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Alternative proteins and gut health: balancing sustainability and uncertainty

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The need to nourish the increasing world population while ensuring the environmental sustainability of the food system boosted research in the field of alternative proteins (AP). AP include vegetable proteins, algae, insects, and proteins from microbial biomass. Several studies suggest that AP consumption may be positively correlated with human health. However, although the increasing research interest, the number of studies addressing the impact of their long-term consumption on the human gut microbiome is still limited. In this review, we summarize current evidence on the impact of different AP on the gut microbiome, highlighting the need for ad hoc-designed clinical trials to study the mechanisms by which AP may affect human health, also through the modulation of gut microbiome activities.

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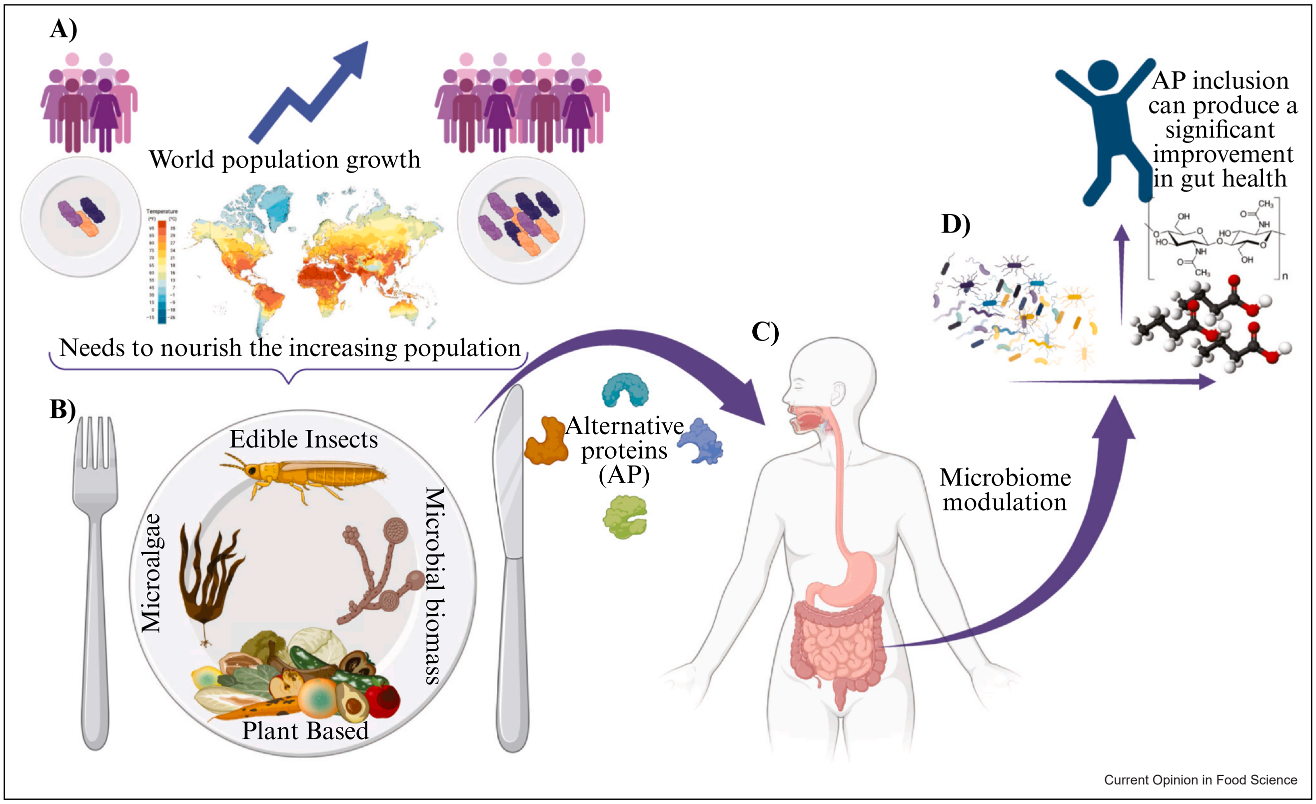
Introduction

Demographical, economical, societal, and climate change issues strongly motivate consumers to change their diet in a sustainable way [1] and dietary guidelines encourage populations to increase protein intake [2] (Figure 1a). Global demand for food is expected to nearly double by 2050. In this context, it is particularly important to find alternatives able to nourish the increasing population without compromising the environment. Alternative proteins (AP), which include plant-based proteins (PBP), algae, insects, and proteins from microbial biomass, have been proposed as a sustainable solution to ensure global food security (Figure 1b) [3]. A summary of the principal advantages and concerns of AP inclusion in the diet is reported in Table 1. Indeed, our knowledge on the impact of AP on health and on human gut microbiome remains limited (Figure 1c and d). The gut microbiota is widely recognized as having a significant impact on human well-being. It plays a fundamental role in modulating the immune system, influencing human behavior, and processing dietary nutrients and drugs. Current evidence indicates that numerous diseases could be linked to a general disturbance in the balance of the gut microbiome (namely, dysbiosis). It can be shaped by a multitude of factors, with nutrition being often regarded as the primary influencer [3]. Microbiome composition in various populations is significantly influenced by diverse dietary habits and eating patterns, which are associated with socio-economic status, lifestyle, ethnicity, and cultural practices that have developed over an extended duration. The recent shift in Western dietary patterns toward increased red meat, fat, and refined sugar consumption has been correlated with the rise of chronic diseases such as diabetes, obesity, allergies, and cardiovascular diseases [4,5]. While long-term dietary patterns play a crucial role, it is also important to consider the effects of short-term dietary changes. Indeed, short-term dietary interventions have been shown to alter the gut microbiome rapidly and effectively, even if these changes tend to be temporary [6].

Dietary proteins, health, and the gut microbiome

Primary dietary sources of protein include milk, meat, fish, eggs, legumes, and cereals, with animal-based proteins typically offering a more complete amino acid profile but lacking in some of the health-promoting components found in plant-based foods [7]. Indeed, plant-based foods are increasingly advocated for the lack of cholesterol, presence of health-promoting bioactive compounds (such as phytosterols, phenolic compounds, dietary fiber, etc.), and their contributions to sustainable agriculture ([8]; Table 1).

Figure 1



Graphical summary of AP sources and their effect on human health. **(a)** Due to the increase in the global population, food systems need alternatives that can help meeting the growing demand for dietary proteins in a sustainable way. Food preferences and availability not only affect human well-being but also impact the environment. **(b)** AP, such as PBP, algae, mycoproteins, and insects, offer potential solutions for global food security, benefiting both our health and the planet. **(c)** However, the impact of AP on human health and the gut microbiome remains an unexplored area. **(d)** The gut microbiome is influenced by shifts in dietary components. Since AP have the potential to support human health by shaping microbiome diversity and function, more research is needed to fully understand how incorporating AP into diets affects gut health. Created with BioRender.com.

Proteins vary in 'quality', defined by their ability to supply nitrogen and essential amino acids (EAAs). High-quality proteins, often animal-based, are well-digested and contain all EAAs in sufficient amounts, whereas plant proteins are generally less digestible, resulting in lower values on the Digestible Indispensable Amino Acid Score scale [9]. Despite these differences, plant proteins can achieve a complete amino acid profile through 'protein complementation', where different plant sources are combined [10]. Additionally, vegetable proteins come with bioactive compounds such as fiber, polyphenols, and phytosterols, which are linked to various health benefits, including improved lipid profiles, glucose regulation, and reduced risks of certain cancers and cardiovascular diseases [11]. A higher intake of plant protein has been linked to reduced risks of several age-related conditions, including metabolic syndrome and its risk factors, cancer, type-2 diabetes, cardiovascular disease mortality, and all-cause mortality [12,13]. In a meta-analysis of cohort studies, the intake of PBP was linked to a decreased risk of all-cause mortality. Indeed, an increase of 3% of daily energy intake from plant proteins was correlated with a 5% decrease in the risk of all-cause mortality [14].

While fiber is extensively studied for its role in modulating the gut microbiota, lower attention was given to proteins. Around 90% of dietary proteins are absorbed in the small intestine, with the remaining reaching the colon, where they serve as nitrogen sources for microbial fermentation. The digestibility of proteins influences the extent of microbial fermentation, with plant proteins, which are less digestible, leading to a higher level of microbial protein fermentation. Proteolysis and amino acid fermentation are mainly performed in the distal colon, where carbohydrates are depleted. Strains belonging to the *Clostridium* clusters (e.g. *Clostridium* spp., *Veillonella* spp., *Peptostreptococcus* spp., and *Fusobacterium* spp.), and *Bacteroides* spp. have been identified as the predominant proteolytic species of the human gut. Fermentation of proteins by the gut microbiota may result in the release of branched-chain fatty acids

Table 1

Summary of the main advantages, concerns, and European regulatory framework of the use of alternative protein sources.

AP source	Advantages	Concerns	Regulatory Framework in EU
Legumes and PBMA	• Presence of other bioactive compounds (vitamins, fiber, and polyphenols) • Part of Western countries cultural and culinary heritage	• Presence of antinutritional compounds • Low digestibility • Proteins lack of some essential amino acids • Allergies are known • Ultra-processed PBMA often contains several additives and high quantity of salt	No specific regulation is needed
Insects	• High-quality proteins • Presence of other bioactive compounds (vitamins, fatty acids, polyphenols, chitin, and minerals) • Low environmental and economic impact	• Possible presence of antinutritional compounds • Potential safety issues (microbial pathogens, chemical toxic compounds, heavy metals) • High-calorie amount • Cultural barriers to acceptability • No human trials available to assess long-term safety • Possibilities of new allergies	Only 4 species approved as novel foods with implementation of Regulation EU 2015/2283: *Tenebrio molitor* (EU 2025/89), *Locusta migratoria* (EU 2021/1975), *Alphitobius diaperinus* (EU 2023/58), and *Acheta domesticus* (EU 2023/5)
Microbial biomass and algae	• Presence of other bioactive compounds (fiber, polyphenols)	• No human trials available to assess long-term safety • Potential safety issues (depends on the quality of the environment where they are cultivated)	Algae: • Chlorella vulgaris and Spirulina platensis are considered as GRAS • Others have to be evaluated as novel foods Fungal biomass: • Quorn (mycoproteins obtained by specific strains of *Fusarium venenatum*) is considered traditional ingredient and does not need previous authorization • Other strains/species are considered as novel foods

(mainly isobutyrate and isovalerate), ammonia, amines (agmatine, spermidine, spermine, and putrescine), organic acids (lactate, succinate, formate, and oxaloacetate), phenolic and indolic compounds (e.g. p-cresol, indole, phenol, and skatole), sulfuric compounds, and gases (mainly CO_2, H_2, H_2S, and CH_4). Some of these compounds may have mutagenic and pro-inflammatory activity, also promoting the development of colon cancer [15]. Since plant proteins have a lower digestibility, it is expected that a higher amount would arrive in the colon compared with a diet with the same intake of animal proteins, leading to protein fermentation. Nevertheless, several cohort studies associated higher plant protein intake with positive health outcomes [16]. Therefore, the intricate relationship of dietary proteins with gut microbiome and human health is yet to be understood. This apparent discrepancy may be due to the concomitant presence of other macro- and micronutrients consumed together with plant proteins (e.g. polyphenols, fiber) that make it difficult to isolate the exclusive contribution of the protein fraction. Moreover, the extent of proteolytic fermentation by the gut microbiota is strictly dependent on the protein/carbohydrate ratio. Indeed, the concomitant presence of fiber in the same meal, as often happens in plant-based diets, may promote the switch from a proteolytic to a saccharolytic fermentation [17].

Plant-based meat alternatives and legumes

PBP are present in many different sources, including legumes, nuts, seeds, and whole grains. Among these foods, legumes are particularly rich in protein (21–25%). However, PBP often lack in one or more EAAs such as methionine, leucine, and lysine (Table 1). Nevertheless, the consumption of a variety of PBPs ensures the intake of all EAAs. Moreover, highly-processed Plant-Based Meat Alternatives (PBMA) often have a long list of ingredients and additives to improve sensorial and technofunctional properties (Table 1). Another challenge is that PBP are often associated with antinutritional factors, such as trypsin inhibitors phytates, and lectins in legumes, that reduce protein digestion and assimilation. However, some processing techniques, such as soaking, cooking, and fermenting, can reduce the presence of antinutritional factors, thereby enhancing nutrient bioavailability [18]. Indeed, a recent trial in mice suggested that the protein intake typical of a vegan diet is linked with the beneficial metabolic effect of such type of diets [19].

Table 2

Intervention studies investigating the effects of legumes and PBMA consumption on gut microbiome and human health.

Type of food/diet	Study design	Participants	Intervention duration	Intervention and control description	Total protein intake (Intervention group)	Pulse proteins intake	Gut microbiome analysis method	Observed Gut Microbiome effects*	Observed Health effects	Reference
Plant-based diet (with pulses)	Randomized controlled trial (RCT); Cross-over (CO)	n=23; Healthy (with low-to-moderate cardiovascular risk) omnivorous; overweight subjects; BMI 29–30 kg/m^2; 18–70 years old	2 periods of 3 months each NO WASHOUT PERIOD	MD: Mediterranean diet (MD); VD: vegetarian diet (VD)	VD group: 54.39 g (1400 kcal/day);[a] 62.51 g (1600 kcal/day);[a] 69.64 (1800 kcal/day)[a] MD group: 66.33 g (1400 kcal/day);[a] 76.20 g (1600 kcal/day);[a] 83.99 (1800 kcal/day);[a]	VD group 7.4 g/day[b] MD group 3.7 g/day[b]	16S rRNA	↑ *Anaerostipes* and *Streptococcus* in VD; ↓ *Clostridium* sensu stricto and *Odoribacter* in VD; ↑ *Enterorhabdus*, *Lachnoclostridium*, *Parabacteroides* in MD	NOT REPORTED	Pagliai et al., 2020 [22] (PMID: 31292752)
Plant-based diet (with pulses)	Randomized controlled trial (RCT); Parallel (P)	n=82; Healthy (with lifestyle risk factors for metabolic disease) overweight and obese omnivorous subjects; BMI 25–35 kg/m^2; 18–65 years old	8 weeks	MedD: individually tailored Mediterranean; ConD: habitual diet.	66.2 g/day[a]	MedD: 5.6 g/day[a]	16S rRNA	↓ *Ruthenibacterium lactatiformans*, *Flavonifractor plautii*, *Parabacteroides merdae*, *Ruminococcus torques,* and *Ruminococcus gnavus*; ↓ *Bilophila wadsworthia*; ↑*Faecalibacterium prausnitzii* clade, *Roseburia,* and *Lachnospiraceae*	↓ TC and HDL in MedD group compared with ConD group (at 4 weeks);	Meslier et al., 2020 [23] (PMID 32075887)
Plant-based meat substitutes (with legumes)	Randomized controlled trial (RCT); Cross-over (CO)	n=36; Healthy omnivores; normal-weight to obese subjects; BMI 23–33 kg/m^2; 18–65 years old	2 periods of 8 weeks each NO WASHOUT PERIOD	Plant phase: participants consumed at least 2 servings of plant-based meat products daily; Animal phase: participants consumed at least 2 servings of phase-congruent types of meat products (animal products) daily	85 g/day[a]	Plant phase: 41 g/day[a]	16S rRNA	↑ *Ruminococcaceae* sp., *Lachnospiraceae* sp. in Plant compared with Animal phase; ↑ *Lachnospiraceae* sp., *Roseburia* sp., *Ruminococcus* sp., in Animal compared with Plant phase	↓ TMAO level, LDL, and body weight in Plant phase	Crimarco et al., 2020 [24] (PMID: 32780794)

Table 2 (*continued*)

Type of food/diet	Study design	Participants	Intervention duration	Intervention and control description	Total protein intake (Intervention group)	Pulse proteins intake	Gut microbiome analysis method	Observed Gut Microbiome effects*	Observed Health effects	Reference
Plant-based meat substitutes (with legumes)	Randomized controlled trial (RCT); Parallel (P)	n=40; Healthy omnivores; normal to overweight subjects; BMI 18.5–30 kg/m^2; 18–65 years old	4 weeks	Intervention group: usual diet + replace a minimum of 4 animal-protein-based meals with a plant-based meat substitute (made from pulses) per week; Control: usual diet based on daily animal products consumption	NOT REPORTED	Intervention group: 11.3 g/day[b]	16S rRNA	↑ *Lachnospira*, *Faecalibacterium*, *Ruminococcaceae*, *Oscillospira*; ↓*Tenericutes*_ML615J-28	NOT REPORTED	Toribio-Mateas et al., 2021 [25] (PMID: 34574149)
Plant-based diet (with legumes)	Randomized controlled trial (RCT); Parallel (P)	n=53; Healthy omnivorous; normal subjects BMI 20–25 kg/m^2; 18–65 years old	4 weeks	VD (vegan diet) group: participants were free to choose their food within their assigned diet (strict vegan diet); This diet includes daily consumption of lentils, peas, beans, tofu products; MD (meat-rich diet) group: participants were free to choose their food within their assigned diet. In this group, participants must eat > 150 g of meat per day	79.5 g/day[a]	NOT REPORTED	16S rRNA	↑ *Alistipes*, *Bacteroides*, *Blautia*, *Coprococcus*, *Dialister*, *Dorea*, *Faecalibacterium*, *Ruminococcus*; ↓*Faecalibacterium* sp. and *Roseburia faecis*	NOT REPORTED	Kohnert et al., 2021 [26] (PMID: 33807447)

Table 2 (*continued*)

Type of food/diet	Study design	Participants	Intervention duration	Intervention and control description	Total protein intake (Intervention group)	Pulse proteins intake	Gut microbiome analysis method	Observed Gut Microbiome effects*	Observed Health effects	Reference
Food (Yellow pea noodles)	Single-arm pre-post study	n=8; Healthy; normal-weight female participants; BMI 23–25 kg/m^2; 18–65 years old	8 weeks (4 weeks of intervention + 4 weeks of post-observation period)	Intervention group: habitual diet + 200 g of boiled yellow pea noodles daily	NOT REPORTED	Intervention group: 14.2 g /day (only from pea noodles)[b]	16S rRNA	↓ *Bacteroides*, *Bilophila*, *Hungatella*, *Parabacteroides* and *Streptococcus*; ↑ *Bifidobacterium longum* and *Ruminococcus bromii* (but decreased after the washout)	↓ lysophos-phatidyl-choline (LPC)	Yamada et al., 2023 [27] (PMID: 37576055)
Food (navy beans)	Randomized controlled trial (RCT); Cross-over (CO)	n=55 Obese surveillance participants with a history of colorectal neoplasia; BMI ≥30 kg/m^2; ≥30 years old	16 weeks	Intervention group: habitual diet + 1 cup of navy beans	90.2 g/day[a]	Intervention group: 14 g/day (only from navy beans)[a]	16S rRNA Shotgun metagenomic sequencing	↑ *Bifidobacterium adolescentis, Eubacterium rectale, Oxalobacter formigenes, Veillonella atypica, Faecalibacterium*; ↓ *Bilophila wadsworthia, Blautia hydrogenotrophica, Christensenella minuta, Clostridium innocuum, Roseburia* sp. CAG:471, *Oscillibacter, Sharpea azabuensis, Streptococcus, Collinsella, Ruminococcus torques*	↑ fibroblast growth factor (FGF)-19; ↓ inflammatory markers	Zhang et al., 2023 [28] (PMID: 38040541)
Legumes	Quasi-Experimental, One-Group Dietary Intervention	n=8; Healthy, participants with some had specific health conditions; BMI 21.3–26.0 kg/m^2; 18–45 years old	8 weeks	Intervention group: replacement of one lunch meal with a vegetarian, legume-based meal (containing chickpeas, beans, lentils, peas, or soybeans) on five weekdays	83.8 g/day (weekdays)[a]	6.2 g/day (weekdays)[b]	qPCR	↑ *F. prausnitzii*, *Lactobacillus, Roseburia* spp., and *Clostridium leptum* subgroup	NOT REPORTED	Ferreira et al., 2024 [29] (PMID: 38964655)

Table 2 (*continued*)

Type of food/diet	Study design	Participants	Intervention duration	Intervention and control description	Total protein intake (Intervention group)	Pulse proteins intake	Gut microbiome analysis method	Observed Gut Microbiome effects*	Observed Health effects	Reference
Plant-based meat substitutes (with legumes) and pulses	Randomized controlled trial (RCT) Parallel (P)	n=127 Chinese prediabetes participants; BMI 19.5–32.0 kg/m^2; 45–75 years old	16 weeks	Intervention group (IG): consumed pre-cooked, low-calorie, ready meals containing mixed legumes 2 times/day; Control group: consumed meat (chicken or fish) 2 times/day	67.9 /day[a]	Intervention group: 46.8 g/day[a]	Shotgun metagenomic sequencing	↑ *Eubacterium rectale, Roseburia faecis, R. hominis, Bifidobacterium*; ↓ *Ruminococcus gnavus, R. torques, R. lactaris, Bacteroides massiliensis, B. stercoris, Bilophila wadsworthia;* ↑ glycoside hydrolases, CAZy genes (arabinoxylan, cellulose, pectin, and starch degradation); ↓ enzymes involved in the digestion of trehalose, lactose, or short fructooligosaccharides, CAZy related to the digestion of mucin and agarose; ↓ Microbial genes associated with histidine metabolism	↓ BMI in both groups; ↓ glycated hemoglobin (HbA1c), TC, HDL-C, LDL-C in IG	Wu et al., 2025 [30] (PMID: 39843443)

BMI, Body Mass Index; TMAO, trimethylamine N-oxide; TC, Total Cholesterol; HDL, high-density lipoprotein cholesterol; CAZy, Carbohydrate-Active Enzymes.

* If not specified, increase or decrease refers to the treated compared with the control group or in the treated group, compared with the baseline, as reported in the original publication.

[a] Data obtained from the information provided in the original article.

[b] Data on protein intake not provided in the original article; values were calculated using official food nutritional tables.

Unfortunately, there is a scarcity of controlled human studies specifically examining the impact of various dietary protein sources on microbiota composition and activities. Consequently, our current understanding is primarily derived from animal studies, and the results cannot be translated easily to humans. Substitution of animal proteins with a combination of soy and pea proteins in a mice model of Inflammatory Bowel Disease (IBD) reduced the IBD severity and led to an increase in fecal butyrate, *Lactobacillus*, and *Leuconostoc* spp. [20]. Conversely, a long-term supplementation with 20% soy protein for eight months led to a decrease in gut microbial diversity, while increasing the relative abundance of *Bacteroidetes* and *Muribaculaceae* [21].

As previously mentioned, the consumption of legumes may enhance gut microbiome composition and function. This hypothesis is supported by human clinical trials on legumes, legume-based meat alternatives, and plant-based diets rich in legumes, as summarized in Table 2, which details the intervention studies. A variety of dietary interventions investigated the effects of legumes on the gut microbiome and related health outcomes. These interventions included incorporating into the diet specific legumes, such as navy beans, pinto beans, and chickpeas, as well as PBMA products containing legumes. Additionally, we also included interventions with broader plant-based dietary patterns, including legumes (e.g. Mediterranean diet). Some of the results from clinical trials are contrasting. Yamada and colleagues [27] reported a reduction in *Bacteroides* with the inclusion in the diet of 200 g of yellow pea noodles daily (14.2 g/day of pea proteins). In contrast, Kohnert et al. [26] observed an increase in *Bacteroides* among participants following a vegan diet rich in legumes.

Lachnospiraceae spp. seem to be positively influenced by the consumption of legumes. They increased with the consumption of PBMA, primarily composed of pulses [24,25], as well as in participants following a Mediterranean diet that included an average of two servings (150 g each) of pulses per week (equivalent to 5.6 g/day of pulse proteins) [23]. In addition, Ferreira et al. [29] reported the increase in *Roseburia* spp. and *Faecalibacterium prausnitzii* when participants substituted one meal per day with a vegetarian, legume-based meal for eight weeks (providing 6.2 g/day of legume proteins). Similarly, Wu et al. [30] in a randomized controlled trial with legumes in 127 prediabetic Chinese participants, observed increase in *Eubacterium rectale*, *Roseburia faecis*, *Roseburia hominis,* and *Bifidobacterium,* correlated with reduction in low-density lipoprotein (LDL) cholesterol and inflammatory markers. While a diet rich in legumes and plant-based foods increases beneficial gut bacteria, it also leads to a decrease in potentially harmful bacteria. Yamada et al. [27] observed a reduction in *Bilophila* after the consumption of yellow pea noodles. *Bilophila wadsworthia* has been linked to colorectal cancer (CRC) through its ability to produce hydrogen sulfide, a genotoxic metabolite [31]. Consistently, Wu et al. [32] found a negative correlation between *Bilophila* levels and dietary plant protein intake, observing that vegetarians, who generally consume higher amounts of plant proteins, exhibited a lower prevalence of *Bilophila* compared to omnivores, despite the similar total protein intake.

Research summarized in Table 1 indicates that diets including legume proteins positively modulate the gut microbiome. Nonetheless, discrepancies exist in the findings. This may be attributed to factors like variations in the study populations, the types and amounts of legumes ingested, and individual differences in gut microbiome composition. Indeed, it is recognized that the individual variability in the gut microbiome, along with long-term dietary patterns and genetic factors, plays a complex role in how diet impacts human health [33]. However, it must be pointed out that different methodologies were used for the analysis of the gut microbiome composition in the studies reported in Table 1 (e.g. 16S rRNA gene or shotgun metagenome sequencing, qPCR). In addition, even when the same method is used (e.g. 16S rRNA sequencing), differences in the study design (e.g. 16S rRNA gene variable region targeted, Polymerase Chain Reaction primers, software used for data analysis) may be present, influencing the results obtained in terms of microbiome taxonomic composition. Therefore, properly designed clinical trials testing the impact of legumes and PBMA are necessary to explore the impact of these products on gut microbiome and, consequently, on the host's health. Another important point to highlight is that plant proteins usually come with other bioactive compounds that may have an effect on health and gut microbiome modulation, such as fiber and polyphenols. Therefore, the effects reported might be only partially attributable to the protein fraction but would be rather the combined results of multiple compounds.

Edible insects

Edible insects (consumed as larvae, pupae, or adults) are considered an ancient traditional food in several parts of the world, with more than 2000 species consumed, including beetles, caterpillars, wasps, ants, bees, grasshoppers, locusts, flies, cicadas, leafhoppers, termites, dragonflies, and crickets, among others [34]. Insects are considered as a substitute of animal or plant foods due to their nutrient composition ([35]; Table 1). The nutritional composition varies in different species but in general insects contain high-quality proteins, ranging from 35% to 60%, fats from 13% to 29%, and fibers from 5% to 13%, [36,37]. Several bioactive compounds have also been identified, including polysaccharides, phenolics compounds, peptides, vitamins, fatty acids (mainly lauric acid), chitin, antimicrobial, and active peptides [38]. Proteins in some insect species contain EAAs (e.g. leucine, histidine, threonine, isoleucine, tryptophan, lysine, and valine) or biologically active peptides with anti-hypertension, anti-hyperglycemia, anti-inflammation, antitumor, and anti-obesity effects. In order to increase insect protein value and their biological properties (e.g. bioactive peptides), enzymatic pre-treatments or microbial fermentation might be required [39]. On the other hand, potential allergic reactions [40] or the presence of unwanted molecules such as antinutritional components (e.g heat-resistant thiaminase, oxalates, tannins, and alkaloids) [41], pathogens, antibiotic resistance genes, or chemicals [36] can represent a safety risk for the consumers (Table 1). These considerations must be seriously taken into account, especially when choosing breeding methods, growth substrate selection, and food preparation methods. In addition, the inclusion of these novel proteins in the diet of Western population may lead to the onset of new allergies (Table 1).

Four insect species have been authorized in the European Union as novel foods pursuant to Regulation (EU) 2015/2283 and its implementation: *Tenebrio molitor* (EU 2025/89), *Locusta migratoria* (EU 2021/1975), *Alphitobius diaperinus* (EU 2023/58) larvae [42], and *Acheta domesticus* (the common house cricket; EU 2023/5). The latter has emerged as one of the most studied insects, not only for its high content of EAAs, but also for being capable of efficiently converting organic materials into insect biomass [43]. Since edible insects can be a new source of proteins and unexplored bioactive compounds in the near future, deep investigation in humans as well as in animal models should be conducted. The supplementation in the diet of monogastric species (such as fish, poultry, pigs, and rabbits) with *Hermetia illucens*, *Tenebrio molitor*, *Acheta domesticus*, and *Bombyx mori* may have a primary influence on growth performance and on beneficial modification in the animal gut microbiota, with an increase in short-chain fatty acids (SCFAs) producing taxa and a reduction in pathogens linked with the high content of proteins, chitin, and lauric acid [44].

Human randomized controlled intervention studies with insect proteins to improve nutritional status and changes in microbial gut composition are limited to draw clear conclusions. To date, only one human trial suggested that cricket consumption in healthy individuals was associated with reduced plasma TNF-α, improved gut health with increased abundance of *Bifidobacterium*, and reduced systemic inflammation [45]. Conversely, other studies on the effects on inflammatory markers, blood concentration of EAAs, and microbiota composition were inconclusive [1,47]. Most of the data available comes from *in vitro* studies, where cricket proteins were able to modify the microbiome composition in batch cultures inoculated with adult feces [46]. Since insect-based protein will be incorporated into food products in the future, it is crucial to assess how they affect the human and animal gastrointestinal tract. The lack of clinical data on humans may depend on food neophobia, especially in Western countries, and this can be a significant barrier in planning human studies. However, consumers' attitudes toward edible insects tend to improve once they are informed about their nutritional profile and sustainability [37]. Since edible insects have the potential to support human health, more research is needed to fully understand how incorporating insect-based foods into diets might shape the microbiome and overall well-being.

Microbial biomass and algae

Single-cell proteins, consisting of biomass produced by fungi, yeast, algae, and bacteria, represent another promising alternative to conventional protein sources ([48]; Table 1). Within this category, microalgae include a heterogeneous group of eukaryotic organisms such as bacillariophytes (diatoms), chlorophytes (green algae), euglenophytes, dinophytes (dinoflagellates), prymnesiophytes (coccolithophorids), and prokaryotes present in both freshwater and marine environments, with some species also distributed in humid soils [49]. Currently, *Chlorella vulgaris* (≈2000 tons annually, dry weight) and *Spirulina platensis* (*Arthrospira* spp., ≈5000 tons annually, dry weight) are the most widely cultivated species [50]. Both are classified as Generally Recognized As Safe (GRAS) according to the Food and Drug Administration, and recognized by the World Health Organization as 'superfoods' [51]. Microalgae are rich in bioactive compounds, including carbohydrates (e.g. oligosaccharides), and phenolic compounds, which may have a potential prebiotic effect [52], although the quantity and the type of compounds vary by species. Due to their high-value nutritional profile, microalgae can be an excellent immunostimulant that plays a role in enhancing fish immunity and improving the capacity of anti-infection [53]. Research on the prebiotic effects of microalgae remains limited, with most studies focusing on purified oligosaccharide extracts and their impact on the growth of specific microbial cultures [52]. Although the prebiotic effect of non-digestible carbohydrates is well established, dietary phenolic compounds seem to be involved in the modulation of the intestinal microbiota and the production of metabolites important for host health. Seaweeds have gained attention for their nutritional and functional properties. Some species contain significantly high levels of dietary fibers (up to 76% of dry matter) along with proteins and phenolic compounds that may promote human health [54]. Due to the prebiotic activities, brown seaweeds are the most studied [55]. Among all, brown seaweed (*Himanthalia elongata*) has been tested in an *in vitro* model of the human colon and demonstrated a prebiotic activity, selectively boosting the growth of specific members of the gut microbiota, such as *Bacteroides* species [56].

Mycoproteins (commercially known as Quorn) represent another novel food ingredient derived from the continuous carbohydrate-fermentation of a fungus called *Fusarium venenatum* [57]. Quorn is rich in both protein and insoluble fiber. Recently, it has been approved by EU as traditional ingredient and does not require prior authorization as novel food (does not apply the Novel Foods Regulation (EU) No 2015/2283; Table 1). Epidemiological evidence suggests that mycoprotein consumers have lower fasting blood glucose and HbA1c protein, a marker of diabetes [58]. The fiber in mycoprotein has been demonstrated to be fermentable [59] and can reduce fecal genotoxins and increase beneficial bacteria in the human gut [60]. Recently, Colosimo and colleagues [61] have reported an increase in three *Bacteroides* species, *B. ovatus*, *B. xylanisolvens*, and *B. uniformis* in a colon *in vitro* model upon administration of mycoproteins and an increase in the production of beneficial SCFAs. Nevertheless, human studies on the impact of mycoproteins on gut microbiome composition and microbial metabolite production are still lacking.

Conclusions and future perspectives

The profound impact of proteins on gut health and overall human well-being is well established. However, only limited data from randomized and properly controlled human trials are available on the role of specific dietary proteins and their interactions with other macro- and micronutrients. Much of our current knowledge comes from correlational studies and animal or *in vitro* models, which, while informative, do not fully capture the complexity of human biology and make it difficult to translate the results to humans. Therefore, future investigations should focus on conducting human clinical trials specifically designed to study the mechanisms by which novel protein sources affect human health, also through the interactions with the gut microbiome. Indeed, the design of updated dietary recommendations that include novel protein sources is advisable, but they cannot ignore the impact on gut microbiome composition and activities. Moreover, citizen-directed campaigns should focus on informing and educating about the health benefits and sustainability of the consumption of novel proteins to break the cultural barriers. Indeed, in most Western countries, there is still a limited cultural acceptability toward these novel products. Besides this, the lack of a clear national and international regulation on APs is another important issue, limiting the industrial interest in investments in this sector and slowing down the uptake of research innovation in this field. Despite these limitations, it is clear that to reach the United Nations Sustainable Development Goals expected in 2030, maintaining the sustainability of the food system, while ensuring healthy and nutritious diets for the increasing world population, AP sources will become increasingly widespread. In this context, microbiologists, food technologists, nutritionists, social scientists, and regulatory bodies must collaborate to develop and make available on the market more and more products containing APs, and at the same time promote consumer awareness and acceptance.

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CRediT authorship contribution statement

Roberto Marotta: Data curation, Writing – original draft, Writing – review & editing. **Erica Pontonio:** Data curation, Writing – original draft, Writing – review & editing, Funding acquisition. **Ilario Ferrocino:** Conceptualization, Data curation, Funding acquisition, Writing – original draft, Writing – review & editing. **Francesca De Filippis:** Conceptualization, Funding acquisition; Supervision, Writing – original draft, Writing – review & editing.

Data Availability

No data were used for the research described in the article.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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- • of special interest
- •• of outstanding interest

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