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Gut microbiota diversity according to dietary habits and geographical provenance

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ABSTRACT

The gut microbiota is an ecosystem including all bacterial species that permanently colonize the gastro intestinal tract and a large number of other microorganisms from the environment. These millions of microorganisms may be unbalanced by a number of external and internal factors. The aim of this review is to summarize recent findings on animal and human studies on the effect of dietary and geographical provenance on gut microbiota-composition. It includes results on the influence of dietary products, type of diet (e.g. vegetarian and omnivorous subgroups), and geographic areas, as well as differences between populations within the same area. In animal models, most results showed contradictory effects on modulation of the intestinal microbiota within the same phylum, while in human studies, dietary products, such as fat, are often reported as being associated with an increase in Bacteroidetes and Actinobacteria species and a decrease in those in the Firmicutes and Proteobacteria phylum. The results of different studies showed that the omnivorous group has a higher diversity of bacteria compared to vegetarians. Gut microbiota composition differs widely between different areas and between different ethnic groups within the same area. However, a higher diversity of bacteria species was encountered in the African population. The conclusions highlight that gut microbiota composition differs according to diet and eating habits which are closely correlated to geographical location suggesting therefore, the need for more in-depth research, looking at ethnic diversity and eating habits.

Introduction

The gut microbiota is an ecological community of symbiotic, commensal and pathogenic microorganisms [1]. This microbial ecosystem includes many bacterial species which permanently colonize the gastrointestinal tract as well as a large number of microorganisms such as Archaea, viruses, parasites and fungi that come from our environment [2]. The number of these microorganisms can reach 10^{12}–10^{14} in the colon, making gut microbiota one of the most densely populated communities, far exceeding that of the soil, the subsoil, and the oceans [3]. Methods for analyzing the composition of microbial communities have progressed rapidly over the past ten years, mainly due to developments in molecular tools, and particularly next generation sequencing [4]. Nevertheless, as the pure culture of microorganisms remains an essential step towards elucidating their pathogenic role [5], a renaissance of culture methods [6,7], favored by the advent of Matrix Assisted Laser Desorption/Ionization Time-of-Flight Mass Spectrometry (MALDI-TOF), a rapid and effective identification tool [8], has recently been observed. Gut microbiota play an important role in the normal functioning of the host organism [9]. In a healthy human adult, the gut microbiota is dominated by two phyla, Firmicutes (which includes mainly *Clostridium*, *Enterococcus*, *Lactobacillus* and *Faecalibacterium* genera) and Bacteroidetes (which includes notably *Bacteroides* and *Prevotella* genera). The others phyla, including Actinobacteria (mainly *Bifidobacterium*), Proteobacteria, Verrucomicrobia and Euryarchaeota, are represented in lower concentrations [10]. Subsequent changes in the microbiota are very important for maintaining host health throughout life. The first microbial inoculate consist of maternal microbiota, and from birth to the first three to five years of life, microbial diversity increases and converges toward adult-like microbiota [11]. After childhood, the microbiota becomes a stable system throughout adulthood, although long-term changes resulting from diet, lifestyle,

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gastrointestinal infections, antibiotic treatments or surgery [9], as well as geographical provenance [12,13], can modify the composition of microbiota, decreasing or increasing the bacterial diversity. This paper reports differences in the composition and diversity of the gut microbiota in relation to food products, dietary habits and geographical origin.

Food products affecting gut microbiota diversity

Our dietary habits are based on foods, usually of plant or animal origin, that contain essential nutrients for our bodies, such as proteins, fats, carbohydrates, vitamins and minerals that can be ingested and assimilated for producing the energy required for growth and life. Diet is one of the most important factors that influence the composition and diversity of the intestinal microbiota [9]. Changes in microbiota composition can be due partly to the microorganisms established in the food that we eat but also to dietary behavior and lifestyle. Thus, the gut microbiota can be modulated by changing eating habits, modifying dietary components (fats, proteins and carbohydrates), introducing probiotics (living microorganisms that have an effect on host health), and prebiotics (ingredients which are selectively fermented and which modulate changes in both the composition and activity of the gut microbiota) [14] (Fig. 1). The types and frequency of food consumed can vary according to dietary habits (such as vegetarian and omnivore) [15,16]. Information on the associations between diet and the diversity of the microbial community vary as researchers complete assessments of the intestinal microflora and strive to find more detailed taxonomic information through DNA sequencing [17]. Most studies on the influence of dietary products in microbiota diversity have been experimental and are based on animal models (e.g. mice) and this data still needs to be validated in human populations [14]. Human studies on the influence of diet on gut microbiota diversity are mainly based on the abundance or lack of the three main dietary components: fats, carbohydrates and proteins. These dietary products serve as an energy source for the microorganisms which compose the intestinal flora and have a profound impact on the gut microbiota [4]. However, most differences in gut microbiota appear to be limited to the phylum and genus levels rather than species [14].

Influence of food products in animal models

Diets rich in carbohydrates or fat

Carbohydrates are one of the major classes of biologically essential organic molecules found in all living organisms. They are the most abundant organic compounds in most fruits, vegetables, legumes and cereals, and are one of the main types of food products that provide an important energy source for the host and gut microbiota [18]. Three types of carbohydrates, resistant starches, non-starch polysaccharides, and oligosaccharides, are non-digestive and reach the gut. Their fermentation, specifically the fermentation of non-digestible carbohydrates, is an important activity of the gut microbiota, providing energy and driving the carbon economy of the colon [19]. Fibers are another type of plant-based carbohydrate composed of complex, non-starch carbohydrates and lignins that are not digestible in the human small intestine but can be completely or partially fermented in the large intestine [20]. Fats are one of the three main macronutrients, along with carbohydrates and proteins, and are found in meat, poultry, nuts, milk products, butters and margarines, oils, lard, fish, grain products and salad dressings. It has been demonstrated that a high fat diet leads to a decrease in *Eubacterium rectale* and *Blautia coccoides* (Firmicutes phylum) and *Bacteroides* spp. from the Bacteroidetes phylum [21]. Turnbaugh et al. observed a bloom in a single uncultured clade within the *Mollicutes* class of the Firmicutes, by assessing the consumption of a prototypic western diet (high-fat/high-sugar) that induced obesity in mice. The authors suggested that the increase in *Mollicutes* might reduce

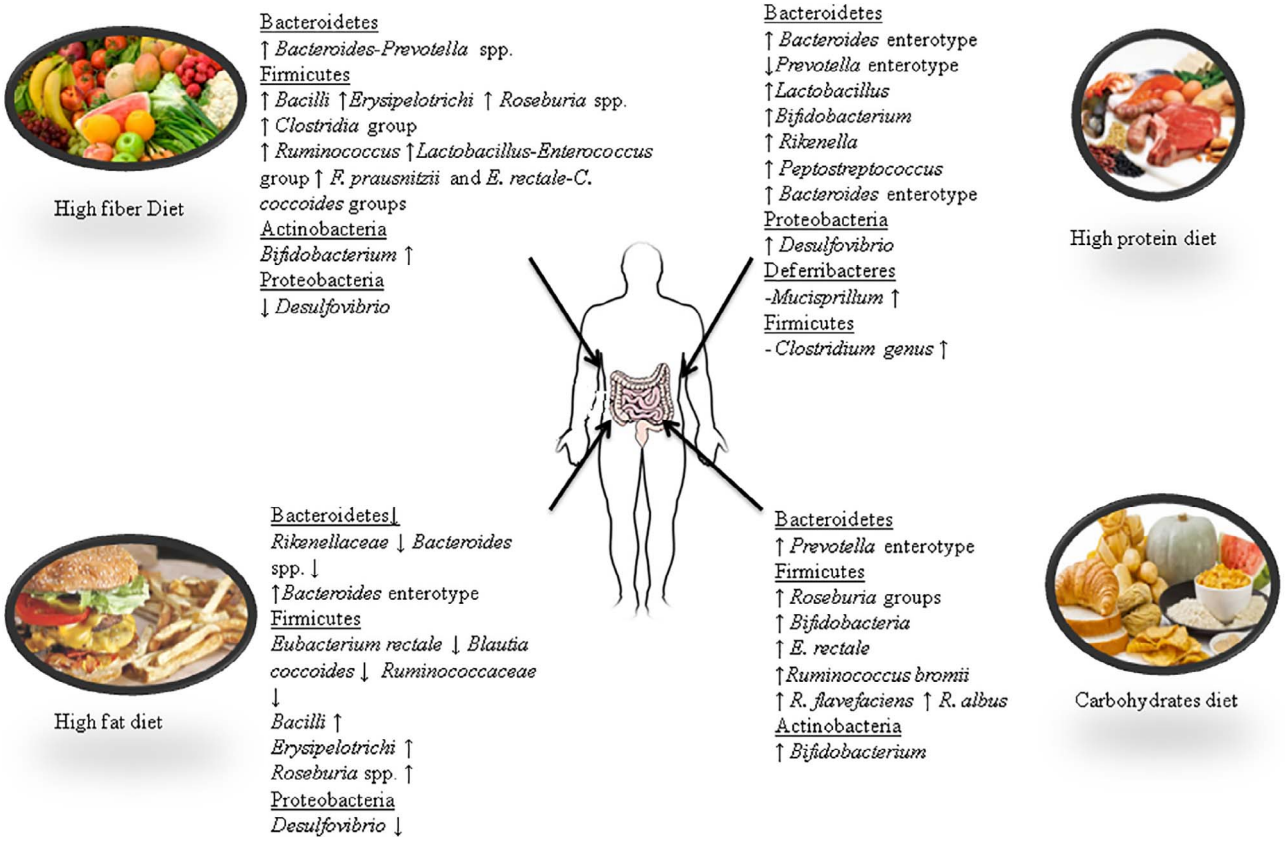

Fig. 1. Influence of the main dietary components in gut microbiota composition.

microbial diversity, including a reduction in the relative abundance of the genus *Bacteroides* [22]. The same authors demonstrated in another study that when animals were switched from a low fat/fiber rich plant diet to a high fat/high sugar diets, they experienced a significant increase in *Bacilli* and *Erysipelotrichi* from the Firmicutes phylum and a significant decrease in members of the Bacteroidetes phylum. These results differ from those of Hildebrandt et al. who compared wild type and resistin-like molecule beta/FIZZ2-deficient mice and assessed the influence of diet on microbiome composition. The authors showed that a high-fat diet decreased the number of gut Bacteroidetes and increased the number of Firmicutes (*Clostridia group*) and *Proteobacteria*, mainly species from the Delta-Proteobacteria family, genus *Desulfovibrio* [23]. Daniel et al. measured the change in caecal bacterial communities in mice which were fed a carbohydrate or high-fat (HF) diet for 12 weeks by high-throughput 16S ribosomal RNA gene sequencing. The high-fat diet caused shifts in the diversity of dominant gut bacteria and caused a decrease in species of the *Ruminococcaceae family* and an increase in those of *Rikenellaceae* [24]. De Wit et al. studied the influence of fat-type from oils (palm, olive and safflower) on mouse microbiota composition by analyzing 16S rRNA of fecal microbiota using a phylogenetic microarray called the MITChip. The results showed that a diet which is rich in fats from palm oil leads to significant changes in the composition of the microbiota by increasing the ratio of Firmicutes to Bacteroidetes and the abundance of *Bacilli* and *Clostridium* cluster XI, XVII and XVIII, reducing the diversity of microbiota [25].

Proteins

Dietary proteins are found in foods such as meats, poultry, fish, meat substitutes, cheese, milk, nuts, and legumes in smaller quantities and in starchy foods and vegetables. They are an important part of a balanced diet [26]. High animal protein intake and a variety of amino acids are highly associated with the Bacteroides enterotype while the Prevotella enterotype presents the reverse association for these groups of amino acids but is associated with high values of carbohydrates and simple sugars [23]. In an experimental study, Sprong et al. quantified the fecal excretion of rats fed with a cheese whey protein isolate or casein, supplemented either with threonine or cysteine. The authors noted significant increases in the numbers of *Lactobacilli* and Bifidobacteria in fecal microbiota [27]. In another study, McAllan et al., used high throughput DNA sequencing and reported that mice fed with increased doses of whey protein isolate presented a significant increase in *Lactobacillus*, *Bifidobacterium*, *Rikenella*, *Peptostreptococcus*, *Desulfovibrio* and *Mucispirillum* genera but a significant decrease in *Clostridium*. The authors reported that the effects of whey protein isolates in the composition of the gut microbiota of mice were dose-dependent [28].

Prebiotics

Introducing prebiotics to a particular diet may induce changes in gut microbiota composition. In an experimental model, Neyrinck et al. fed mice with a control diet (CT), a high fat (HF) diet, or a HF diet supplemented with wheat Arabinoxylan (10%) for a period of four weeks. The quantitative polymerase chain reaction (qPCR) analyses of different bacterial groups showed that the HF diet induced a drop in *Roseburia* spp. and B*acteroides-Prevotella* spp. compared to the CT. However, the addition Arabinoxylan induced a significant increase in *Bacteroides–Prevotella* spp. and *Roseburia* spp. as well as a marked increase in caecal Bifidobacteria content, in particular *Bifidobacterium animalis lactis* [29]. Mujico et al. used qPCR to investigate the ability of an oleic acid-derived compound (S1) and a combination of n-3 fatty acids (S2) to modulate the gut microbiota composition in high fat diet (HFD)-induced obese mice. The authors demonstrated that the HFD led to a modification in the gut microbiota. However, S1 supplementation clearly increased total bacterial density and restored the proportions of bacteria that had increased (i.e. *Clostridial* cluster XIVa and Enterobacteriales) or decreased (i.e. *Bifidobacterium* spp.) during HFD feeding. In contrast, S2 supplementation significantly increased the quantities of Firmicutes (especially the *Lactobacillus* group) [30]. Other prebiotics, such as fructans, have been linked with changes in the gut microbiota, resulting in positive health benefits. In animal models, it has been demonstrated that the administration of fructans leads to an increase in potentially beneficial species, notably *Bifidobacterium* spp. (Phylum: Actinobacteria) and species in the Bacteroidetes phylum (2).

Salt effect

Few studies have investigated the impact of a salty diet on the composition of gut microbiota. Wilck et al. showed that an increase in dietary sodium chloride alters gut microbiome composition. Indeed, by Pyrosequencing the V4 region of the 16S rRNA gene, the authors demonstrated that a high-salt diet (4% sodium +1% in drinking water) created a distinct gut microbiome composition compared to a purified normal salt-diet (0.5% sodium). While a normal diet induced a gut microbiome mostly composed of operational taxonomic units from the Bacteroidetes phylum (70% of reads), the authors showed that a high-salt diet caused a shift in relative abundance to other phyla (increase in the Firmicutes to Bacteroidetes ratio). In addition, an increase in the genus *Allobaculum* was significantly higher after high-salt feeding [31]. The salt effect on gut microbiota was also studied by Mell et al., who identified the fecal microbiota composition of Dahl salt-sensitive (S) and resistant (R) rats by using 16S rRNA gene sequencing to targeted the variable regions V1–V3. Their findings showed that rats are not identical in their fecal microbiota compositions. Indeed, bacteria of the phylum Bacteroidetes were significantly higher in the S rats compared with the R rats, while Proteobacteria showed the opposite association. All other phyla, including Firmicutes, were not altered between S and R rats, although a family within the phylum Firmicutes, *Veillonellaceae*, was significantly higher in the S rats compared with the R rats. The same difference was found in the family of bacteria under the phylum Bacteroidetes, known as S24-7 [32].

Short and long term-diet modifications

Heinritz et al. examined the effect of two different diets on microbial composition, using pigs as a model for humans. Eight pigs were fed a low-fat/high-fiber (LF) or a high-fat/low-fiber (HF) diet for seven weeks. Dietary effects on fecal microbiota were assessed using qPCR, DNA fingerprinting and metaproteomics. The authors showed that gene copy numbers of *Lactobacillus*, Bifidobacteria and *Faecalibacterium prausnitzii* were significantly higher in the LF pigs, while *Enterobacteriaceae* were more abundant in the HF pigs [33]. In general, in animal models, most results show contradictory effects on the modulation of the intestinal microbiota at species level within the same phylum.

Influence of dietary products in human

Fat and fiber

In humans, it has been reported that Bacteroidetes and Actinobacteria have a positive association with fat but a negative association with fibers, whereas Firmicutes and Proteobacteria show the reverse association [34]. However, it has been demonstrated in overweight or obese men and women that high-fat diets are not associated with species of the *Bifidobacterium* genus of the Actinobacteria phylum [35]. In an in vitro colonic model, Shen et al. demonstrated that the increase in dietary fiber led not only to a significant growth of species from the *Bifidobacterium* genus and *Ruminococcus* and *Lactobacillus-Enterococcus* groups, but also a significant increase in the numbers of *F. prausnitzii* and *E. rectale-Clostridium coccoides* groups from the *Clostridial* cluster XIVa [36]. This modulation at the species level of the gut

microbiota by dietary fibers is also reported in recent studies using 16S rRNA gene sequences to investigate the potential of specific non-digestible dietary carbohydrates (apple pectin and inulin) to modify the gut microbiota. The results showed highly specific enrichment of particular bacterial operational taxonomic units (OTUs). Indeed, two OTUs derived from *Bacteroides* related to *Bacteroides uniformis* and *Bacteroides caccae*, became strongly enriched in the inulin fermentors, while six different OTUs, namely *Bacteroides cellulosilyticus/intestinalis, Bacteroides eggerthii*, *Bacteroides ovatus*, *Bacteroides stercoris*, *Bacteroides thetaiotaomicron* and *Bacteroides vulgatus/dorei*, became enriched in the pectin fermentors [37].

Carbohydrates

Changes in the amount and/or type of dietary carbohydrates can have a profound and rapid influence on the composition of the human gut microbiota [38,39]. Walker et al. compared two groups of subjects provided with a fixed dietary intake. One consisted of a meal with high RS, containing added type III RS and the other consisted of a meal of high NSP, containing additional wheat bran, for a three-week period. At the phylum level, no significant effect of diet was observed on the fecal microbiota proportions of Bacteroidetes, Firmicutes, Actinobacteria and Proteobacteria; however a finer taxonomic analysis showed a significant increase in the proportions of *E. rectale* and *Ruminococcus bromii* (*Roseburia* groups) in the RS diet. Further supplementary analysis by qPCR for these bacterial groups including relatives of *R. bromii, Ruminococcus flavefaciens* and *Ruminococcus albus*, revealed a significant increase of around 4.5-fold on the RS diet compared to the NSP diet. They suggested that increasing the levels of non-digestible carbohydrates can increase levels of bacterial species in the Firmicutes phylum [38]. These findings were reported by Ducan et al., who showed that a decrease in non-digestible carbohydrates in the diet significantly reduces the levels of *Roseburia* spp. and *E. rectale* subgroup of cluster XIVa from the Firmicutes phylum and also the level of *Bifidobacterium* from the Actinobacteria phylum [40].

Short and long term-diet modification

Short-term changes in dietary patterns can have some influences on intestinal microbiota composition, while long-term dietary changes can cause substantial modifications to microbiota composition [38,39]. Wu et al. carried out a short-term controlled-feeding experiment in ten subjects who were randomly allocated a high-fat/low-fiber or low-fat/high-fiber diet and used16S rDNA analysis to investigate the stability of the gut microbiome. The findings showed that a short-term identical diet does not have an influence on the *Bacteroides* and *Prevotella* enterotypes, while a long-term diet, particularly one encompassing proteins, animal fats and carbohydrates, was strongly associated with *Bacteroides* and *Prevotella* enterotypes, respectively [38]. David et al. used 16S rDNA pyrosequencing to study the effects of short-term diet on the microbiota of six healthy American volunteers over five consecutive days after being administered two different diets: an animal-based diet (rich in meats, eggs and cheeses) and a plant-based diet (rich in fruits and vegetables, legumes and grains). The first led to a decrease in the levels of Firmicutes, in particular *Roseburia* spp., *E. rectale* and *R. bromii,* capable of metabolizing plant polysaccharides, while the second increased the abundance of bile-tolerant microorganisms (e.g., *Alistipes* spp., *Bacteroides* spp. and *Bilophila* spp.) [41]. Seasonal dietary changes may also modify the composition of the gut microbiota. A study exploring the impact of lifestyle and seasonal dietary changes on Mongolian gut microbes showed that in residents of Khentii, a typical pasture area of Mongolia, who maintains a traditional nomadic lifestyle and diet, the genera *Lactobacillus, Olsenella*, *Oribacterium, Prevotella*, *Succinivibrio*, *Solobacterium* and *Escherichia coli/Shigella group* were most abundant. In contrast, the genera *Alistipes, Anaerosporobacter*, *Akkermansia, Bacteroides, Barnesiella, Butyricimonas, Coprobacillus, Coprococcus, Oscillibacter, Odoribacter, Parabacteroides, Parasutterella, Roseburia, Subdoligranulum* and *Victivall* were abundant in residents of Ulan Bator, the capital of Mongolia, whose urban lifestyle is characterized by modernization and economic development [42]. Fewer experimental studies on the effect of food products have been carried out in humans, although the results are more consistent with dietary products such as fat often being associated with an increase in species in the phylum Bacteroidetes and Actinobacteria and a decrease in Firmicutes and Proteobacteria.

Gut microbiota diversity according to dietary type

There are two major dietary groups in humans: omnivores who eat both animals and plants, and vegetarians who choose to exclude the consumption of meat. Within vegetarianism, there are different subgroups: vegetarians who do not eat meat, fish, or poultry; vegans who avoid all meat and animal products; lacto-ovo-vegetarians who include eggs, milk and milk products in their diets; pesco-vegetarians who include fish, eggs, milk and milk products [43]; semi-vegetarians who occasionally eat meat, poultry and fish; and ovo-vegetarians who avoid all meant and dairy produce but who include eggs in their diets [44]. The relationship between vegetarianism and health benefits is often difficult to demonstrate and some studies have even shown contradictory effects [45]. In modern science, research has not only focused on dietary habits [46] but also the association between dietary patterns and microbiota diversity. This relationship is increasingly studied as the result of the advent of new technologies DNA sequencing techniques. Thus, it is now possible to observe differences between vegetarian subgroups and omnivore diets [47,48]. However, the most part of the available studies in the gut microbiota compared the microbiota diversity of vegetarians or vegans or vegetarian subgroups and omnivores [10,48], but few have compared diversity between the subgroups of vegetarianism [47].

Gut microbiota diversity in vegetarian subgroups

The dominant feature of strictly vegetarian gut microbiota is the detection of a high proportion of *Clostridium* rRNA sub cluster XIVa and *Clostridium ramosum* (*Clostridium* rRNA cluster XVIII) [49]. It has also been shown that a vegetarian diet affects intestinal microbiota, specifically by decreasing and modifying the diversity of the *Clostridium* cluster IV [50]. Microbial counts of *Bacteroides* spp., *Bifidobacterium* spp., *E. coli, Enterobacter* spp., *Enterococcus* spp, *Clostridium* spp., *Klebsiella* spp. and *Lactobacillus* spp. are not significantly different between vegans and vegetarians [47]. In contrast, Ferrocino et al. used a specific culture method (Glutamate Starch Phenol Red agar) to show that counts of *Pseudomonas* spp. and *Aeromonas* spp. were significantly higher in the ovo-lacto-vegetarian group compared to vegan, while *Coliforms* and *Bifidobacterium* spp. counts were lower in the vegan group than in the ovo-lacto-vegetarian group [51].

Diversity between vegetarian groups and omnivores

Reiss et al. compared the gut microbiota composition of vegans and omnivores using qPCR analysis. They showed that Firmicutes (58.6% vs. 56%) and Bacteroidetes (39.1% vs. 39%) were the most abundant phyla in the vegan and omnivore group, respectively, while the phyla Verrucomicrobia, Proteobacteria, Actinobacteria, and Euryarchaeota accounted for minor proportions in both groups. However, significant differences between vegan and omnivore groups were observed with Proteobacteria being higher in the omnivore group and Verrucomicrobiota being higher in the vegan group [10]. Kabeerdoss et al. used real-time PCR to quantify the fecal microbiota of a group of lacto-vegetarians and omnivores, and demonstrated an increase in the *Clostridium* cluster XIVa and *Roseburia/Eubacaterium rectal* in the omnivorous group compared to the lacto-vegetarians, while the ratio of *F.*

prausnitzii was higher in the lacto-vegetarian group [52]. Zimmer et al. used a classical bacteriological isolation of the main anaerobic and aerobic bacterial genera to study the fecal microbiota composition of a group of vegetarians and vegans in comparison to an omnivorous group. The results showed that the vegetarian and vegan samples had significantly lower microbial counts of *Bacteroides* spp., *Bifidobacterium* spp., *E. coli,* and *Enterobacteriaceae* compared to the omnivorous group. On the other hand, no significant differences between the vegetarian subgroups and omnivorous group were seen for the following species: *E. coli biovars, Klebsiella* spp., *Enterobacter* spp., other Enterobacteriaceae, *Enterococcus* spp., *Lactobacillus* spp., *Citrobacter* spp. and *Clostridium* spp. [47]. Ruengsomwong et al. compared a vegetarian group (ovo-lacto vegetarians, lacto-vegetarians, ovo-vegetarian and vegans) with a non-vegetarian group and showed that the *Prevotella* genus was significantly higher in vegetarians than in non-vegetarians. In contrast, the non-vegetarian subjects showed higher numbers of Bacteroides, *C. coccoides-E. rectale* and *Bifidobacterium* groups. The *Enterobacteraceae*, *Lactobacillus*, *Bifidobacterium*, *C. coccoides-E. rectale* group and the *C. leptum* group proportions did not differ significantly between the two groups. No comparison within the vegetarian subgroups was performed, probably due to the low number (36 in total), but also to the fact that all had been vegetarians for at least three years before taking part in this study [53]. Another study comparing healthy omnivores, ovo-lacto-vegetarians and vegans, using culture methods, ribosomal RNA Denaturing Gradient Gel Electrophoresis (rRNA-DGGE) and 16S rRNA gene sequencing, showed no significant difference in bacteria counts between the three diets when considering all the culture media. However, considering each culture medium, only counts of *Pseudomonas* spp. and *Aeromonas* spp. were significantly higher in the ovo-lacto-vegetarians compared to omnivorous group. *Coliforms* and *Bifidobacterium* sp counts were lower in the vegan group than in the omnivorous group. The *Bacteroides* and *Prevotella* loads targeted on Wilkins-Chalgren Anaerobe Agar plus Gram-Negative Anaerobe Supplement, showed a significant reduction in the omnivorous group, compared to the other groups. In addition, the population of *Bacteroides fragilis* was higher in the omnivorous group. In the same study, data from the V3 region of 16S rRNA gene sequences showed that *B. salanitronis, Bacteroides coprocola* and *Prevotella copri* are associated with an omnivorous diet, while *Prevotella micans* and *Bacteroides vulgatus* were specific to the vegetarian group and *Bacteroides salyersiae* were characteristic of the vegan group. The RNA-DGGE fingerprints of the V9 region showed that *Veillonella parvula*, *F. prausnitzii* and *E. coli* were specific to the vegan, ovo-lacto-vegetarian and omnivorous groups, respectively [51]. In a recent study comparing vegetarian and non-vegetarian groups, Ruengsomwong et al. showed a low diversity in the first group with only three species, *Clostridium nexile*, *Eubacterium eligens*, and *P. copri,* being increased, whereas more diversity was noted in the second group, with the presence of *Ruminococcus torques*, *Collinsella aerofaciens*, *Escherichia*, various species of *Bacteroides*, *Parabacteroides*, *Clostridium*, and *Eubacterium* [54]. In general, higher proportions of Proteobacteria, Firmicutes (*Clostridium* cluster XIVa, *Roseburia/Eubacaterium rectal, C. coccoides-E. rectale*) Actinobacteria (*Bifidobacterium* groups) Bacteroidetes (*Bacteroides fragilis* group, *Bacteroides salanitronis, B. coprocola* and *Prevotella copri*) were reported in the omnivore group, while in the vegetarian group, an increase of Verrucomicrobia (*Verrucomicrobiota*), Firmicutes (*F. prausnitzii*), Bacteroidetes (*Prevotella micans* and *Bacteroides vulgatus*, *Bacteroides salyersiae*) were often reported (Table 1).

Table 1
Diversity of gut microbiota according to dietary types.

Microbiota assessment technique	Omnivorous	Vegetarians	Vegan	Ovo-lacto-vegetarians	References
qPCR	↑ *Clostridium* cluster XIVa, *Roseburia/Eubacaterium rectale*			↓ Decrease: *Clostridium* cluster XIVa, *Roseburia/Eubacaterium rectale*	[52]
Classical bacteriological isolation	↑ *Bacteroides* spp., *Bifidobacterium* spp., *Escherichia coli, Enterobacteriaceae*	↓ *Bacteroides* spp., *Bifidobacterium* spp., *Escherichia coli, Enterobacteriaceae*	↓ *Bacteroides* spp., *Bifidobacterium* spp., *Escherichia coli, Enterobacteriaceae*		[47]
qPCR/PCR-DGGE fingerprinting	↑ *Bacteroides* spp.	↑ *Bacteroides*-to-*Prevotella* ratio, *Bacteroides thetaiotaomicron, Clostridium clostridioforme*, and *Faecalibacterium prausnitzii* and *Clostridium* cluster XIVa			[48]
PCR-DGGE fingerprinting	↑ *Bacteroides* spp.	↑ *Prevotella* spp.			[53]
Classical bacteriological isolation, rRNA-DGGE fingerprinting	↓ *Pseudomonas* spp. and *Aeromonas sp, Coliforms and Bifidobacterium* spp. ↑ *Bacteroides fragilis*		↓ *Pseudomonas sp.* and *Aeromonas* spp., ↑ *Coliforms and Bifidobacterium* spp.	↑ *Pseudomonas* spp. and *Aeromonas* spp.	[51]
16S rDNA pyrosequencing (V6-V8 region)	↑ *Collinsella aerofaciens, Ruminococcus torques*, various species of Bacteroides, Parabacteroides,	↑ Clostridium nexile, Eubacterium eligens, and Prevotella copri			[54]

Geographical dietary diversity

Diets differ significantly around the world, due to differences in the development level of countries as well as to agricultural and cultural practices. From west to east, diets are obviously different. The Western diet is mainly followed by American and European populations. In contrast, the Eastern diet is mainly followed by the Chinese population

and neighboring countries. The key differences include, among other things, types of food, how meals are prepared, drinks, desserts, kitchen utensils, and rituals for meals [55]. The Western diet is characterized by plant-based nutrition in combination with animal products such as meat, fish, milk and eggs which are high in fat and sugar and low in plant polysaccharides [10]. The diet of people living in western countries is usually rather low in fiber and provides a high amount of fat and refined carbohydrates compared with the diet of people living in rural countries [56]. In the Eastern diet, the main meals are lunch and dinner, which usually consist of a staple such as rice or noodles, soup, and several dishes with vegetables and meat [55]. The African diet is quite similar to that of Eastern countries, as it is mainly based on local products. In general, however, Africans eat more grains, but consume less fruit per day. The main meal of the day is lunch, which usually consists of a mixture of rice, legumes, fish and, sometimes, meat [57]. Several countries around the Mediterranean have adopted a traditional food practice now referred to as the Mediterranean diet. This diet is characterized by frequent consumption of large quantities of cereals, vegetables, nuts and fruit, which are important source of fibers as well as by a low consumption of fish or seafood, white meats and eggs, poultry and dairy products [58]. However, between inhabitants within a same geographical zone and sometimes, within the same country, eating habits may differ between those living in urban or rural areas and between populations which have separate socio-cultural practices.

Diversity within different countries

Variability in dietary behavior is an understandable explanation for the strong influence which geography has on the composition of gut microbial populations [41]. It has been demonstrated that the *Bacteroides* enterotype is increased in the guts of people living in Western countries eating a western diet with high fat and protein content, while *Prevotella* enterotype is common in non-Western countries where the population consumes lots of fiber [59]. This contrast in the gut microbiota composition has also been reported by De Filipo et al., who used multiplex pyrosequencing of the V5 and V6 hyper variable regions of 16S rRNA gene to compare gut microbiota of Italian (Europe) and Burkina Faso (Africa) children. The authors reported enrichment in Bacteroidetes, Actinobacteria and *Enterobacteriaceae* (*Shigella* and *Escherichia*) in the Burkina Faso children, while Firmicutes were most present in those from Italy. In addition, the genus *Prevotella*, *Xylanibacter* (Bacteroidetes) and *Treponema* (Spirochaetes) were only found in Burkina Faso. According to the authors, this geographical difference in microbiota diversity is due to the difference in dietary patterns between the modern Western and rural African diet in Italy and Burkina Faso, respectively [60]. Nam et al., comparing the gut microbiota composition of Korean, Japanese and American subjects, showed that the amount of fecal microbial community varied from one geographical area to another. At the phylum level, Firmicutes (61.0%) were higher in the American population than in other countries (55.6%); Actinobacteria (22.1%) in Japanese people than the others (2.5%) and Bacteroidetes-rich gut microbiota (30.2 and 36.6% in Korean and Japanese subjects, respectively) than the American cohort (18.2%). At the genus level, *Bifidobacterium* (20.6%) and *Clostridium* (10.3%) showed a higher abundance in the Japanese group while the genus *Bacteroides* (30.3%) were higher in China than in other countries [61]. In another study, fecal microbial communities of US American children and adults were compared with those of Malawians and Amerindians (Venezuelan) using 16S rRNA pyrosequencing targeting the variable region V4. In this study, the authors reported significant differences in the phylogenetic composition of fecal microbiota between individuals from the three countries, with especially pronounced separation occurring firstly between US and Malawian, and secondly between US and Amerindians' gut microbiota. In general, the microbiotas of Malawian and Venezuelan inhabitants were more diverse than those living in the US [13]. The same findings were reported between Bangladeshi and American children. The microbiota of was enriched in *Prevotella Butyrivibrio* and *Oscillospira* and depleted in *Bacteroides* [62]. Grzeskowiak et al. used three methods: FCM-FISH, bacterial count and qPCR, to compare differences in the gut microbiota composition of Malawian and Finnish infants from Turku and neighboring areas in southwestern Finland. The count of *Bifidobacterium*, *Bacteroides-Prevotella*, *C. histolyticum* groups and the total number of bacteria detected by FCM-FISH was significantly higher in the Malawian infants compared to the Finnish children. The results of qPCR showed higher amounts of the *Bifidobacterium* genus group and the species of *B. longum* and *B. bifidum* in Malawian children compared to the Finnish infants. *B. catenulatum*, *C. difficile* and *A. muciniphila* species were rare in Malawian infants and bacteria belonging to the *Bifidobacterium adolescentis*, *C. perfringens* and *Staphylococcus aureus* species were only detectable in the Finnish infants [63]. Another difference between countries was reported between African children from a rural area outside the town of Empangeni in the KwaZulu-Natal Province of South Africa, compared with African Americans in the Pittsburgh area of Pennsylvania and surrounding counties with an enrichment in *Prevotella Succinivibrio* and *Treponema* in the former group [64]. Schnorr et al. explored the variation in gut microbiota of a community of hunter-gatherers in Hadza in Tanzania with those of Italian people. The authors reported a relatively higher abundance of the genus *Prevotella*, *Eubacterium*, *Oscillibacter, Butyricicoccus*, *Sporobacter*, *Succinivibrio* and *Treponema* in Tanzanian people, while in the Italians, the genus Bacteroides, *Blautia*, *Dorea*, *Roseburia*, *Faecalibacterium* and *Ruminococcus* were encountered in higher numbers. Interestingly, in the Tanzanian gut microbiota, the authors reported a relative enrichment of opportunistic bacteria species in members of Proteobacteria, *Succinivibrio* and *Treponema* genus. These differences appear to be more important as the authors reported many unclassified genera belonging to Bacteroidetes, Clostridiales and *Ruminococcaceae* in the Hadza, and others belonging to *Erysipelotrichaceae* and *Lachnospiraceae* families in the Italian gut microbiota [65]. Dehingia et al. compared the gut microbiota profile of Indian populations to those of peoples living in various geographical areas of the world. The results showed that the genus *Prevotella* was most present in Indian, Malawian, Mongolian and Venezuelan populations, while in the American, Italian and Tanzanian groups, *Faecalibacterium* was the dominant genus [66]. Gomez et al. had compared the gut microbiota composition of two Central Africa Republic ethnic groups (the BaAk and the Bantu) to that of US Americans by targeting the V1 and V3 region of the 16SRNA. The authors demonstrated overall that the gut microbiome of each African group was more similar to the other than either was to that of US Americans. Higher bacterial diversity was observed in both the BaAk and Bantu groups compared to the US Americans, with no difference between the two African groups [67]. Fecal microbiota in different European adults and elderly persons from France, Germany, Italy and Sweden were studied by Mueller et al. and showed a country difference effect. These differences were observed for the following phylogenetic groups: *Eubacterium rectale-C. coccoides*, *Bacteroides-Prevotella*, *F. prausnitzii* and *Atopobium*, especially between Germany and Italy. At the genus level, German adults had a 2–3.5-fold lower proportion of *Bacteroides-Prevotella* than those from France, Italy and Sweden. In contrast, elderly members of the Italian group showed lower proportions of these bacteria than those of the three other countries. The *Bifidobacterium* genus represented two to threefold-higher proportions of Bifidobacteria in Italian adults and elderly. At the species level, the highest proportion for *F. prausnitzii* was noted in Swedish adults. Significantly higher levels of *F. rausnitzii* were found in the Italian adults than in the elderly group, while between the French groups, no difference was found for these bacteria [68]. Overall, people living in African countries have higher gut microbiota diversity dominated by Actinobacteria (*Bifidobacterium*); Bacteroidetes (*Bacteroides-Prevotella*); Firmicutes (*C. histolyticum; Eubacterium*, *Oscillibacter, Butyricicoccus*, *Sporobacter*); Proteobacteria (*Succinivibrio, Shigella* and *Escherichia*) and Spirochaetes (*Treponema*) and depleted in only

Fig. 2. Gut microbiota diversity according to geographical areas.

Actinobacteria (*Bifidobacterium catenulatum*), Firmicutes (*Clostridium difficile, Akkermansia muciniphila*). Meanwhile, people living in Western countries such as in Europe and America, gut microbiota is enriched in Firmicutes (*Blautia, Dorea, Roseburia, Faecalibacterium*, *Ruminococcus, Oscillospira, C. perfringens, C. difficile* and *S. aureus);* Actinobacteria (*B. adolescentis* and *B. catenulatum*); Verrucomicrobia (*A. muciniphila*) and Bacteroidetes (*Bacteroides*). Interestingly, Asian people appear to have an intermediate gut microbiota diversity, with dominant bacterial species such as Bacteroidetes (*Bacteroides*), Firmicutes (*Prevotella*) encountered in some African people and in some which are particularly dominant in Actinobacteria (*B. adolescentis*), Firmicutes (*Butyrivibrio, Clostridium perfringens* and *S. aureus*), which were encountered in a large proportion in Western countries (Fig. 2).

Gut microbiota diversity within the same country

Microbiota appears to be similar in people living within the same area who are in contact with one another [13]. However, within the same country, geographical and socio-economical differences between localities may contribute to shaping the human gut microbiota [51]. In China, Kowk et al. compared a major ethnic group known as the Han, with 55 official ethnic minority groups. The 10 groups of bacteria targeted exhibited different degrees of variation across seven ethnic groups but no significant difference was observed in the *Prevotella* genus between these ethnic groups. Meanwhile, significant differences were noted for the other bacterial groups (*C. coccoides* group, *Desulfovibrio* genus, *Atopobium* cluster, *Bifidobacterium* and *Lactobacillus* genus, *Clostridium leptum* group, *Bacteroides fragilis* group, *C. perfringens* group). At the family level, the most variable group within the ethnic groups was the *Enterobacteriaceae* family [69]. A strong ethnicity and socio-economic-linked bacterial diversity was reported by Wie et al., comparing three Malawian ethnic groups (Malays, Chinese and Orang Asli) with a relatively narrow range of socio-economic discrepancy. A detailed taxonomic analysis of the composition of the gut flora showed that children in Orang Asli ethnic group harbored significantly greater *Aeromonadales*, an unclassified order affiliated to *Bacteroidetes* and genus under *Ruminococcaceae* and *Deltaproteobacteria* compared to those of the Malay and Chinese. These lineages included bacteria species that are commonly involved in degradation in the human gut of dietary fiber found in vegetables and grains that represent a larger proportion of the Orang Asli diet [70]. Greenhill et al. used qPCR to target dominant and sub-dominant groups of bacteria currently reported in the human gut microbiome of people living in highland and lowland regions in rural areas in Papua New Guinea. The results of principal coordinates analysis revealed two groups, the first including *Prevotella*, clostridia, *Atopobium*, *Enterobacteriaceae*, *Enterococcus* and *Staphylococcus*, and the second *B. fragilis*, *Bifidobacterium* and *Lactobacillus*. Differences were observed between highland and lowland participants with the former having higher numbers of most groups of bacteria detected [71]. Dehingia et al. studied the effects of ethnicity and geography on the gut bacterial profile of Proto-Australoid tribes spread across four geographical locations (Assam, Telangana, Sikkim and Manipur) of India with distinct cultures, traditions and dietary habits. The NGS-based analysis showed that the gut microbiota of tribes in Manipur had a significantly lower Firmicutes to Bacteroidetes ratio in comparison to the tribes of Telangana and Assam. On the other hand, the Actinobacteria phylum was significantly higher in the tribes from Sikkim compared to the other tribes. The proportion of *Bacteroides, Bifidobacterium*, *Clostridium*, *Enterobacter*, *Escherichia*, *Gordonibacter*, *Klebsiella Odoribacter*, *Pantoea, Parabacteroides* and *Slackia,* representing the core gut bacterial genera, varied significantly across the Indian tribes. For example, *Enterobacter, Klebsiella* and *Pantoea* were significantly lower in the Sikkim tribes in comparison to the tribes from Assam, Telangana and Manipur, while *Escherichia* was more present in the Assam tribes than in those from Telangana and Sikkim [66]. Ethnicity and socio-cultural practices could have an effect on the modulation of gut microbiota within inhabitants of the same geographical area.

Conclusion

Dietary products and the associated eating habits and geographical provenance of individuals all have an influence on gut microbiota diversity. Most studies comparing eating habits have shown that omnivorous groups have greater bacterial species diversity, probably due to the high spectra of dietary products consumed. According to

geographical provenance, people living in non-Western countries, particularly Africans, showed higher gut microbiota diversity than other areas. However, further study of individuals representing different cultural traditions and ethnic origins will allow us to observe greater diversity in the gut microbiota composition according to individual provenance. Most gut microbiota diversity is related at higher taxonomy levels, such as phylum, family and genus. For a better understanding of gut microbiota diversity at different levels, this review suggests the use of recent advances in new technologies which enable the sequencing and characterization of the human microbiome, increasingly revealing new species in the human gut.

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Conflict of interest

None to declare.

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