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DIETS AND HEALTH BENEFITS OF GUT MICROBIOTA-FERMENTED SHORT-CHAIN FATTY ACIDS: A PERSPECTIVE OF THE MALAYSIAN DIET CONTAINING PALM OIL

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ABSTRACT

A healthy diet provides a favourable environment that allows the essential bacteria to grow and ferment beneficial metabolites, short-chain fatty acids (SCFA) through various metabolic pathways. SCFA, including linear- and branched-SCFA (BSCFA) are important in regulating energy haemostasis, inflammation, and appetite. A plant-based diet is associated with increased SCFA levels and SCFA-producing bacteria that regulate nutrient metabolism. Conversely, an animal-based diet is associated with lower SCFA levels and its producing bacteria. The Malaysian dietary guidelines are in line with other healthy eating recommendations that promote vegetables and fruit intake. Very few clinical studies are available to explore the association of gut microbiota and SCFA profiles following a Malaysian diet and the detailed amount of oil consumption was not reported. The available data demonstrated that acetate, propionate, and butyrate were the most abundant SCFA, while BSCFA, isobutyrate, was less abundant in Malaysian. Firmicutes and Bacteroidetes are the predominant phyla, while Faecalibacterium *and* Prevotella *are the dominant SCFA-producing genera in Malaysian.* Prevotella *is associated with metabolic pathways for carbohydrates and fatty acids. However, more long-term cohort studies are needed to further elucidate the association between gut microbiota composition, SCFA profiles and the potential health effects of palm oil consumption in Malaysian diet.*

Keywords: dietary pattern, gut microbiota, Malaysian diet, palm oil, short-chain fatty acids.

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INTRODUCTION

A healthy diet provides a friendly environment for diverse gut microbiota compositions to ferment essential metabolomes particularly SCFA to improve gut health (LeBlanc *et al.*, 2017). In an increasingly fast-paced world, the traditional human healthy diet rich in whole grains, vegetables and fruits is quickly replaced with processed foods added with sugars, salt, food additives and preservatives which are low in nutritional value (Atzeni *et al.*, 2022). The long-term consumption of these ultra-processed foods has been associated with diet-related chronic diseases such as obesity, type 2 diabetes (T2D), and cardiovascular disease (CVD) (Kopp, 2019).

More recently, studies reported that unhealthy dietary patterns promote gut dysbiosis (Liu *et al.*, 2021; Zsálig *et al.*, 2023), which is characterised by a lower proportion of commensal bacteria (Levy *et al.*, 2017). The commensal bacteria have diverse gene families and are important in improving the efficiency of metabolic pathways for nutrient assimilation (Asnicar *et al.*, 2021; Bolte *et al.*, 2021; Tomova *et al.*, 2019; Xiao *et al.*, 2022). Gut dysbiosis has been linked to diseases such as diarrhoea, constipation, diverticulosis, irritable bowel syndrome (IBS), Crohn's disease (Priya *et al.*, 2022) and colorectal cancer (Sánchez-Alcoholado *et al.*, 2020).

The composition of the gut microbiota is generally stable, as evident that it is resilient to short-term dietary modification (Schwedhelm *et al.*,

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2018). A study has shown that an abrupt shift from a purely plant-based diet to a purely animal-based diet induced a rapid change in the gut microbiota profile but this change was promptly restored within 48 hr after discontinuing the animal-based diet (David *et al.*, 2014). Similar temporal effects of diet on gut microbiota have also been reported with a low-carbohydrate or low-fat diet (Fragiadakis *et al.*, 2020), suggesting that sustained dietary change should extend beyond 3 months (Pagliai *et al.*, 2020), which had been shown in cross-sectional studies with different populations (De Filippo *et al.*, 2010; Wu *et al.*, 2011). Long-term adherence to a diet enriched with fruits, vegetables, legumes, and grains as is the case with the Mediterranean and vegetarian diets, leads to a constant elevate in SCFA levels and cultivation of SCFA-producing bacteria such as *Prevotella copri* and *Blastocystis* spp. (Asnicar *et al.*, 2021; Gibiino *et al.*, 2021; Pagliai *et al.*, 2020). Conversely, prolonged consumption of red meat and processed foods reduces the diversity of the gut microbiota and lowers SCFA levels (Agus *et al.*, 2016) due to insufficient fibre to support the growth of gut microbiota (An *et al.*, 2021).

Dietary pattern affects the proportion of macronutrient residues, including polysaccharides from carbohydrates, peptides from proteins, and fatty acids and glycerol from fats. These residues are fermented by bacteria into a wide range of SCFA (*Figure 1*). SCFA is a group of fatty acids consisting of six or fewer carbon atoms and exists as linear or branched chain molecules (*Figure 1*). They are typically obtained from various foods such as cheese, vinegar, yoghurt, palm kernel oil and coconut oil. Among these SCFA, acetate, propionate, and butyrate are the main linear chain SCFA, and they are mainly produced through anaerobic fermentation of dietary fibre (Wang *et al.*, 2019) by saccharolytic bacteria, and through degradation of fatty acid residues by bacteria. Furthermore, a relatively small percentage of SCFA is also obtained from the fermentation of glycerol and ketone bodies such as beta-hydroxybutyrate and acetoacetate (Puchalska and Crawford, 2017). BSCFA, namely isobutyrate, isovalerate, and 2-methylbutyrate are mainly produced through the degradation of branched amino acids such as leucine, isoleucine and valine by proteolytic bacteria (Xu *et al.*, 2020a).

The Malaysian diet is unique as it offers a wide variety of foods while still ensuring a balanced nutrient intake. Palm oil is versatile and has been extensively used in Malaysia either as cooking oil or for food preparation. Palm oil has an almost equal proportion of saturated fatty acids (SFA) and unsaturated fatty acids (UFA), with palmitic acid comprising about 45%, oleic acid about 40% and linoleic acid about 10%. Palm oil can be fractionated into palm olein (liquid) and palm stearin (solid). The UFA content of palm olein increases by 5%-7% compared to palm oil. Palm

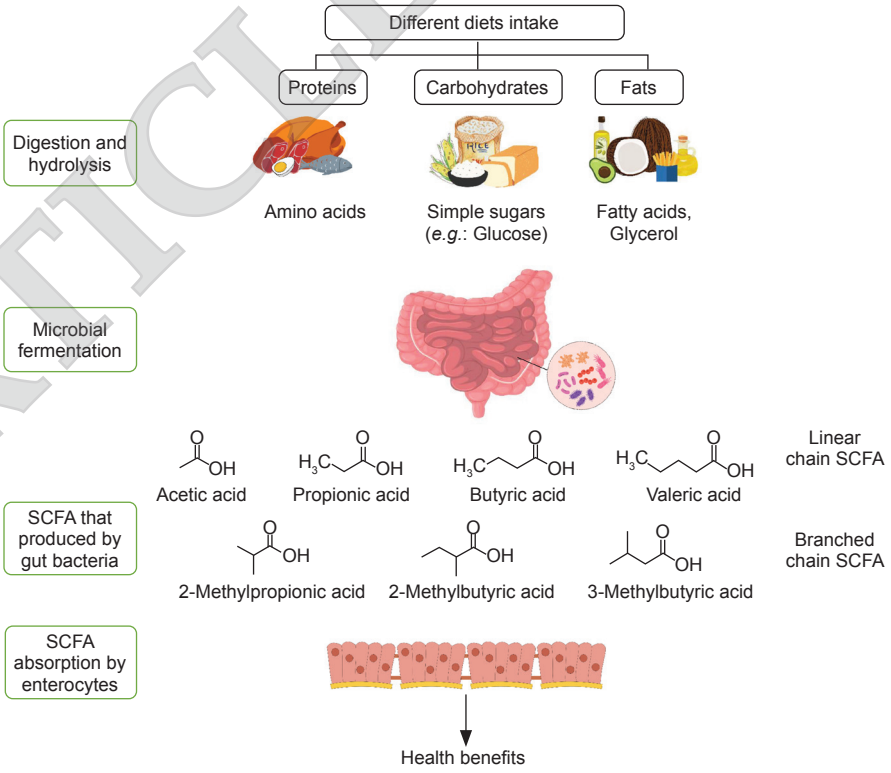


Figure 1. The roles of gut microbiota in producing SCFA after fermenting different types of food. These SCFA are absorbed into the host and provide health benefits to the host.

olein has a lower proportion of linoleic acid, which makes it very stable at high temperatures and ideal for deep frying. Additionally, solid palm stearin is often used as a hard fat and is blended with other soft oils such as sunflower or soybean oil to produce margarine, and shortening which are widely used in the confectionery and food industries (Dian *et al.*, 2017).

The effects of SCFA on health are complex. Clinical randomised and cross-over trials have been conducted to investigate the effects of different individual dietary components on the profile of the gut microbiome and SCFA produced on potential health benefits, but an understanding of these effects is still lacking. Few studies have examined the effects of dietary patterns on the composition of the gut microbiota and the long-term effects of gut-fermented SCFA in healthy adults. There is limited information on the potential benefits of the effects of habitual consumption of palm oil-containing Malaysian food on the diversity of the gut microbiota and its effects on SCFA profiles. However, given the uniqueness of Malaysian cuisine and palm oil, the bacterial profile is expected to be more complex than in diets containing only SFA or UFA oils, although some core bacterial strains are previously identified in SFA and MUFA diets (Yap *et al.*, 2022). This review explains the composition of the gut microbiota and SCFA content of people following specially designed diets that are high in certain dietary components and the long-term effects of different dietary patterns to adult health. Furthermore, this review also examines the potential effect of the Malaysian diet in this context.

SCFA AND GUT HEALTH BENEFITS

A balanced physiological level of SCFA is essential to promote gut health. The direct beneficial effects of SCFA have been demonstrated in the studies of oral administration in animals (den Besten *et al.*, 2013; Vieira *et al.*, 2012). In studies in which stable acetate-, propionate-, and butyrate- isotopes were infused into mice, different SCFA were reported to regulate different pathways (den Besten *et al.*, 2013). Approximately two-thirds of the infused propionate was used for glucose production, while a higher proportion of acetate and butyrate was involved in lipid and cholesterol synthesis (den Besten *et al.*, 2013). Acetate and butyrate are precursors in lipid metabolism and are especially important for the metabolism of fatty acids and cholesterol to yield palmitate and cholesterol. Vieira and co-workers reported that mice with ulcerative colitis in the caecal lymph nodes have reduced inflammation after oral ingestion of butyrate (Vieira *et al.*, 2012).

Later, researchers have also found that a high-fibre diet increases the levels of faecal acetate as well as butyrate and reduces pathogens or toxins such as bacterial lipopolysaccharides (LPS) (Biswas *et al.*, 2022). At physiological concentrations, butyrate regulates the expression of tight junction proteins such as cladin-2 which consequently prevents LPS (Kelly *et al.*, 2015). Otherwise, high levels of LPS in the blood will trigger the immune cells in the lamina propria of the gut, leading to an increase in pro-inflammatory cytokines and interferons which increases the risk of an inflammatory response (Rowart *et al.*, 2018). Along with acetate, butyrate also stimulates mucus secretion to prevent pathogens or toxins from adhering to the colonic epithelium (Kelly *et al.*, 2015; Pelaseyed *et al.*, 2014) and to stop the growth and specification of cancer cells (Donohoe *et al.*, 2011). Therefore, faecal butyrate concentration could be a useful preliminary biomarker for the diagnosis of colonic diseases such as diarrhoea, inflammatory bowel disease (IBD), IBS, and colon cancer.

SCFA can also suppress appetite by activating the G-protein coupled receptors (GPR) 41 and 43 on L-enteroendocrine cells in the gut and pancreas (*Figure 2*). The binding of propionate and butyrate is more selective for GPR41, while acetate and propionate have higher affinity for GPR 41 and 43 (Tazoe *et al.*, 2009) (*Figure 2*). Consequently, these activated receptors induce the secretion of gut hormones such as glucagon-like peptide 1 (GLP-1) and peptide tyrosine tyrosine (PYY) (Larraufie *et al.*, 2018) to suppress appetite, resulting in lower food intake (Byrne *et al.*, 2015).

SCFA, especially butyrate and propionate, can also ameliorate the effects of a high-fat diet on insulin resistance and obesity. These SCFA activate the AMP-activated protein kinase (AMPK) by increasing the AMP/ATP ratio and consequently trigger the expression of Peroxisome proliferator-activated receptor-gamma coactivator-1 alpha (PGC-1a). This in turn increases adiponectin secretion and, enhances glucose uptake in skeletal muscle and liver, leading to increase energy utilisation and improved insulin sensitivity (Sanna *et al.*, 2019) (*Figure 3*). Mice fed with a high-fat diet (45% calories from fat) supplemented with 5% sodium acetate lost 30% of their body weight compared to their non-supplemented counterparts (den Besten *et al.*, 2015). Moreover, SCFA particularly via the free fatty acid receptor 2 (FFAR-2) dependent pathway has been associated with an increase in leptin secretion, stimulating fatty acid oxidation (*Figure 3)* to reduce appetite and food intake (Mithieux, 2013). This concomitantly suppresses the insulin signalling to inhibit fat storage in adipose tissue.

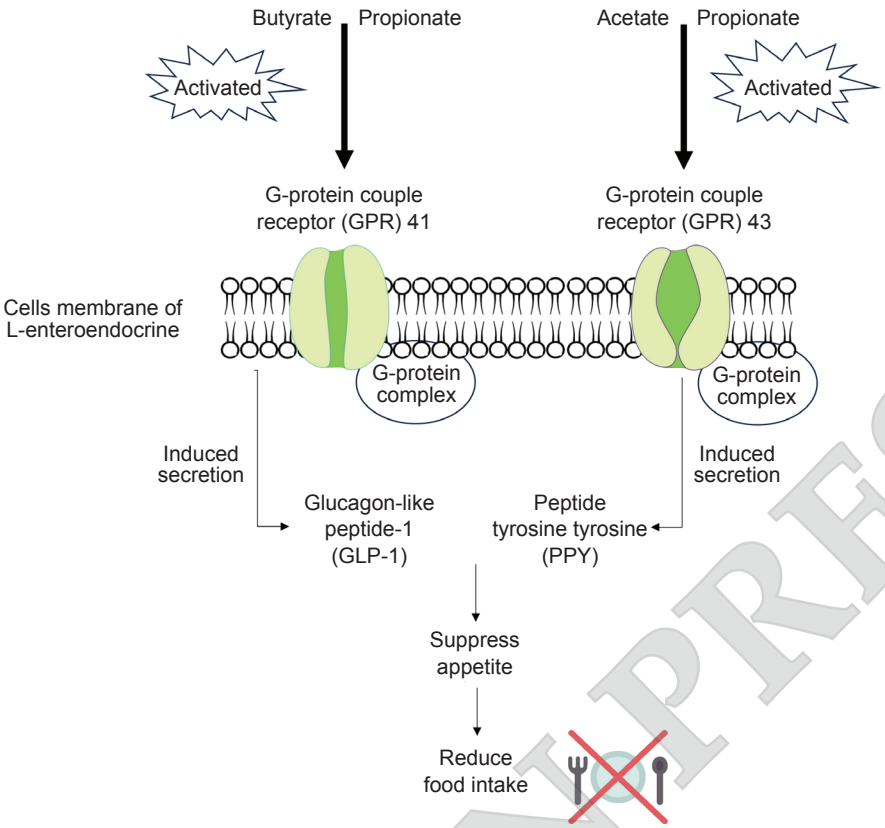
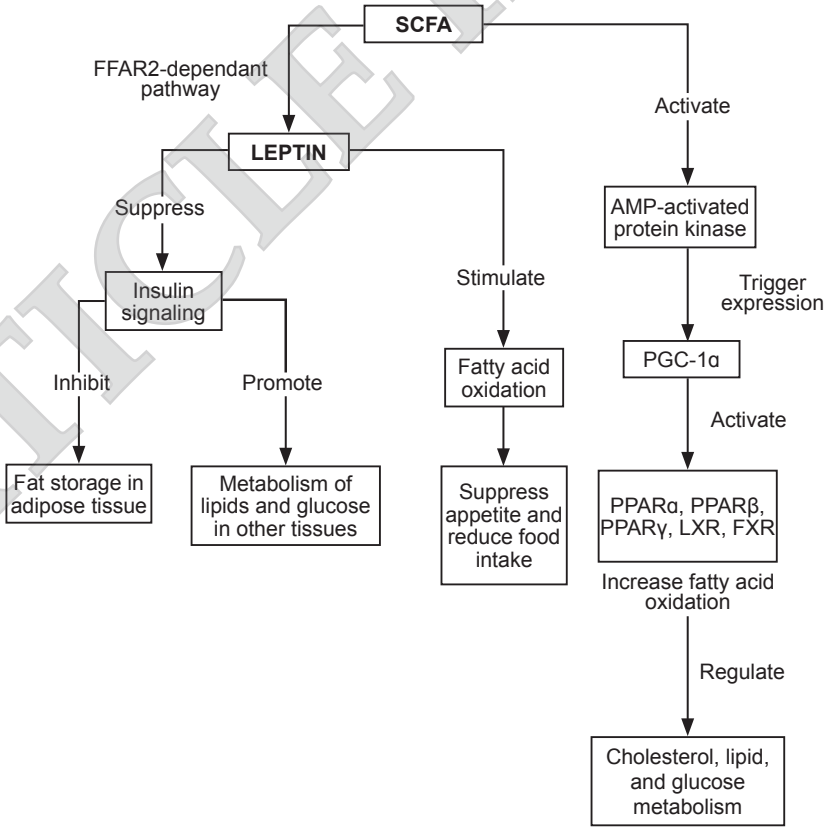


Figure 2. The important of different G-proteins couple receptor on selection of different SCFA binding and affecting the food intake.



Note: PGC-1a - peroxisome proliferator activated receptor-gamma coactivator-1 alpha; PPAR - peroxisome proliferator-activated receptor; LXR- liver X receptor; FXR - Farnesoid X receptor.

Figure 3. SCFA in regulating various metabolisms in the host.

The health benefits of BSCFA are still poorly understood. A six month study of severely obese individuals who had undergone bariatric surgery found decreased total linear SCFA and increased BSCFA due to higher protein and fibre intake, resulting in increased proteolytic fermentation by gut bacteria (Farup and Valeur, 2020). Another 12-month study of obese adults who had also undergone bariatric surgery found gut isobutyrate levels that are inversely correlated with changes in BMI and insulin resistance (Martínez-Sánchez *et al.*, 2023). These results suggest that BSCFA also have the potential to promote weight loss and improve insulin sensitivity (Mohammadifard *et al.*, 2022).

GUIDELINES OF DIFFERENT DIETARY PATTERNS

Dietary guidelines serve as a reference to form a dietary pattern which is tailored to the needs of different populations to meet nutritional requirements while preventing malnutrition and deficiencies. Adherence to these dietary guidelines yields a unique SCFA and gut microbiota profile of each population. The dietary guidelines of 96 countries have been comprehensively reviewed (Rong *et al.*, 2021) and found that a healthy and balanced diet is commonly recommended, although there are minor differences due to the availability of local foods, cultural practices, and health status.

The dietary guidelines of most countries advise a high consumption of various vegetables and fruits of at least 300-500 g/day, maintaining a moderate protein intake, limiting fat intake to 25-30 g daily, reducing sugar consumption and sugary drinks, limiting salt intake to 6 g/day, and at least 1.5 to 2.0 L of water a day (Rong *et al.*, 2021). There are some minor differences in the recommendations. For example, India discourages alcohol consumption, while Mediterranean countries typically recommend 2-3 glasses of alcohol intake in their diets (*Table 1*). Some Mediterranean countries such as Spain recommend consuming olive oil instead of other oils (*Table 1*), and Greece has no limit for olive oil intake. The United States, on the other hand, recommends consuming vegetable oils instead of solid fats, and China recommends consuming 25-30 g of oil daily (Wang *et al.*, 2016). India recommends limiting the intake of ghee, butter and hydrogenated vegetable oils (Manual, 2011), while Japan advocated an adequate intake of vegetable oil and fish oil (Gabriel *et al.*, 2018) (*Table 1*).

Some common guidelines for dietary patterns used in long-term cohort or epidemiological studies are summarised in *Table 1*. The USDA dietary guidelines recommend a well-balanced diet across all food groups, emphasising a high proportion of fruits, vegetables, legumes, nuts and whole grains. It also suggests limiting fats (less than 30% of total energy, of which less than 10% is saturated fat), industrially produced trans fats, added sugars and salt. In a similar vein, the Dutch diet encourages a high intake of vegetables, fruits, whole grains, legumes and nuts, and reasonable quantities of dairy products, fish, fats and oils, tea and coffee (*Table 1*). The diet also discourages the consumption of red meat, *trans* fats, sugar, sweetened beverages, processed foods and salt (*Table 1*).

The Mediterranean diet, originating in Mediterranean countries such as Greece and Italy, promotes a healthy diet by reducing red meat consumption and prioritising consumption of plant foods such as fruits, vegetables, grains and legumes (*Table 1*). Poultry, seafood and dairy products are recommended to be consumed in moderate amounts, with olive oil being the main source of fat (Widmer *et al.*, 2015). Over the last two decades, vegan and vegetarian diets have increasingly gained popularity. These diets consist primarily of plant sources and exclude or limit animal products. Although vegetables are rich in fibre, they are relatively poor in protein content, leading vegetarians to rely on plant-based protein sources.

The Malaysian Ministry of Health revised the food pyramid (Ganapathy *et al.*, 2019) to improve the healthy eating habits of the Malaysian population (*Figure 4*). In line with other healthy diet recommendations, the updated guidelines recommend more than 50% of vegetables and fruits. This should be supplemented by complex carbohydrates found in brown rice, whole grains products, unprocessed cereals, and oats. These natural foods are rich in vitamins and minerals which strengthen the immune system. The guide also emphasises a moderate intake of proteins from animals, seafood and plants such as nuts and legumes. The guide also recommends staying hydrated with plain water and reducing sugar, salt and oil intake (*Figure 4*).

Of note, there are also specific short-term dietary patterns such as Atkins and ketogenic diets, which are mainly adopted by individuals with certain health conditions such as obesity, pre-diabetes, epilepsy, and mild cognitive impairment (Haji-Ghazi Tehrani *et al.*, 2022; Nagpal *et al.*, 2019). The Atkins diet encourages a higher protein intake from meat while reducing carbohydrate consumption. This approach has been heavily modified recently and is now known as the modified Atkins diet, serving as a transition towards the ketogenic diet (Kossoff *et al.*, 2013). The modified Atkins diet has demonstrated promising results in weight loss (Bueno *et al.*, 2013).

TABLE 1. DIFFERENT DIETARY PATTERNS AND RECOMMENDED INTAKE PORTIONS

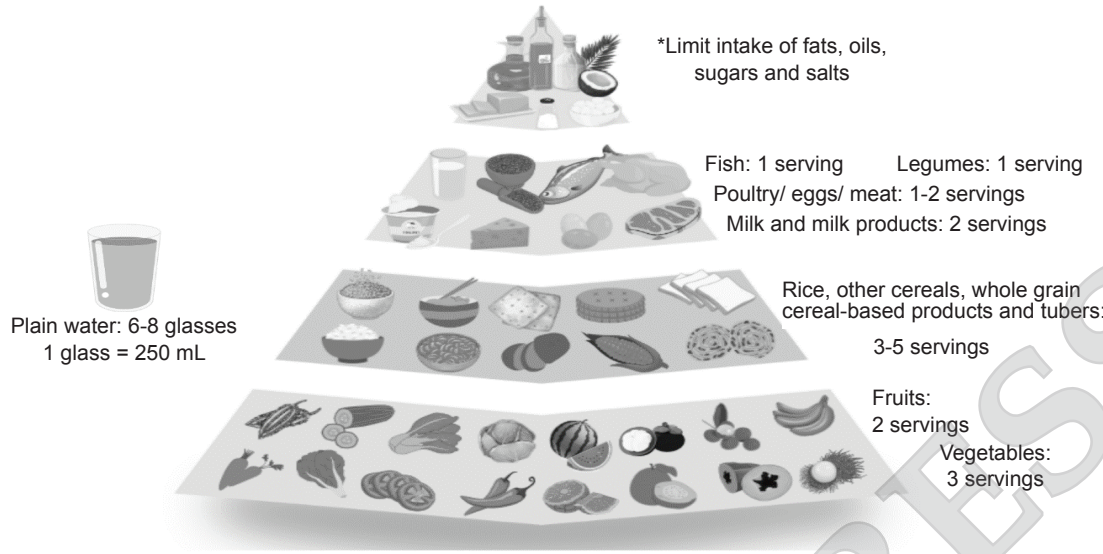
Dietary patterns	Proximate ratio of macronutrients, % kcal	Food recommendation	References
USDA diet	• Carbohydrates, ~55%-60% • Proteins, ~15% • Fats, 21%≤30%	• Consume large portion of grains (preferrable whole grains), vegetable (variety of vegetables, including legumes, starchy) • Variety fruits, preferable whole fruits (2-4 servings) • Variety proteins from lean meat, poultry, fish, eggs, seafood, dry beans, soy products, lentils, peas and nuts (2-3 servings) • Moderate dairy, including milk, cheese, yogurt, fortified soy beverages (2-3 servings) • Sufficient Vitamin D and calcium supplements • Sufficient intake of vegetable oils • Limit *trans* and saturated fats, red meat, butter, salt, sugars, refined grains and alcoholic beverages	DeSalvo *et al.* (2016); Fernandez *et al.* (2021)
Dutch diet	• Carbohydrates, 40%-70% • Proteins, 10%-25% • Fats, 20%-40%	• Eat plenty of vegetables, fruits, wholegrain, nuts, and legumes • Moderate dairy, fish, fats and oils, tea and coffee • Limit consumption of red meat, processed meat, sweetened beverages, alcohol, salt	Looman *et al.* (2017)
Japanese diet	• Carbohydrates, 50%-70% • Proteins, 20%-30% • Fats, 15%-25%	• 5-7 servings of grain dishes • 5-6 servings of vegetables • 3-5 servings of fish and meat dishes • 2 servings of milk or milk products • 2 servings of fruits • Moderate intake of snacks, confection and alcohol • Drink plenty of water or teas	Gabriel *et al.* (2018)
Indian diet	• Carbohydrates, 50%-60% • Proteins, 10%-15% • Fats, 20%-30%	• Eat plenty of cereals, millets, and pulses • Milk as protein source • Moderate intake of eggs, fish, and animal proteins • Reduce intake of butter, ghee, and hydrogenated fats and red meat • Eat nuts • Eat plenty of vegetables and fruits • Diversify food choice • Avoid alcohol and smoking	Manual (2011)
China diet	• Carbohydrates, 55%-65% • Proteins, 20%-30% • Fats, 15%-20%	• 5-6 servings of cereals, tubers, legumes • 4-5 servings of vegetables (priorities dark-coloured vegetables) • 3-4 servings of fruits • 2-3 servings of lean meat, eggs and fish • 2-3 servings of soybeans or soy products, nuts and dairy products • Moderate intake of oil • Limit salt, sugar, and alcohol intake • Drink plenty of water	Wang *et al.* (2016)

TABLE 1. DIFFERENT DIETARY PATTERNS AND RECOMMENDED INTAKE PORTIONS (continued)

Dietary patterns	Proximate ratio of macronutrients, % kcal	Food recommendation	References
Spain diet	• Carbohydrates, 50%-60% • Proteins, 25%-35% • Fats, 20%-30%	• Moderate intake of meat and meat products, fish and eggs • 2-4 servings of milk and dairy products • 2 or more servings of legumes and nuts • 4-6 servings of cereals and potatoes • 2 or more servings of vegetables (250-300 g daily) • 3 servings of fruits • Moderate lean meats and plant oils intake; recommended use olive oil • Limit animal fats and trans-fat intake • Reduce sugary foods and drinks • Drink plenty of water, moderate intake of tea • Reduce alcohol intake	Aranceta *et al.* (2001)
Mediterranean diet	• Carbohydrates, ~55%-60% • Proteins, ~15% • Fats, 21%≤30%	• Drink plenty water • 2 portions of vegetables with a variety of colours/textures • Olive oil as the main choice of fat source • 1-2 portion(s) whole grain bread/ pasta/ rice/ couscous/ cereals/ potatoes • 1-2 portion(s) nuts/ seeds • Herbs/ spices/ garlic/ onions • Legumes • 2 portions of dairy • Variety of flavours • 1/3 portion of egg /fish/ seafood/ white meat • Less read meat and processed meat and sweet	Serra-Majem *et al.* (2020)
Vegen diet (without all flesh foods) Vegetarian diets (without all flesh foods, but also include egg (ovo) and/or dairy (lacto) products)	• Carbohydrates, ~60% • Proteins, ~10%-15% • Fats, ≤20%	• Legumes, soya foods and meat analogues, nuts and seeds, grains, potatoes, tomatoes, avocados, fruits and vegetables. • Some amounts of eggs and dairy products for those following the ovo-lacto diet • Low intake of sweets, snack foods,and soda drinks • Drink plenty of water	Orlich *et al.* (2014)

TABLE 1. DIFFERENT DIETARY PATTERNS AND RECOMMENDED INTAKE PORTIONS (continued)

Dietary patterns	Proximate ratio of macronutrients, % kcal	Food recommendation	References
Atkins diet	• Carbohydrates, ≤40% • Proteins, ~30% • Fats, 30%-55%	• Large portion of protein sources such as fish, seafood and beef, poultry, pork and soy products • Vegetables – green leafy vegetables (2 cups per day); broccoli, cauliflower, spinach, asparagus (1 cup per day) • Fruits – blueberries, pears, raspberries, avocados • Oils – vegetable and seed oils • Unlimited eggs • cheese and milk (4 ounces per day) • Legumes, nuts and whole grain foods • Carbohydrate (25 to 50 g/d) • 8-ounce glasses of water (at least 6 cups)	Atkins (2002)
Ketogenic diet	• Carbohydrates, ~5%-10% • Proteins, ~10%-20% • Fats, 50%-70%	• Natural fats – Olive oil, coconut oil, avocado • Moderate amounts of meats, fish, poultry • Dairy (cheese, heavy cream, butter, ghee) • Eggs • Vegetables (green leafy vegetables, avoid starchy root vegetables) • Small amounts of berries, dark chocolate (>90% cocoa) • Avoid soda drinks, milk, yogurt, candy, pastries, all starch foods including grains, limit intake of beans and lentils	Carroll and Koenigsberger (1998)



Note: 1. The recommended number of servings is calculated based on 1500, 1800 and 2000 kcal.
2. Less active / sedentary adults should choose the minimum number of servings.

Figure 4. The Malaysian Food Pyramid 2020 illustrated the proportion of food groups in a healthy Malaysian diet in daily food intake (adopted from the Ministry of Health Malaysia).

The ketogenic diet is characterised by consuming exceptionally high-fat content, moderate protein intake and very little carbohydrates (*Table 1*). Foods commonly found in the ketogenic diet include olive oil, coconut oil, avocado, moderate amounts of meat, poultry, seafood, eggs, nuts and green leafy vegetables, berries and dark chocolate (*Table 1*). This diet induces a state of ketosis, where the body utilises fat instead of glucose for energy, resulting in elevated levels of ketone-bodies. This metabolic shift has been associated with a reduction in pro-inflammatory Th17 cells in the gut and visceral adipose tissue (Ang *et al.*, 2020), which may reduce the risk of inflammation and obesity (Mohammadifard *et al.*, 2022). Notably, a meta-analysis on individuals following a ketogenic diet has shown that BSCFA levels are increased due to the degradation of branched amino acids from protein sources (Ferraris *et al.*, 2021), but total SCFA levels decrease due to limited fibre intake (Rew, 2022). These dietary changes are reflected in the gut microbiota composition, which is characterised by a lower abundance of butyrate-producing bacteria (Louis and Flint, 2017).

MACRONUTRIENTS AND PATHWAYS FOR FERMENTING SCFA

Recent studies have shown that diets rich in certain dietary components significantly affect gut microbiota compositions. These bacteria exhibit different abilities to ferment SCFA based on different rate-limiting catalytic enzyme pathways (Xu *et al.*, 2020b). Short-term dietary intervention studies, ranging from a single day to several months (David *et al.*, 2014; Pagliai *et al.*, 2020), have shown that altering macronutrient proportions can influence gut microbiota composition and SCFA profiles.

Effects of Macronutrients on SCFA-Producing Bacteria in Short-term Interventions

Carbohydrates. A diet rich in unprocessed, high-fibres foods is a good food source for the gut microbiota especially for the phyla Actinobacteria and Firmicutes, which play an important role in SCFA metabolism (Bolte *et al.*, 2021). Resistant starch (RS) is a type of carbohydrate naturally found in grains, legumes, seeds, raw bananas and potatoes, and precooked rice (Ashwar *et al.*, 2015). It serves as an excellent precursor for gut-fermented SCFA (Abreu *et al.*, 2021). A study of 20 healthy volunteers who consumed 48 g of raw potato starch, containing 50% RS for one week showed a significant increase in the relative abundance of SCFA producing bacteria, particularly *Ruminococcus bromii*, *Bifidobacterium adolescentis*, and *Eubacterium rectal* (Venkataraman *et al.*, 2016). These bacteria are responsible for RS degradation and butyrate production (Ze *et al.*, 2012). Of particular interest, *R. bromii* has a distinct organisation of some amylolytic enzymes that form complexes through cohesion and dockerin

interaction, enhancing their ability to degrade starch (Xu *et al.*, 2015). Furthermore, *Clostridiales* and *Dorea* are also involved in the assimilation of starch, as shown in a study with mice that were fed isotopically labelled RS (Herrmann *et al.*, 2018).

Other indigestible starch components such as soluble dietary fibre also increase SCFA levels. Consumption of 5-12 g of inulin or oligosaccharides, which consist of highly branched molecules, was found to result in significant fermentation by *Faecalibacterium prausnitzii* and *Bifidobacterium* (Holscher *et al.*, 2015; Vandeputte *et al.*, 2017). This finding is in accordance with a meta-analysis conducted by So *et al.*, (2018), who found higher faecal butyrate with a high abundance of *Bifidobacterium* spp. and *Lactobacillus* spp. in individuals following a high-fibre diet.

Foods rich in whole grains and high in insoluble fibre such as cellulose are also excellent sources of nutrition for the gut microbiota but to a lesser extent. A diet rich in cellulosic materials promotes the growth of acetate and propionate producers, especially *Xylanibacter* and *Prevotella* (Iljazovic *et al.*, 2021; Ueki *et al.*, 2006). High proportions of *Prevotella* and *Xylanibacter* are often linked to vegetarian and high-fibre diets, suggesting their role in the hydrolysis of cellulose and xylan from dietary fibre (De Filippo *et al.*, 2010; Sánchez-Tapia *et al.*, 2019).

Proteins. The effect of proteins on gut microbiota compositions has not yet been fully researched. Depending on the type of diet, approximately 6-18 g of proteins is further degraded in the colon to peptides or amino acids daily by the host or bacterial-derived proteases and peptidases (Neis *et al.*, 2015). These degradation products can be further utilised by proteolytic bacteria and lead to the production of SCFA and BSCFA. Excessive protein consumption has been associated with an increased abundance of peptide and amino acid-fermenting bacteria that degrade branched-chain amino acids, such as *Bacteroides* and *Clostridium*, leading to increased levels of BSCFA, namely isovaleric acid and isobutyric acid, and smaller amounts of 2-methylbutyric acid (Aguirre *et al.*, 2016). These bacteria are also known to possess strong peptidase activity (Oliphant and Allen-Vercoe, 2019). A study of 17 obese men who underwent a high-protein but low-carbohydrate diet for 4 weeks showed that a high-protein diet increased BSCFA concentrations in the presence of toxic compounds such as phenylacetic acid and N-nitroso compounds while lowering butyrate levels and decreasing *Roseburia* and *E. rectale* (Russell *et al.*, 2011).

Some SCFA-producing bacteria such as *Prevotella bryantii* (Trautmann, *et al.*, 2020) and *Lactobacillus casei* (Chen *et al.*, 2019) can efficiently degrade peptides especially peptides that consist of more than three amino acids in their chain such as casein into nitrogen for growth (Kim *et al.*, 2017; McIntosh *et al.*, 2009). These bacteria possess dipeptidyl peptidase activity that is involved in protein digestion and the host metabolism such as regulating the secretion of glucagon-like peptide 1 (GLP-1) and gastric inhibitory polypeptide (GIP) involved in glucose haemostasis (Olivares *et al.*, 2018). Studies have also shown that different protein sources in the diet have an impact on gut bacterial species and BSCFA (*Table 2*). Consumption of chicken meat promotes the growth of *Faecalibacterium, Prevotella* 9, *Dialister* and *Megamonas*, but consumption of pork leads to the growth of *Bacteroides, Faecalibacterium, Roseburia, Dialister* and *Ruminococcus* 2. This results in different levels of SCFA and BSCFA in the gut (Shi *et al.*, 2021). Similarly, animal-derived protein sources such as fish promote the growth of *Lactobacillus* and *Oscillibacter* (An *et al.*, 2014), while consumption of dried skimmed milk and milk casein increased *Lactobacilli* and *Bifidobacterium* (Zhang *et al.*, 2020) but lower *Staphylococci, Coliforms* and *Streptococci* counts (Zhao *et al.*, 2018) in porcine and rat. Conversely, less digestible plant proteins such as peanuts and soybeans (Day *et al.*, 2022), consist of indigestible cell wall components that demonstrated a higher fermentability. This leads to an increased content of acetic and lactic acid and an increased abundance of *Bifidobacterium*. Different proteins possess different amino acids that make up the protein structure and yield different gut microbiota compositions. For example, vegetarians showed significantly higher plasma concentrations of methionine, tryptophan, alanine, glutamate, glycine, and tyrosine but lower lysine compared to meat- and fish-eaters (Schmidt *et al.*, 2016). Gut microbiota synthesises butyrate from lysine and glutamate, while propionate is mainly synthesised from alanine, methionine and threonine and acetate from glycine, alanine and lysine (*Figure 3*).

Dietary fats. The effects of fats on gut microbiota composition and SCFA production generally depend on the degree of fat saturation and the amount of dietary fat consumed. Extensive clinical studies in human and animals have consistently demonstrated that diets high in SFA promote the growth of *Firmicutes*, *Enterobacteriacea* and *Proteobacteria*, while concurrently reducing the abundance of *Bacteroidetes* and *Lactobacillus* (Heinritz *et al.*, 2016; Ley *et al.*, 2006; Wu *et al.*, 2011; Zhang *et al.*, 2012). High SFA content is often used as a comparator when studying the effects of dietary fats on gut microbiota. However, it is important to note that an increase in fat intake may inadvertently lead to lower energy intake from other macronutrients such as complex carbohydrates, and this reduces the abundance of saccharolytic

TABLE 2. EFFECTS OF DIET COMPONENTS ON GUT MICROBIOTA PRODUCING SCFA

Diets	SCFA	Gut microbiota	References
Resistant starch	Butyrate, acetate	*Ruminococcus bromii, Bifidobacterium adolescentis, Eubacterium rectal*	Venkataraman *et al.* (2016)
		Bifidobacterium	Alfa *et al.* (2018)
Oligosaccharides	Butyrate	*Bifidobacterium* spp. *Lactobacillus* spp.	So *et al.* (2018)
Insoluble fibres	Acetate, propionate	*Xylanibacter, Prevotella, Faecalibacterium*	Iljazovic *et al.* (2021); Ueki *et al.* (2006); Holscher *et al.* (2015); Vandeputte *et al.* (2017)
Proteins	SCFA and BSCFA (isobutyric, isovaleric, and 2- methylbutyric acids)	*Bacteroides, Clostridium, Faecalibacterium, Roseburia, Dialister,* and *Ruminococcus 2*	Aguirre *et al.* (2016); Smith and Macfarlane (1998)
High SFA	SCFA	*Firmicutes, Enterobacteriacea, Proteobacteria, Lactobacillus, Prevotella,* and *Alistipes*	Heinritz *et al.*, 2016; Wu *et al.* (2011); Zhang *et al.*, 2012; Zhao *et al.* (2018)
High MUFA	Propionate	*Oscillspira, Faecalibacterium prausnitzii,* and *Roseburia*	Haro *et al.* (2016); Muralidharan *et al.* (2019)
High PUFA (EPA, DHA)	Butyrate	*Coprococcus, Roseburia,* and *Blautia*	Ochoa-Repáraz and Kasper (2016)

Note: SCFA - short chain fatty acids; SFA - saturated fatty acids; MUFA - monounsaturated fatty acids; PUFA - polyunsaturated fatty acids; EPA - eicosapentaenoic acid; DHA - docosahexaenoic acid.

bacteria such as *Bifidobacterium, F. prausnitzii,* and *Ruminococcus* (Fava *et al.*, 2013; Shen *et al.*, 2012).

In a study comparing the effects of diets high in SFA, MUFA, carbohydrate, or sugar on the gut microbiota of 88 subjects at risk of metabolic syndrome over a 24 weeks period, it was found that a diet high in SFA yielded greater SCFA abundance compared to other diet groups (Fava *et al.*, 2013). Conversely, a diet rich in MUFA, akin to the Mediterranean diet, increases the abundance of SCFA-producing bacteria (Haro *et al.*, 2016; Muralidharan *et al.*, 2019). It is noteworthy that the Mediterranean diet is also high in vegetables and fruits and the effect of MUFA could be confounded by these dietary fibres. PUFA-rich diets, particularly those rich in omega-3 fatty acids, have been shown to elevate the abundance of butyrate-producing colonic bacteria, namely *Coprococcus*, *Roseburia*, and *Blautia* (Ochoa-Repáraz and Kasper, 2016) (*Table 2*).

Some researchers suggest that various dietary fats indirectly influence the gut microbiota composition by influencing bile acid secretion from the colon (Just *et al.*, 2018). It is known that a high-fat diet increases bile acid secretion, resulting in these bile acids being converted into secondary forms to prevent reabsorption in the colon (Park *et al.*, 2022). These secondary bile acids may subsequently reshape the composition of the gut microbiota by enhancing the abundance of bile-tolerant bacteria (Yokota *et al.*, 2012).

Pathways involved in SCFA production. The pathways of SCFA production have been summarised in detail by Xu and colleagues (Xu *et al.*, 2020b). Four general pathways for SCFA production have been identified. First, SCFA is produced from carbohydrates, which involves the degradation of dietary fibre to monomers (pentoses) and various sugars and oligosaccharides. These substrates are degraded by glycolysis, yielding pyruvate molecules (*Figure 5*). In addition, SCFA can be synthesised from acetate and ethanol by extending the carbon chain. Acetate, derived from beta-oxidation of dietary fats and deamination of amino acids from proteins, reacts with coenzyme A (CoA) to form acetyl-CoA (*Figure 5*). Pyruvate and acetyl-CoA serve as the main precursors in the citric acid cycle and contribute to the production of SCFA. Third, amino acids such as valine, leucine and iso-leucine undergo decarboxylation and reduction to synthesise BSCFA. Lastly, unique substrates such as carbon dioxide molecules are involved in the synthesise of acetate via the Wood–Ljungdahl pathway, while lactate contributes to the synthesise of propionate (*Figure 5*).

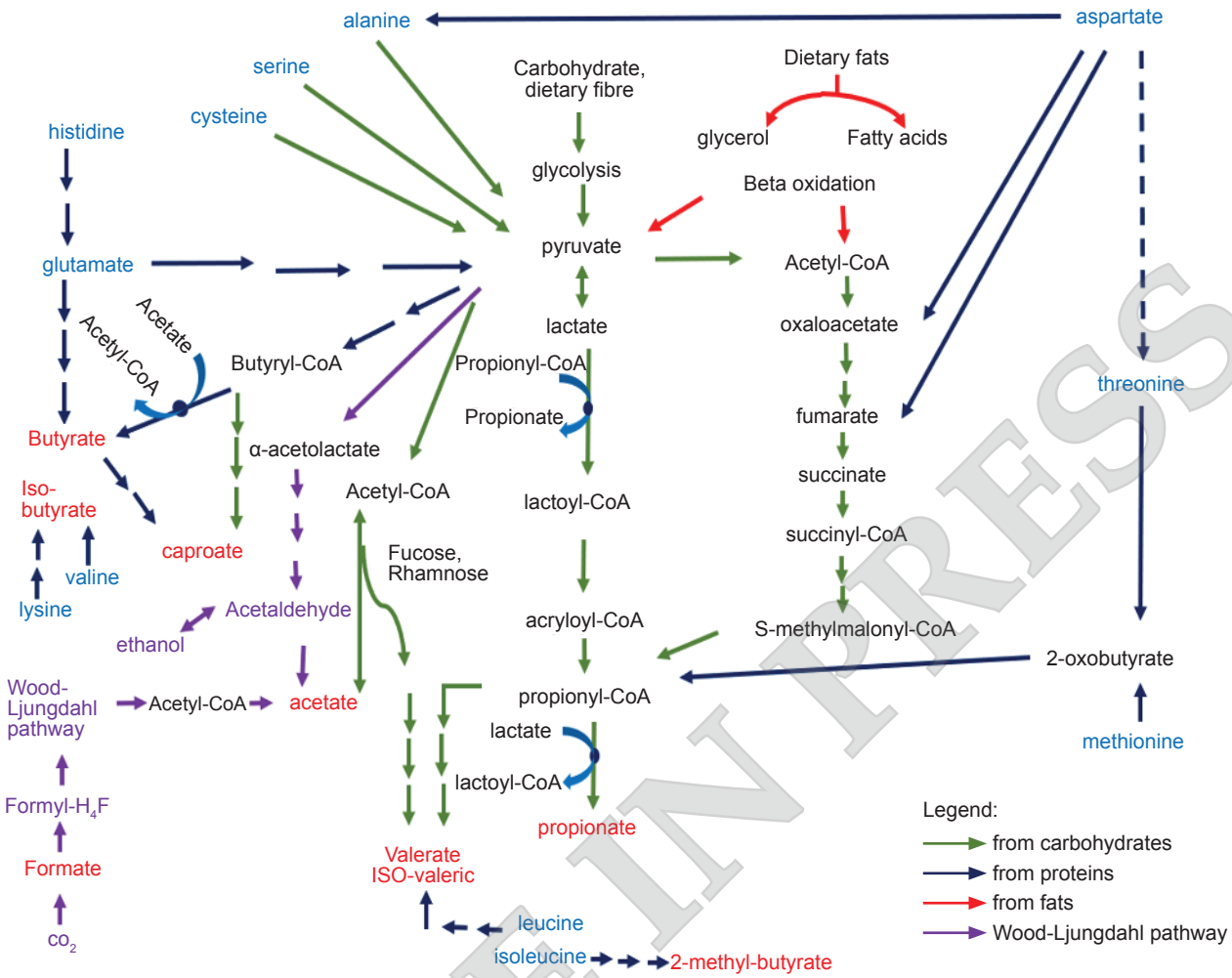


Figure 5. Pathways of SCFA production from macronutrients.

Recent studies have identified 74 key SCFA-producing bacterial species in different research groups (Xu *et al.*, 2020b). Approximately 80% of these SCFA-producing bacteria are members of Firmicutes phylum, mainly from the *Clostridiaceae* and *Lachnospiraceae* families. Of these, many species are recognised as butyrate producers, including *Clostridium*, *Eubacterium*, *F. prausnitzii*, *Subdoligranulum variabile*, *Anaerostipes*, *Coprococcus*, and *Roseburia*. Some of these bacteria such as *Clostridium* sp., *Coprococcus* and *Roseburia*, *A. muciniphila*, *Ruminococcus* spp. produce acetate and propionate in addition to butyrate (Flint *et al.*, 2015; Reichardt *et al.*, 2014).

Certain bacterial strains such as *Prevotella copri* and *P. stercorea* are major producers of longer-chain SCFA valerate (C5) (Almeida *et al.*, 2019), whereas *Veillonellaceae*, such as *Megasphaera elsdenii* and *Megasphaera* sp. *Roseburia*, *Megasphaera* and *Clostridium* have demonstrated an excellent ability to produce multiple types of SCFA (Reichardt *et al.*, 2014). These results suggest that certain gut bacterial species can efficiently utilise different food residues, possibly highlighting the role of a few "core" gut bacteria in regulating SCFA production pathways.

Roseburia and *Faecalibacterium* (*Table 2*) are most abundant in those following high-protein and high-fat diets. These bacteria are postulated to have diverse genes which are involved in several important functional metabolic pathways or that their genes interact with other dietary components. Although short-term replacement of dietary components may affect overall gut health, the gut microbiota is resilient and tends to regenerate back to its original composition when the original diet is resumed. Therefore, holistic nutritional epidemiological studies, can shed light on the true effects of the whole diet and provide a better understanding of the complex relationship between the diet, gut microbiota composition, and the functional pathways for the production of metabolites.

EFFECTS OF LONG-TERM DIETARY PATTERNS ON GUT MICROBIOTA COMPOSITIONS AND SCFA PROFILES ON HEALTH OUTCOMES

Long-term dietary patterns have been explored in detail in several large human cohort studies. Their profound effects on gut microbiota composition, SCFA profiles, associated metabolic pathways and resulting health outcomes are summarised in *Table 3*.

In general, a plant-based diet, such as vegan or vegetarian diet, is associated with higher total SCFA content and promotes greater numbers of SCFA-producing bacteria such as *Roseburia, Ruminococcus, Lachnospira*, *Dorea*, *Lactobacillus, Bifidobacterium* and *Prevotella* (*Table 3*). Conversely, high consumption of animal foods has been associated with a reduction in gut bacterial diversity, higher levels of valeric acid, capric acid and BSCFA, and dominance of *Firmicutes*, *Streptococcus* and *Ruminococcus*, possibly stimulating endotoxin synthesis pathways.

The Mediterranean diet promotes a healthy diet high in fibre (*Table 3*). High adherence to this diet results in increased total SCFA, particularly acetate (Mitsou *et al.*, 2017) and growth of butyrate-producing taxa such as *Roseburia faecis, R. bromii,* and *Oscillospira plautii*, with a strong association observed for *Bifidobacterium animalis*. In addition, consumption of animal proteins inhibits the growth of *Bacteroidetes*, while consumption of PUFA, particularly from fish and vegetal proteins, tends to cultivate *Prevotella copri*, *Dorea* and *Lactobacillus* (*Table 3*).

Both the Mediterranean and vegetarian diets, which are both rich in plant-based foods, exhibit slight differences in intake of animal protein and olive oil, resulting in slight variations in the composition of gut microbiota at the genus level, while alpha diversity, richness and evenness remain similar (*Table 3*). When comparing the effects of gut microbiota composition of a vegetarian and vegan diet to an omnivorous diet (*Table 3*), Shannon index, which indicates bacterial richness, are found to be significantly different between those who follow vegetarian and omnivorous diets (Ghosh *et al.*, 2020; Trefflich *et al.*, 2021). It is noteworthy that faecal SCFA levels, especially acetate, propionate and butyrate, are higher in plant-eaters, suggesting a correlation between gut microbiota composition, gut fermented SCFA, and dietary fibre content.

Comparative studies between the Mediterranean diet and different dietary habits among the British, French, Dutch, Italians, and Poles revealed some interesting patterns. Strong adherence to the Mediterranean diet for an extended period enhances the abundance of SCFA-producing bacteria. These bacteria have anti-inflammatory properties as evidenced by the negative correlation with proinflammatory markers such as the highly-sensitive C-reactive protein (hsCRP) and IL-17, and this ultimately lowers the risk of frailty in the elderly (Ghosh *et al.*, 2020). Conversely, low adherence to the Mediterranean diet is associated with an abundance of taxa such as *Collinsella aerofaciens*, *Coprococcus comes*, *Clostridium ramosum*, and *Veillonella dispar*, which are associated with a higher risk of T2D, colorectal cancer, and IBD (*Table 3*).

Vegetarian diets typically result in higher proportions of butyrate and valerate, but lower concentrations of branched-chain amino acids. However, in a small cohort study in southern India, contradictory results have reported omnivorous diets increase the abundance of *Clostridium* cluster XIVa and upregulation of the butyryl-CoA: CoA transferase gene, leading to increased butyrate production compared to vegetarian diets (*Table 3*). In a larger cohort of healthy adults following vegan or omnivorous diets, no significant difference was found between SCFA and BSCFA levels (*Table 3*).

Specific core taxa are identified in shaping the effects of a long-term dietary pattern. Omnivorous diets are dominated by three specific core taxa, namely *Lachnospira*, the NK4A136 group of the *Lachnospiraceae* and *Ruminiclostridium*. Conversely, the vegetarian diet resulted in an abundance of seven core taxa, mainly SCFA-producing bacteria together with three rare genera. The rare taxa are *Tyzzerella, Succinivibrio* and *Shuttleworthia*, which are positively correlated with SCFA and BSCFA levels (*Table 3*).

A well-studied Dutch cohort study provided insight into certain bacterial taxa with significant health implications. Of these bacterial taxa, *Christensenellaceae* stands out as being inversely proportional to the size of very-low-density lipoprotein (VLDL) particles, small high-diversity-lipoprotein (HDL) particles and triglycerides in medium HDL. These results suggest a possible role in lipid metabolism, cardiovascular risk reduction and body weight regulation (Goodrich *et al.*, 2014). *Clostridiaceae* 1 and the genus *Clostridium sensu stricto* are associated with very large and large HDL particles, suggesting an association with lower BMI and lower blood triglyceride levels, which reduces the risk of stroke and CVD. *Ruminococcaceae* is associated with acetate production, while *Lachnospiraceae* and *Blautia* are involved in upregulating 7α-dehydroxylation genes to accelerate metabolism from primary to secondary bile acids (Ridlon *et al.*, 2013; Vital *et al.*, 2019) and producing butyrate from lactate (Duncan *et al.*, 2004). Overall, these long-term cohort studies have shown that diet undoubtedly affects the gut microbiota composition at the lower phylogenetic level and the metabolome produced by these bacteria. Adherence to certain dietary patterns is important to maintain a stable "core" community of gut microbiota to perform certain core functional metabolic pathways.

TABLE 3. EFFECTS OF DIFFERENT DIETS PATTERN ON SCFA PRODUCING GUT MICROBIOTA (continued)

Diet	Study design, duration, participants	Main food sources/ food components	Outcomes	References
Mediterranean diet	Cross-sectional, Healthy 251 F and 109 M, 45.0 ± 10.5 yo; BMI: 25-30 kg/m^2	Macronutrients intake: Carbohydrate 54%-55% Proteins 21%-22% Fats 23%-24% Fibre 24%-36%	• A strict Mediterranean diet is associated with increased abundance of butyrate-producing bacteria such as *Roseburia faecis*, *R. bromii* and *Oscillospira plautii* • *Bifidobacterium animalis* are strongly associated with the Mediterranean diet	Rosés *et al.* (2021)
Mediterranean diet	116 subjects: 61 M, 55 F; mean age 42 yo; BMI 25-30 kg/m^2. Adherence of med diet was accessed using MedDietScore. Low MedDietScore indicates high intake of fast food, high fats, sugar and processed food	Non-refined cereals, potatoes, legumes, fruits, vegetables, olive oil, fish; moderate meat, meat products, poultry, dairy; low alcohol	• 68% subjects showed moderate to high adherence to the Mediterranean diet • High adherence in MedDietScore tertiles showed higher levels of acetate but lower levels of caproic acid • A high MedDietScore was positively associated with total bacteria and *Candida albicans* counts and the ratio of bifidobacterial to *Escherichia coli* but negatively associated with the concentration of valeric acid and *E. coli* after adjusting for the BMI, gender and age • Fast food intake suppressed the abundance of *Lactobacilli* and butyrate-producing bacteria	Mitsou *et al.* (2017)
Mediterranean diet	27 healthy adults (11M, 16 F; 39.5 ± 7.3 yo; lived in Valencia-Spain): PREDIMED score	Non-refined cereals, potatoes, legumes, fruits, vegetables, olive oil, fish; moderate meat, meat products, poultry, dairy; low alcohol	• High protein intake lowers the abundance of *Bacteroidetes*, whereas animal proteins, saturated fats and sugars reduced bacteria diversity • High intake of vegetal protein was associated with high abundancy of butyrate-producing bacteria such as *Dorea, Coprococcues*; as well as *Roseburia* and *Bifidobacterium* • Higher intake of PUFA/SFA increased the abundancy of *Dorea* and *Lactobacillus* • High intake of plant-based nutrients increases the bifidobacterial counts, and total SCFA levels • Higher adherence to MedDiet Score also increased total SCFA	Garcia-Mantrana *et al.* (2018)
Mediterranean, vegan dan vegetarian diets	Cohort study: 153 healthy Italian; 51 omnivores (23M, 28F; BMI 22.1 ± 2.0 kg/m^2); 51 vegan (23M, 28F, BMI 21.3 ± 2.2 kg/m^2); 51 vegetarian (18M, 33F; 21.9 ± 2.5 kg/m^2), with 88% of them are medium or highly adhered to the Mediterranean diet.	High intake of cereals, fruits, vegetables and legumes	• Alpha diversity did not significantly vary across these three diets • Significant relationship between genus-level microbiota composition and habitual diet in PCA plot • *Lachnospira, Roseburia* and *Prevotella* was associated with a plant-based diet, while *L-Ruminococcus* and *Streptococcus* were associated with an animal-based diet • Faecal acetate, propionate and butyrate were associated with a high plant-based foods intake, while valeric and caproic acids were associated with a high protein and high fat diet intake	Filippis *et al.* (2016)

TABLE 3. EFFECTS OF DIFFERENT DIETS PATTERN ON SCFA PRODUCING GUT MICROBIOTA (continued)

Diet	Study design, duration, participants	Main food sources/ food components	Outcomes	Reference
Mediterranean diet *vs*. control diet	Mediterranean diet = 141 M, 182 F, from UK, France, Netherlands, Italy, and Poland; Control diet = 145 M, 144 F, 1 year	Mediterranean (NU_AGE) diet (tailored for elderly): Whole grains, fruits, vegetables, and legumes, dairy and cheese, seafood, meat and poultry, nuts, potatoes, rice, eggs, and olive oil Control diet: Normal habitual local diet intake Accessed with MedDiet score	• Data from these countries showed no significance, but high adherence to Mediterranean diet increased microbiota biodiversity • The control group had higher fat intake than Mediterranean Diet intervention group • Among the 44 Predictive OTUs positively associated with a high MedDiet score were *F. prausnitzzi, Roseburia hominis, Eubacterium, Bacteroides thetaiotaomicron, P. copri* and *Anaerostipes hadrus*. These bacteria are associated with SCFA or BSCFA production and possess anti-inflammatory properties, showing negative correlation with proinflammatory markers hsCRP and IL-17 • Predictive OTUs inversely associated with MedDiet score primarily belonged to taxa of *Collinsella aerofaciens, Ruminococcus torques*, *Coprococcus comes, Dorea formicigenerans, Clostridium ramosum, Veillonella dispar, Flavonifractor plautii* and *Actinomyces lingnae*. Increase abundance of these taxa has been associated with higher risk of T2D, colorectal cancer, IBD • The commercial gut microbiota is positively correlated with dietary fibre, vitamins C and D, plant proteins, and carbohydrates, resulting elevated SCFA levels and decreased secondary bile acids	Ghosh *et al.* (2020)
Vegetarian diet (VD) *vs*. omnivorous (O)	32 lacto-vegetarian and 24 omnivorous women from South India Age, 19 yo; BMI 20-21.9 kg/m^2 FFQ, 24-hr diet recall	VD, Dietary intakes: Simple Carbohydrate: 29.5 (g/d) Complex Carbohydrate: 225 (g/d) Proteins: 30 (g/d) Fats: 21.5 (g/d) Fibre: 2.9 (g/d) O, Dietary intakes: Simple Carbohydrate: 25.5 (g/d) Complex Carbohydrate: 246 (g/d) Proteins: 32 (g/d) Fats: 20.5 (g/d) Fibre: 2.95 (g/d)	• In the omnivorous group, the faecal microbiota composition exhibited an increase in *Clostridium* cluster XIVa, specifically *Roseburia–E. rectale* • *Clostridium* cluster XIVa and *Roseburia–E. rectale* are positively associated with faecal butyrate, with a weaker correlation observed for *Clostridium leptum* and *F. prausnitzii* • Omnivores have displayed a higher proportion of *Clostridium* cluster XIVa and butyryl-CoA:CoA-transferase gene compared to vegetarians	Kabeerdoss *et al.* (2012)

TABLE 3. EFFECTS OF DIFFERENT DIETS PATTERN ON SCFA PRODUCING GUT MICROBIOTA (continued)

Diet	Study design, duration, participants	Main food sources/ food components	Outcomes	Reference
Vegetarian diet (VD) *vs*. omnivorous (O)	healthy vegans (n = 57) and omnivore (n = 33) subjects. Cross-sectional study 3 days dietary record	VD, Dietary intakes (g/d): Carbohydrate: 250 Proteins: 69 Fats: 70 Fibre: 33 O, Dietary intakes (g/d): Carbohydrate: 232 Proteins: 81 Fats: 83 Fibre: 18	• Long-term adherence to a vegan diet has greater effects (43.3%) on faecal metabolomes than the feacal bacterial genera • Vegans diet resulted in higher proportion of polysaccharide fermentation products such as MCFA, SCFA (especially butyric and valeric acids) and their derivatives in faeces, and lower proportion of branched chain amino acid compared to omnivores • Of 58 genera detected in both vegetarian and omnivorous diets, ten genera are identified as the core microbiome. Three of them (*Lachnospira*, *Lachnospiraceae* NK4A136 group, and Ruminiclostridium) were found to be more abundant in the omnivores, whereas seven genera (*Anaerostipes, Blautia, Alistipes, Dorea, Fusicatenibacter, Bifidobacterium, and Ruminococcaceae*_uncultured) were less abundant in the vegans compared to omnivores	Prochazkova *et al*. (2022)
Vegetarian diet (VD) *vs*. omnivorous (O)	Healthy vegans (n = 36); omnivores (n = 36) Cross-sectional study	VD: Vegetables, legumes, mushroom, confectionery, fruits, cereal, wholegrains, nuts, vegetable oils, soy milk, soy-products, vegetarian spread O: meat, fish, poultry, processed meat, dairy products, animal fats, alcohol, vegetables, grains, fruits, confectionery, butter.	• Random forest regression analysis indicated no significant SCFA and BCFA concentration differences between vegans and omnivores, implying bacterial adaptability to diverse nutrient availability in these diets • At the species level, omnivores exhibited significantly higher Shannon diversity (p = 0.04) than vegans • In vegans, a cluster of *F. prausnitzii, Prevotella copri, Dialister* spp. and *Eubacterium* spp. affect • SCFA and BCFA concentrations • For omnivores, *Bacteroides* spp., *Clostridium* spp., *Ruminococcus* spp. and *Prevotella copri* affect SCFA and BCFA concentrations	Trefflich *et al*. (2021)

TABLE 3. EFFECTS OF DIFFERENT DIETS PATTERN ON SCFA PRODUCING GUT MICROBIOTA (continued)

Diet	Study design, duration, participants	Main food sources/ food components	Outcomes	Reference
Dutch diet	1425 subjects from four cohorts: Crohn's disease, ulcerative colitis, irritable bowel syndrome and the general population	Dairy, cheese, meat (sausage, meatball), breads, potatoes, cereals, boiled vegetables, salad, fruits, butter, egg, legume, alcohol. Dietary intakes (g/d): Carbohydrate: 208.24-228.37 Proteins: 67.09-74.79 Plant protein: 27.34-30.85 Animal protein: 38.65-44.05 Fats: 71.77-80.66 Alcohol: 4.13-8.53	• Regular intake of processed and animal-derived foods correlated with higher abundance of *Firmicutes*, *Ruminococcus* and *Blautia*; along with pathways related to endotoxin production • Conversely, plant-based foods and fish were positively associated with SCFA-producing bacterial and pathways related with nutrient metabolism	Bolte *et al.* (2021)
Dutch diet	2309 individuals from Rotterdam Study and the LifeLines-DEEP cohort	Grains, dairy, fruits, vegetables, legumes, potatoes, poultry, meat, processed meat, eggs, tea, coffee, soda, alcohol	• The *Christensenellaceae* family, being highly heritable, has an inverse correlation with various VLDL particle sizes, small HDL particles and triglycerides in medium HDL • *Clostridiaceae 1* and genus *Clostridium sensu stricto* are associated with very large and large HDL particles, and potentially decrease risk of stroke and CVD • *Clostridiaceae 1* is inversely related to BMI and blood TG levels • *Ruminococcus gnavus* is associated with serum triglycerides levels • *Lachnospiraceae* and *Blautia* are associated with small HDL particle • *Ruminococcaceae UCG-005* was associated with acetate • *Ruminococcaceae, Lachnospiraceae* and *Blautia* convert primary bile acids into secondary bile acids and production SCFAs	Vojinovic *et al.* (2019)

Note: RCT - Randomised cross over trial; T2D - Type 2 Diabetes; %en - percent energy; hsCRP - high-sensitivity C reactive protein; IL-17 - interleukin 17; BMI - body mass index; MCFA - medium chain fatty acid; VLDL - very low density lipoprotein; HDL - high density lipoprotein; TG - triglycerides; yo - years old.

PROSPECTIVE OF MALAYSIAN DIET CONTAINING PALM OIL

The Malaysian diet is unique in that it offers a wide variety of food choices. However, findings from the National Health and Morbidity Survey NHMS 2019 Technical Report (Ganapathy *et al.,* 2019) revealed a concerning high consumption of energy-dense foods and sugary beverages. Approximately, 94.9% of Malaysians have neglected to consume the recommended amounts of fruits and vegetables coupled with inadequate dietary fibre intake. Therefore, the Malaysian public is encouraged to reduce the consumption of refined sugar and sugary drinks and increase consumption of fruits, vegetables and unprocessed foods. When high adherence to this dietary guideline is achieved, a healthy gut environment with a stable gut microbiota community follows.

Around 25 years ago, a study examining the fat intake of Malaysians found that the nation diet contained 40-66 g of fat daily which is equivalent to 22%-26% of total calorie intake (Ng, 1997). Two decades later, Malaysians are found to typically consume 58 g of fat, accounting for 29.2% of total calorie intake. This approaches the upper bound of the recommended limit (Lee and Muda, 2019). Malaysians are also found to have a marginal increase in protein consumption and decreased carbohydrate intake, albeit dipping slightly below the recommended range (Lee and Muda, 2019).

Malaysian Diet and SCFA-Producing Bacteria

A comprehensive understanding of the composition of gut microbiota and its SCFA profiles in the context of long-term Malaysian dietary patterns remains limited. Some noteworthy works have been conducted to investigate either the SCFA or the gut microbiota profiles alone for specific aspects. These include studies conducted in pre-adolescents (Chong *et al.,* 2015) and young adults following *Helicobacter pylori* eradication (Yap *et al.,* 2016), probiotic intake in adolescents (Joseph *et al.,* 2019) and the effects of fermentable oligosaccharides, disaccharides, monosaccharides and polyols (FODMAP) (Khoo *et al.,* 2023) in both healthy adults and patients with IBD (Huda-Faujan *et al.,* 2010), and the effect of ethnicity on gut microbiota composition and SCFA profile (Dwiyanto *et al.,* 2021) (*Table 4*). Of these, only two studies (Dwiyanto *et al.,* 2021 and Khoo *et al.,* 2023) provide detailed dietary records and explore the correlation of SCFA to gut microbiota.

Very few studies have been conducted to investigate the composition of the gut microbiota and the corresponding SCFA concentrations in people following a typical Malaysian diet. Analysis of some available data in *Table 4* suggests that the SCFA profiles of healthy adults (control) contain mainly acetate, propionate and butyrate, and relatively low levels of BSCFA such as isobutyrate (*Table 4*). The higher concentration of butyric acid compared to propionic acid suggests a higher consumption of starchy staple foods, particularly rice, by the Malaysian population (Huda-Faujan *et al.,* 2010) or subtle differences in the diets of different ethnic groups (Shafiee *et al.,* 2022).

Firmicutes and Bacteroidetes are the main phyla among healthy Malaysians, and Actinobacteria and Proteobacteria were also found in lower abundance. In addition, SCFA-producing genera such as *Faecalibacterium* and *Prevotella* have also been identified. Indigenous children were found to have a higher abundance of *Aeromonadales* and *Ruminococcaceae* (*Table 4*), which is probably related to the degradation of high-fibre foods such as *ulam*, a popular food in the indigenous diet (Shafiee *et al.,* 2022). A multi-ethnic study by Dwiyanto *et al.* (2021) demonstrates that the influence of ethnicity on the composition of gut microbiota is related to different lifestyles and dietary patterns of different ethnic groups (*Table 4*). Conversely, Khine *et al.* (2019) found that dietary habits affect gut microbiota composition even among individuals from the same ethnic group living in different geographical areas, including Chinese from Guangzhou city (China), Penang city (west coast of Malaysia) and Kelantan city (Malaysia). However, these studies lack detailed information on dietary intake, especially on the type and quantity of edible oils.

The inclusion of palm oil in a balanced Malaysian diet has promising health benefits and should be further explored. Palm oil is known for its unique fatty acid profile and antioxidant properties and has long been used as an important ingredient in Malaysian cuisine. High adherence to the balanced Malaysian diet, which is typically prepared with palm oil, has the potential to create a favourable environment for gut microbiota (Yap *et al.,* 2022) and improve SCFA production in promoting gut health in Malaysians.

CONCLUSIONS AND FUTURE PRESPECTIVES

A healthy Malaysian diet should consist of a large proportion of complex carbohydrates from fruits and vegetables which are mainly indigestible fibre, approximately 25% of proteins and 25% of fats, and the remainder being carbohydrates from fruits and vegetables, and also staple foods such as rice. This composition is broadly in line with the recommended ratios of macronutrients found in other notable dietary patterns. Strict adherence to the recommended intake promotes a healthy intestinal environment for gut bacteria.

TABLE 4. STUDIES ON SCFA CONTENTS AND GUT MICROBIOTA COMPOSITIONS IN MALAYSIANS

Study	Diet	Results / outcomes	Reference
Malays (n = 24), Chinese (n = 17) and the *Orang Asli* (indigenous) (n = 20). 7-12 yo 5 weeks on normal Malaysia diet	Not provided	• The prominent phyla of gut microbiota were *Firmicutes* and *Bacteroidetes*, while *Feacabacterium* and *Prevotella* are the dominant genera • Analysis of 16S rRNA sequencing revealed elvevated abundance of *Aeromonadales* and an unclassified genus related to *Ruminococcaceae* in *Orang Asli* children compared to Malays and Chinese	Chong *et al.* (2015)
Young healthy volunteers, with Helicobacter pylori positive, 18-30 yo, n=17	Not provided	• Alpha indexes indicated no significant diversity shifts between baseline and post-eradication; likewise, beta diversity indexes showed no substantial alternations in bacterial community composition across these time point • At baseline, the most abundant phyla were *Bacteroidetes*, *Firmicutes, Actinobacteria*, and *Proteobacteria* • No SCFA was tested	Yap *et al.* (2016)
Healthy and overweight (BMI ≥ 23 kg/m^2) adults. 4 weeks MCP supplement, n=12 placebo, n=14	No dietary record	• No notable differences were observed in fasting blood glucose, body weight, waist circumference, and SCFA content between the treatment and the control group • The content of acetate was 242.0±107.7mmol/g; propionate, 36.8 ±16.4 mmol/g; and isobutyrate, 204.4±116.3 mmol/g at the baseline. Results after MCP supplement are not of interest of this article • Gut microbiota composition was not measured	Mahadzir *et al.* (2017)

School children, 7-10 yo,
normal weight, n=19 (BMI, 16.07 kg/m^2);
overweigh, n=21 (BMI, 23.82 kg/m^2);
Probiotic drink was provided to the treatment group.
	No dietary record	• At the baseline, acetic concentration was 20.5 mmol/g, butyric, 23.07 mmol/g and propionate, 58.03 mmol/g, respectively
		• Overweight children showed higher total faecal SCFAs concentration, particularly butyrate and propionate than normal weight children
		• Only investigated the abundance of *Lactobacillus* spp and *Bifidobacterium spp.* None of these bacteria were detected in the control group
			Joseph *et al.* (2019)

Compared SCFA content in normal healthy adults (M = 18, F = 32) to IBD patients (M = 6, F = 2)	Normal Malaysian diet, details were not provided	• The concentration of SCFA μmol/g wet faeces (mean ± SEM) in healthy adults are listed below: • Acetate = 209.7 ± 14.0 • Butyrate = 176.0 ± 16.0 • Propionate = 93.3 ± 5.3 • Formic acid = 21.5 ± 9.7 • Isobutyrate = 17.9 ± 13.2 • Gut microbiota composition was not measured	Huda-Faujan *et al.* (2010)
Investigated impact of FODMAP and ethnicity on gut microbiota variation in IBS patients (n = 34, 14M, 19F, 8 Chinese, 20 Malay, 6 Indians; BMI of 23.9 kg/m^2) and healthy controls (n = 15, 6 M, 9 F, 2 Chinese, 11 Malay, 2 Indian, BMI of 20.6 kg/m^2)	3 days self-dietary record. Diet record for control group was not highlighted	• Healthy adults have higher proportions of fermenter bacteria, such as *Succinivibrio dextrinosolvens* and *Intestinibaculum porci* along with SCFA producer *F. prausnitzii* when compared to IBS patients	Khoo *et al.* (2023)

TABLE 4. STUDIES ON SCFA CONTENTS AND GUT MICROBIOTA COMPOSITIONS IN MALAYSIANS (continued)

Study	Diet	Results / outcomes	Reference
Gut microbiota composition of different ethics in Segamant area n = 214 (46 Malay, 65 Chinese, 49 Indian, and 54 Jakun), 10 to 83 yo	Main food items are *ulam*, pork, beef, chicken, fish, fermented food fruits, coffee, tea, probiotics, raw food	• When all variables were adjusted, ethnicity (Malay, Chinese, Indian, and indigenous people) emerged as the most influential factor shaping the gut microbiota compositions in Malaysian (PERMANOVA, p = 0.002). • Three distinct enterotypes were identified: *Prevotella*-dominant, *Bacteroides*-dominant and *Bifidobacterium*-dominant. Jakun volunteers exhibited a higher prevalence of *Prevetella*-dominant enterotype, Chinese had more *Bacteroides*-dominant enterotype; while Malays and Indians showed similar distribution between the first two enterotypes. • Among volunteers, Malay displayed an increased abundance of *Clostridiales*, while Jakun and Indian participants exhibited unique taxa associations attributed to variations in health-related factors. • Functional pathway analysis of the gut microbiota revealed ethnic disparities. Jakun participants displayed elevated pathways connected to pyruvate fermentation, NAD biosynthesis, protocatechuate degradation, methylglyoxal degradation, and maltose degradation. Indians had elevated in L-arginine and fatty acid biosynthesis pathways compared to Chinese and Malays and they are associated respectively to demographic and health-related factors.	Dwiyanto *et al.* (2021)

Note: FODMAP - fermentable oligosaccharides, disaccharides, monosaccharides, and polyols; BMI - body mass index; IBD - inflammatory bowel disease; MCP - microbioal cell preparation; yo - years old.

Although the health benefits of SCFA are well known, there is limited data on the SCFA profile of healthy Malaysians who regularly consume palm oil. Therefore, more clinical data is needed to establish a link between the SCFA profile and other potential health benefits of regular palm oil consumption. This data would not only guide researchers in designing human clinical trials but also allow comparisons with other dietary oils in a balanced diet. These results can also provide valuable insights for policy makers to facilitate the effective implementation of health-conscious dietary recommendations, hopefully reducing the burden of medical costs.

Awareness of healthy diets can be achieved through collaboration between the government and private sectors to create a stable market for healthy foods while providing nutrition education programmes to enhance the public's understanding of good eating habits.

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