2018a).

MST methods are either library-dependent (LDM) or library-independent (LIM) and are analyzed either based on their phenotypic and/or genotypic characteristics, as shown in Table 2.

Table 2: Techniques under library-dependent and library-independent MST methods

Library-dependent		Library-independent	
Culture-based			Culture-independent
Phenotypic (Biochemical)	Genotypic	Phenotypic or Genotypic	Molecular
• Antibiotic resistance (ARA and MARA) • Carbon utilization • FAME profiling	• Rep-PCR • RAPD • AFLP • PFGE • Ribotyping • DGGE • LH-PCR • T-RFLP	• Bacteriophage	• Host-specific viral PCR • Host-specific bacterial PCR

LDM entails creating a comprehensive database of isolates from known sources that will serve as the basis for cross-referencing. Firstly, fecal samples are collected from potential or suspected sources (i.e., humans, cattle, swine, etc.) of water contamination. Then, bacteria from feces are isolated and subjected to either phenotypic or genotypic analysis to create a pattern referred to as a fingerprint used for cross-referencing. Phenotypic analysis may include antibiotic resistance analysis (ARA), multiple antibiotic resistance analysis (MARA), carbon source utilization analysis, and FAME profiling. Conversely, genotypic analysis includes patterns in repetitive DNA sequences (Rep-PCR), random amplification of polymorphic DNA (RAPD), amplified fragment-length polymorphism (AFLP), pulse-field gel electrophoresis (PFGE), ribotyping, denaturing-gradient gel electrophoresis (DGGE), length heterogeneity PCR (LH-PCR), and terminal restriction fragment-length polymorphism analysis (T-RFLP) (Hagedorn et al. 2003; Meays et al. 2004; Duran et al. 2006; Ballesté and Blanch 2010). However, a major limitation in LDM is that it is highly tedious to make a reliable database because it requires numerous isolates to be tested and even then, the minimum number of isolates needed to construct a reliable library has not been fully established (Ahmed et al. 2005).

Alternatively, LIM does not require the construction of a database but depends on the concept that bacteria or viruses taken directly from the environment come from species-specific host/s or sources of fecal contamination; thus, a library is not needed for cross-referencing. A significant advantage of LIM, as opposed to LDM, is that it saves time and resources as it removes the need to construct a library starting with the isolation, purification, and culture of microorganisms. In LIM, detection of MST-specific markers (or simply MST markers) is used. There have been various MST markers developed to discriminate human fecal from other fecal animal sources like viral MST markers (Wong et al. 2012), bacterial MST markers, and recently, the use of mitochondrial DNA (mtDNA) as MST markers (He et al. 2016). The most common type of MST marker is the use of *Bacteriodes* spp. as indicators of the type of host animal serving as the source of fecal pollution. *Bacteroides* MST markers are designed to target specific diagnostic sequences within the *Bacteroides* 16S rRNA gene present in feces from different animals (Layton et al. 2006).

Bacteroides-based MST markers

Bacteroides-based MST marker is the most extensively used MST marker. Due to the anaerobic nature of *Bacteroides*, it has minimal capacity for growth outside the GIT of its host. This makes it ideal for MST because it provides a more accurate count in terms of the degree of fecal pollution. It has shown a high level of host specificity as *Bacteroides* adapt to the GIT conditions of its host and has even co-evolved with its host species (Bernhard and Field 2000). Also, the traditional FIB only represents less than 2% of the gut microbiota. FIB can remain viable and multiply in environmental waters, giving a false alarm of fecal pollution (Zheng and Shen 2018). Lastly, there is a strong positive correlation that the presence of *Bacteroides* also indicates the presence of fecal pathogens like *E. coli*, *Salmonella,* and *Campylobacter,* as shown in Table 3, as opposed to detecting the presence of traditional FIB that does not show a similar correlation. Therefore, due to all those characteristics, many LIM are designed to target specific sequences within the *Bacteroides* 16S rRNA gene to discriminate the different sources of contamination by PCR. Some of the known *Bacteroides*-based MST markers are shown in Table 4.

Table 3: Studies reporting strong positive correlation between the presence of *Bacteroides* and the presence of fecal pathogens

Analysis	Studies
Bacteroides and fecal coliform	Schriewer et al. 2010; Villemur et al. 2015
Bacteroides and *Escherichia coli*	Ahmed et al. 2008; Mauffret et al. 2012; Nshimyimana et al. 2014
Bacteroides and enteroviruses	Noble et al. 2006; Sauer et al. 2011
Bacteroides and *Enterococcus*	Eichmiller et al. 2013; Gordon et al. 2013
Bacteroides and *Salmonella, Campylobacter*	Schriewer et al. 2010; Stea et al. 2015

Bacteroides and *Giardia, Cryptosporidium*	Staley et al. 2012; Marti et al. 2013

Table 4: Known *Bacteroides*-based MST markers and its target host

Specific target host	MST marker/s
Human	*HF183* (Bernhard and Field 2000)
	HuBac (Layton et al. 2006)
	BacHum (Kildare et al. 2007)
	BacH (Reischer et al. 2007)
	HumM2 (Shanks et al. 2009)
	HumM3 (Shanks et al. 2009)
Pig	*PigBac-1* and *PigBac-2* (Okabe et al. 2007)
	Pig-1-Bac and *Pig-2-Bac* (Mieszkin et al. 2009)
Cow	*BacCow* (Kildare et al. 2007)
	BoBac (Layton et al. 2006)
Dog	*BacCan* (Kildare et al. 2007)
Horse	*HoF597* (Dick et al. 2005)
Muskrat	*MuBa01* (Marti et al. 2011)
General Ruminant	*Rum-2-Bac* (Mieszkin et al. 2010)
	BacR (Reischer et al. 2006)
Chicken	*ChickenBac* (Kobayashi et al. 2013)
Duck	*DuckBac* (Kobayashi et al. 2013)
Canada Goose	*CGOF1-Bac* (Fremaux et al. 2010)
	CGOF2-Bac (Fremaux et al. 2010)
General Feces	*AllBac* (Layton et al. 2006)

The effectivity of MST and its *Bacteroides*-based markers have been tried and tested in several research globally since their development. *HF183* gene marker was used as a tracer in discriminating between human and ruminant sources of fecal pollution in New River, Pasco County, Florida, USA (Chase et al. 2012), in Lake Pontchartraine, Louisiana, USA (Xue et al. 2018), in Nijo River, Kenya (Jenkins et al. 2009), in Danube River (Kirschner et al. 2017) and Daoulas River catchment, Britanny, France (Mauffret et al. 2012). It was also used in determining whether sand and other submerged sediments in the waters of Lake Superior, Minnesota, USA can also serve as a reservoir of fecal pollution and thus can be an alternative source for MST sampling other than water samples (Eichmiller et al. 2013). Conversely, *HF183* was the MST marker used to establish the positive correlation of MST markers with enterococci in the Gulf of Mexico waters (Gordon et al. 2013). *HuBac* marker was used in the coastal water of Puerto Rico and Trinidad and Tobago to assess fecal pollution (Bachoon et al. 2010). In Ireland, the human MST marker *BacHum* was used to assess the water quality of Mattock River catchment (Flynn et al. 2016), Ware and Oyster Creek, North Carolina, USA (Gonzalez et al. 2012), Sava River Basin that borders three countries such as Serbia, Bosnia and Herzegovina, and Croatia (Vrzel et al. 2016), and Monterey Bay, central California coast, USA (Schriewer et al. 2010). *BacH* was developed in 2006 to detect and discriminate human fecal pollution in the Northern Alps, Austria (Reischer et al. 2006). In Israel, *BacH* marker was the human MST marker used to assess the water quality of Karst springs found in the Sea of Galilee (Ohad et al. 2015), alpine springs in Austria (Reischer et al. 2007), coast of Odisha, Bay of Bengal (Odagiri et al. 2015) and in Cornwalis watershed, Nova Scotia, Canada (Ridley et al. 2014).

Pig-2-Bac is often used to detect and source track pig fecal pollution (Bae and Wuertz 2015). *Pig-2-Bac* was the pig marker used to assess the freshwater quality of Taige and Taihu Lake in China (He et al. 2016), in Danube River (Kirschner et al., 2017), Daoulas catchment, France (Mieszkin et al. 2009; Mauffret et al. 2012), in Sava River Basin in Central Europe (Vrzel et al. 2016), and Tha Chin watershed in Thailand (Somnark et al. 2018b). MST marker assessment showed that *BacCow*, as the cow MST marker, was used for India (Odagiri et al. 2015) and Thailand (Somnark et al. 2018b). It was also used to identify fecal sources of contamination in the Njoro River watershed, Kenya (Jenkins et al. 2009), surface waters of the central California coast, USA (Schriewer et al. 2010), and coastal waters in Odisha, India (Odagiri et al. 2015). Alternatively, *BoBac* cow MST marker was used to assess the NPS of fecal pollution in stream waters of Brandywine Creek that pass by the states of Pennsylvania, and Delaware, USA (Duris et al. 2011), Harris Neck estuarine marshes in Georgia, USA (Markand et al. 2011), pond waters, the primary source of water for hygiene purposes in Bangladesh (Knappett et al. 2011), and sediment water in Saginaw Bay, Michigan, USA (Oun et al. 2017). Cow MST marker *BacBov* was used to assess the water quality in the Grand River watershed, southwestern Ontario, Canada, and in Mattock River catchment that supplies water to 7% arable land in Ireland (Flynn et al. 2016). *Rum2Bac* is a specific marker for detecting fecal contaminants of generally all ruminants that includes domesticated animals such as cows, carabaos, sheep, and goats and nondomesticated ones like giraffes and elks. Ruminants are mammals composed of four gastric compartments namely: rumen, reticulum, omasum, and abomasum. The first three mentioned stomachs are collectively known as pro-ventriculus as they share a common function. They contain bacteria that break down ingested cellulose from grasses that ruminants usually eat (Teixeira et al. 2009). Thus, *Rum2Bac* is commonly used to screen for the presence of feces from other ruminants other than that of cows. *Rum2Bac* has been used in France in their development of MST tools to identify the origins of fecal pollution in bathing and shellfish harvesting waters (Gourmelon et al. 2010; Mauffret et al. 2013) and in assessing the water quality in Daoulas catchment, Justicou, Pen an Traon, and La Fresnaye, Britanny, France (Mauffret et al. 2012; Jardé et al. 2018). *Rum2Bac* (with other markers) was used in a study conducted in South Fork Broad River, Georgia, USA, to show the relationship between MST markers and FIB. They could establish a positive correlation between Shiga-toxin, *Campylobacter,* and *Rum2Bac* MST marker (Bradshaw et al. 2016).

BacCan is the only known/developed *Bacteroides*-based MST marker for dogs. It is the MST marker used to determine the water quality and source track the waters of Ningi Creek, Queensland, Australia (Ahmed et al. 2008), coastal surface waters, central California, USA (Schriewer et al. 2010), different dog fountains and ponds across Calgary, Alberta, Canada (Tambalo et al. 2012); coast of Odisha, part of Bay of Bengal, India (Odagiri et al., 2015), and Gulf of Nicoya, Costa Rica (Symonds et al. 2017). In 2011, an MST marker for muskrat (*Ondatra zibethicus*) was developed to determine the presence and extent of the muskrat's fecal pollution contributions to South Nations River, Canada. *MuBa01*, when tested, showed a sensitivity of 66% and specificity of 100% (Marti et al. 2011). Muskrats are wide-ranging semi-aquatic mammals common to North America and considered a normal and very common feature of the wetlands. They have very high fecundity, producing 2–3 offspring per year. Additionally, muskrats born in that year can also breed within that year due to their fast growth (Sadowski and Bowman 2021).

AllBac is primarily a screening or preliminary MST marker to first check the presence (if any) of fecal contamination in a body of water. It is the initial test before performing or using more host-specific MST markers. Such as in the research by Stapleton et al. (2009), in which they used *AllBac* to first detect fecal contamination in the recreational bathing waters in the UK. A similar study was conducted in France, but other than bathing waters, it also included shellfish harvesting waters and the Daoulas catchment (Gourmelon et al. 2010; Mauffret et al. 2012). The same was done in rural and urban watersheds in Canada by using *AllBac* to monitor fecal pollution (Ridley et al. 2014; Stea et al. 2015), in the Danube River (Mayer et al. 2016; Kirschner et al. 2017), in the Sava River Basin, Central Europe

(Vrzel et al. 2016), and in the beach area of Duluth-Superior Harbor, Minnesota, USA (Zhang et al. 2016). In Bangladesh, *AllBac* was used to generalize that there are other sources of fecal contamination other than humans and cows in several pond waters used for hygiene purposes (Knappett et al. 2011).

As can be seen, most of the markers are for mammalian fecal samples. However, *Bacteroides* has been identified in other warm-blooded and cold-blooded vertebrates such as ducks, geese, frogs, and toads. Unfortunately, for avian MST, only three MST markers have been developed. Many migratory waterfowls such as ducks and geese and non-migratory birds like chickens are also carriers of pathogens. Hence, the three avian-specific MST markers developed are insufficient in better monitoring and managing water pollution. After development, *ChickenBac* and *DuckBac* were immediately used to check the water quality by MST in Kamogamo River, Toyohira River, and Oono pond, Hokkaido, Japan, and showed an abundance of fecal contamination from ducks (Kobayashi et al. 2013). Alternatively, Canada's geese population was estimated to be at 3 million and often occupy regions within urban settings. For that reason, the *CGOF* MST markers were developed to determine the extent of fecal pollution that Canadian geese may have contributed. True enough, using the developed *CGOF* markers, water samples from Wascana Lake detected high prevalence and abundance of *Bacteroides* markers (Fremaux et al. 2010).

However, there have been reports of a cross-reaction of *Bacteroides*-based MST gene markers with other fecal samples. There are numerous cases where several MST markers supposed to be for a specific host would vary in their specificity. The two MST markers for pigs (*Pig-1-Bac* and *Pig-2-Bac*) would usually vary in their specificity depending on the geography (Mieszkin et al. 2009; Heaney et al. 2015). Another would be among the different human associated *Bacteroides* MST markers. Although *HF183* is the most widely used, it is not always the best performing MST marker. *HF183* was identified as a high-performing marker in California, USA, and Australia. However, the MST marker *BacHum* was the better performing MST marker in Kenya and India. The 16S rRNA gene is a highly conserved region among bacteria. Thus, it is for this reason that cross-reactivity happens when this gene is amplified in MST. Therefore, it is important that marker sensitivity and specificity are established before performing actual MST research as they are the two major performance indicators of an MST marker and determine which MST marker to use (Ahmed et al. 2016).

MST sensitivity is defined as the percentage of samples from a targeted host positive for the chosen market. Likewise, the greater the sensitivity of a marker, the closer it is to 100% host sensitivity. It is empirically measured by testing a collection of fecal samples from the target host, or it is simply expressed in Equation 1, mathematically (Nshimyimana et al. 2014). Currently, there is no consensus on the number of samples, type of sample, and sample volume needed to determine the sensitivity of a marker. Unfortunately, there is also no universal benchmark for sensitivity, but a value of > 80% is acceptable for MST use (Ahmed et al. 2016). Also, sensitivity varies due to geographical variations. This means that an MST marker with high sensitivity used in a given location does not necessarily mean that it will also have an increased sensitivity if used in a different location, because it has precedence from a previous site as being a highly sensitive marker. Thus, MST marker sensitivity should always be verified in every geographic region before performing a study (Harwood et al. 2014).

$$\text{Equation 1: Sensitivity} = \left(\frac{TP}{TP + FN}\right) \times 100$$

Where: TP = true positive

FN = false negative

Conversely, specificity is the number of non-target host samples that test negative for the assayed marker and mathematically shown in Equation 2 (Nshimyimana et al. 2014). Much research worldwide shows that most MST gene markers have variable specificity in different geographic areas. Studies have shown that an MST marker specific to a particular organism would cross-react to different organism/s. Unfortunately, like sensitivity, there is no recognized standard about the number of samples for specificity testing. However, statistically, analyzing as many non-target fecal samples as possible will increase confidence (Harwood et al. 2014).

$$\text{Equation 2: Specificity} = \left(\frac{TN}{TN + FP}\right) \times 100$$

Where: TN = true negative

FP = false positive

Ultimately, sensitivity and specificity vary with geographic area and time, highlighting the need for local validation. Therefore, before conducting any MST study, it is critical to first establish sensitivity and specificity, and validate MST marker accuracy using Equation 3 (Nshimyimana et al. 2014). Moreover, since the number of samples to reliably establish sensitivity and specificity is currently not yet standardized, some recent studies have reported that between 12–20 samples is acceptable (Reischer et al. 2006; Kildare et al. 2007; Haugland et al. 2010; Ebentier et al. 2013).

$$\text{Equation 3: Accuracy} = \left(\frac{(TP + TN)}{(TP + FP + TN + FN)}\right) \times 100$$

Where: TN = true negative

TP = true positive

FP = false positive

FN = false negative

Future research avenues

Bacteroides, either as a "good" or "bad" bacterium, do not receive much attention as opposed to *Lactobacillus* and *Bifidobacterium* for being "good bacteria" and different fecal coliform bacteria as being "bad bacteria." At times, they are described simply as gut microorganisms. In Europe, the

European-wide surveillance on antibiotic resistance of *Bacteroides* is conducted annually, to determine the current state of antimicrobial resistance (AMR) among the *Bacteroides* group (Kierzkowska et al. 2020; Sóki et al. 2020). Thus, more research on the AMR of *Bacteroides* must also be conducted in other countries in a similar way that other bacteria such as the AMR of *E. coli*, *Staphylococcus,* and *Klebsiella* are being extensively monitored. Another avenue for *Bacteroides* research is on *Bacteroides* from animals. Most of the research on *Bacteroides* is human-centered. However, more than half of the world's antibiotic usage is for animal husbandry, but ironically, a meager 10% of publications on antibiotic resistance are about animals, and the rest are on humans (He et al. 2020).

There are many animals globally that contribute to fecal water pollution, and yet there are only a handful of MST markers developed. Understandably, the only MST markers made were for those that contribute large volumes of feces into the aquatic environment, such as humans and domesticated farmed animals. However, to create a long-term water conservation policy, more MST markers should be developed because other non-domesticated animals are also carriers of virulent microorganisms. Also, even among the domesticated animals, there are still many of which are without a developed MST marker like goats, sheep, and poultry like turkey.

Different kinds of migratory flying animals like pigeons, sea gulls, pelicans, herons, geese, swans, and bats have been associated as disease carriers of *Borrelia* (Lyme disease), West Nile virus (viral encephalitis), *Mycobacterium avium/genevense* (mycobacteriosis), influenza A virus (avian flu), Nipah virus, rabies virus, and SARS coronavirus. These migratory flying animals come by hundreds to thousands bringing with them pathogens. However, there are only two *Bacteroides*-based MST markers developed for migratory flying animals, which include for ducks (*DuckBac*) and for Canada geese (*CGOF*) (Reed et al. 2003; Calisher et al. 2006). Therefore, more MST markers should be developed for migratory flying animals.

Another aspect that can be enhanced is the accuracy of the MST markers developed. Note that diet serves as a strong evolutionary pressure on the gut microbiome. For example, *DuckBac* marker was developed using wild migratory ducks; hence, it may or may not be sensitive or specific enough if it is used for farmed ducks due to obvious differences in the diet of wild and farmed ducks. Thus, this also brings the issue of marker cross-reactivity. Therefore, it may be time to use a different approach in developing *Bacteroides*-based markers to increase specificity and sensitivity, like using other genes (housekeeping genes, virulence genes, antibiotic resistance genes).

In conclusion, *Bacteroides* are an interesting group of bacteria found in the gut of many animals occupying an important ecological niche of the gut microbiome. Most of their attributions are on their role in the gut microbiome. However, their use on MST has now become a critical tool in helping to curb the problem of fecal water pollution. Lastly, it is noticeable that most of the countries that perform MST are highly developed countries like Canada, the USA, China, Japan, and France. After emphasizing the advantage of MST over the traditional FIBs, it is time for other countries, through their scientists, to explore the use of MST in monitoring water pollution. There is an imminent need for collaboration and cross-disciplinary research between countries' environmental managers, microbial ecologists, and government environmental policymakers to transfer and share the MST technology so that its use can be a norm.

ACKNOWLEDGMENTS

This study was financially supported by the National Research Council of the Philippines (Project No. E-249) and the Philippine Council for Industry, Energy and Emerging Technology Research and Development.

CONFLICT OF INTEREST

The authors declare that there is no conflict of interest.

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