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Hybrid plant-based meat alternatives structured via co-extrusion: A review

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ABSTRACT

Background: Hybrid foods, which combine plant-based proteins with conventional animal sources and/or future-forward alternatives, have emerged as a promising strategy to gradually bridge the gap between current animal-based diets and sustainable alternatives. Extrusion technology has also proven its potential in structuring diverse proteins into fibrous, meat-like textures.

Scope and approach: This review explores the co-extrusion of plant-based proteins with meat, fish and/or emerging alternative sources, including insects, algae, mycoproteins, and cell-cultured meat, as an innovative approach to the development of hybrid meat alternatives. We have discussed how the co-extrusion of plant-based proteins with conventional and/or alternative sources can complement them in mimicking conventional meats' fibrous structure or achieve appealing textural, taste, color, and nutritional features. Challenges such as phase separation, off-flavors, and thermal instability or incompatibility are discussed, along with potential solutions through processing innovations, enzymatic modifications, and technological advancements.

Key findings and conclusions: Overall, precise optimization of extrusion parameters and mixing ratios for every two sources are critical to maintaining protein structuring and essential nutrients during co-extrusion. A shift toward utilizing co-extrusion to develop hybrid products that transcend fibrous texture—integrating enhanced nutritional value, color, flavor, cost and health benefits through the complementary and unique potentials of diverse sources and reactions during co-extrusion—should define the future direction. By leveraging extrusion and hybrid formulation advancements, the food industry can develop scalable, nutritionally rich, and environmentally sustainable alternatives that align with evolving dietary preferences and global food security goals.

1. Introduction

The role of meat in human diets is complex, involving diverse human attitudes and various conflicting factors. It is well established that excessive consumption of red and processed meats can lead to health issues such as obesity and chronic diseases (Wang et al., 2024a,b,c). Conversely, meat remains a valuable source of highly digestible proteins, essential amino acids, heme iron, vitamin B12, and fatty acids. Thus, dietary guidelines often recommend reducing but not eliminating it (Ruxton & Gordon, 2024). Beyond health implications, the negative impact of meat production on the environment and animal welfare has also been extensively criticized (Ha et al., 2024).

As a response to the health, environmental and ethical challenges posed by conventional meat production, the global shift towards

alternative protein sources is gaining momentum. Consequently, alternative sources including plant-based proteins, fermentation-derived ingredients, insects, algae and cultured meat have emerged as promising solutions to mitigate the concerns associated with traditional livestock farming and meet the consumers growing demands for healthy and sustainable foods (Ha et al., 2024). However, each of these resources has its own limitations and cannot fully compete with animal-based products in terms of nutritional value, convenience, cultural relevance, affordability, sensory attributes, and consumer acceptance (Malila et al., 2024). For instance, while plant-based proteins are sustainable and widely available, they often lack a complete amino acid profile or have lower digestibility and may require significant processing to achieve desirable textures and flavors and cannot fully meet consumers' sensorial expectations (Kumar et al., 2022). Fermentation-derived

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ingredients, despite their precision and efficiency, are constrained by high production costs and scalability challenges (Knychala et al., 2024). Cultured meat, while nutritionally comparable to conventional meat, faces hurdles in affordability, production scalability, and regulatory approvals (Treich, 2021).

In this context, the concept of hybrid foods has emerged as a promising solution, either by partly substituting traditional meat with plant proteins or, more recently by combining plant-based proteins with emerging alternatives to harness the strengths of each, while compensating for their individual weaknesses. By integrating complementary components, hybrid foods can deliver products that are nutritionally balanced, economically viable, sensorially appealing, and more closely aligned with consumer preferences, ultimately paving the way for a more sustainable and widely accepted dietary transition (Olivas et al., 2024).

A critical aspect of developing meat analogues is replicating conventional meat's complex texture and structure, a challenge that extrusion technology is uniquely positioned to address. This scalable and efficient thermomechanical processing method has become a cornerstone of plant-based meat analogue production due to its ability to texturize plant proteins into fibrous, anisotropic structures that closely mimic the texture and mouthfeel of animal products (Morantes et al., 2020). In this sense, extrusion technology, especially high-moisture extrusion (HME), enables the alignment of protein molecules into organized muscle-like fibers while allowing for the incorporation of fats, flavors, and binders to enhance sensory attributes (Samard & Ryu, 2019). However, while extrusion technology offers numerous advantages—such as cost-effectiveness, continuous production, and adaptability to various protein sources, challenges remain in achieving the intricate textures, juiciness, mouthfeel, and nutritional optimization necessary to fully replicate meat. Hybridization (i.e. combining various conventional and emerging food sources) presents a unique opportunity to address these gaps by integrating diverse alternative protein sources into the extrusion process (Jareonsin et al., 2024). In addition, its versatility makes HME an attractive platform for hybrid foods, where plant proteins can be effectively combined during extrusion (i.e. coextruded) with other alternatives e.g. fermentation-derived ingredients or algae-based components to overcome limitations in texture, juiciness, and overall palatability. It could also be used sequentially for texturizing plant proteins to the base material for subsequent enrichment or fermentation or as scaffolds for the subsequent development of hybrid foods by cultivating microorganisms or cells.

Hence, this comprehensive review explores the intersection of hybrid food production and extrusion technology, from hybrids that combine conventional resources (such as meat and fish) with plant proteins to innovative combinations of plant-based proteins with emerging alternative food sources, including single-cell proteins and pigments, algae, insects, and cell-cultured meat. The review aims to uncover the implications and contribution of extrusion technology within the context of hybrid foods and the benefits of hybridization in mitigating the limitations of plant-based meat analogues. Through rigorous analysis, we examine how the addition, substitution, or combination of various sources during extrusion (i.e. co-extrusion), especially HME, modifies the physicochemical properties of ingredients, thereby influencing the texture, flavor, and stability of the resulting extruded products. Furthermore, the review addresses the nutritional advantages of hybrid meat alternatives and their consumer acceptance.

2. Hybrid foods definitions, their necessity in the diet shift and protein diversification

Consumer food choices are increasingly influenced by nutritional value, flavor, texture, and sustainability considerations (Siegrist & Hartmann, 2020). Strategies that maintain established meal structures—where animal protein traditionally plays a central role—offer a promising way to encourage a broader shift toward alternative

protein-based diets. Unlike the traditional binary view of meat consumption or complete abstention, reducing meat intake enables consumers to cut down on meat without eliminating it (Schösler et al., 2012). Hereby, to promote a lasting dietary shift, transitioning toward a partially plant-based diet that includes sustainable plant proteins would encourage long-term adoption rather than short-term changes (Hoek et al., 2013).

In this line, flexitarianism promotes reducing meat intake without strict restrictions and supports sustainability, animal welfare, and health (Derbyshire, 2017) by moderating meat consumption, incorporating alternative protein-based meals, or adjusting portion sizes to favor plant-based sources (Kemper & White, 2021). As consumer preferences evolve, there is a growing demand for products that balance familiarity with sustainability, offering both the taste and texture of meat and the benefits of a plant-based diet (Olmedilla-Alonso et al., 2013). Here, a more conventional definition of hybrid products emerges which combines animal and plant-based elements to offer a compromise between traditional meat consumption and alternative proteins-forward diets (Neville et al., 2017). Although there is no official definition for this category of hybrid products, they are generally categorized as animal products containing varying proportions of plant-based ingredients. Products in this category and their consumer acceptance have been comprehensively reviewed by Grasso and Jaworska (2020) and Ataman (2024).

Beyond plant-based sources, there is growing interest in diversifying sustainable alternative food sources by including algae, fermentation-derived sources, insects, and cultured meat. This shift aligns with the increasing consumer adoption of meat-free days and replacing meat with nutritionally balanced but sustainable alternatives (Lang, 2020). Combined with the nutritional and sensorial limitations of plant-based meat alternatives, this trend has led to the emergence of a new category of hybrid products. Within this category, hybrid foods are defined as products where plant-based proteins are partially combined with other alternative sources, such as algae, insects, microbial single cells, and cell-cultured meat, or enriched with fractions or compounds from these alternatives, including fats, heme proteins, flavors, and vitamins (Neville et al., 2017). This approach improves the sensory and nutritional quality of plant-based alternatives while enhancing consumer acceptance of novel ingredients that face high production costs, scalability issues, and limited familiarity. Successful examples, such as the Impossible Burger, demonstrate how recombinant yeast-produced heme enhances flavor and texture, making plant-based proteins more meat-like (Baune et al., 2023).

3. Extrusion as a technology for the development of hybrid foods

Despite the long history and widespread application, the capacity to induce fibrous structures in plant proteins to mimic anisotropic textures of animal muscle products has brought special attention to extrusion technology. A combination of high temperature (120–160 °C), shear and pressures (5–30 MPa) during the extrusion process induces protein denaturation and partial realignment, resulting in the formation of fibrous porous structures that resemble the texture of ground meat or fibrinous gelled structures similar to meat chunks, depending on the moisture content and machine configuration. Food extrusion has been a key technology in the food industry for over 150 years. It originated in 1870, when meat extruders were used to produce sausages (Egal & Oldewage-Theron, 2020). Since then, the configuration, automation, and optimization of various components and overall performance have been continuously adapted to meet modern needs (Chaiyakul et al., 2009). The modern structure and functioning of an extruder have been described by P. Singh et al. (2025) and depicted in Fig. 1. However, extrusion techniques can vary between low (dry) and high moisture methods, with the choice often dictated by the specific requirements of the product being manufactured (Fellows, 2022).

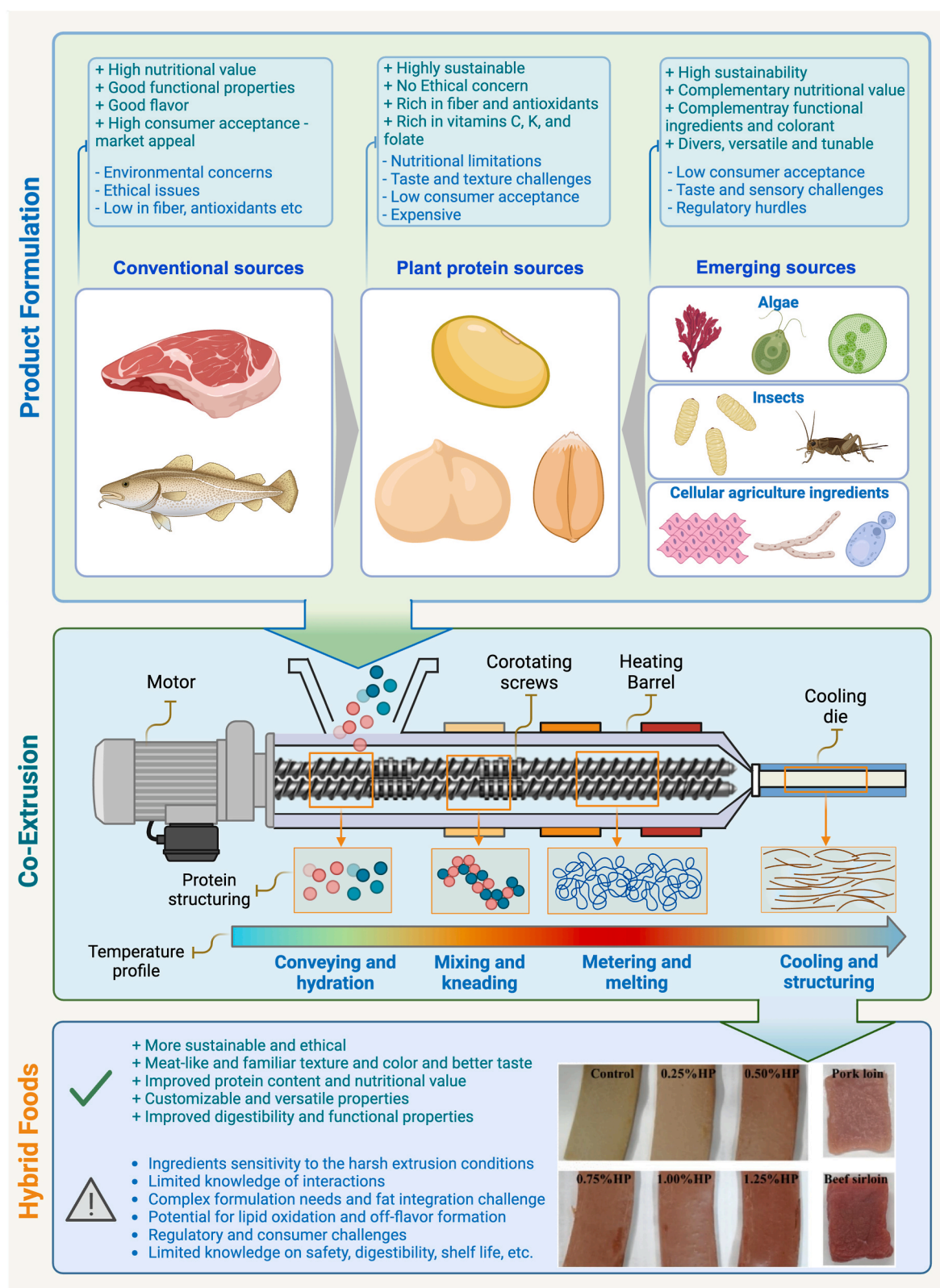


Fig. 1. Schematic overview of hybrid food development via co-extrusion cooking. The figure also shows the pros and cons of each biomass in the process, as well as some aspects of the final product.

Dry or low moisture extrusion (LME) is a cost-effective, energy-efficient and well-established process used for producing textured vegetable proteins (TVPs) for meat analogue applications traditionally using single screw extruders. The use of a short die promotes rapid

expansion as the material exits the extruder, leading to the formation of expanded, porous products with a spongy texture that resembles ground meat. Dry extrusion typically operates at lower moisture levels (10–40 %) compared to HME, making it suitable for shelf-stable products. While

it is advantageous for its simplicity, scalability, and reduced water usage, the method may produce TVPs with less anisotropic texture, requiring further soaking, substantial flavoring and/or other polishing steps to achieve the products consumers' acceptance (Liu et al., 2005). Here there is significant, yet underexplored, potential for hybridizing alternative sources to produce tastier TVPs, facilitated by twin-screw extruders. This approach is well-suited for the sequential development of hybrid products, allowing the incorporation of other alternative sources to enhance sensory qualities or serve as scaffolds for cultivating microorganisms or animal cells (Baune et al., 2023).

High-moisture extrusion (HME) is one of the most common methods for creating plant-based meat and fish analogues, and more recently, hybrid products via co-extrusion. HME requires protein-rich powders, with water added separately to achieve a moisture content above 40 %. Its success is owed to the development of twin-screw extruders (McClements & Grossmann, 2022). The high moisture content of the protein structure is preserved in the final product by using a long cooling die, which prevents a rapid pressure drop and aligns melted protein molecules to form fibrous structures. As the extrudate exits the die, it develops a fibrinous gelled structure resembling meat chunk, which can then be cut and further processed, e.g., marinated, frozen, fried, or shredded (Schmid et al., 2022). The effect of ingredients and processing on the fiber formation of plant proteins during HME and its mechanism has been extensively discussed in other reviews (Tang et al., 2025; Zhang et al., 2022a,b).

HME can be effectively employed to develop hybrid products, either by directly co-feeding a mixture of plant proteins and other conventional or alternative sources into the extruder as the bulk (fiber-forming) or functional component (e.g., as colorant or fat source) here called co-extrusion, which is the main focus in this review (Fig. 1), or by subsequently combining the extruded product with ingredients from alternative sources, such as biotechnologically produced, heme proteins, flavoring agents, colorants, vitamins, and other functional components. A summary of various examples of hybrid plant-based meat and seafood alternatives developed via co-extrusion of different plant proteins with meat, fish, insects, microalgae, fungi, yeast and cell cultured meat and their main purpose, extrusion conditions and key findings are summarized in Table 1.

4. Status of the development of hybrid food products with co-extrusion

4.1. Plant-based hybrids co-extruded with meat

Animal meat from various sources such as beef, pork, lamb or poultry is often associated with a good amount of nutrients but also good taste and mouthfeel. However, both TVPs and HMEs made of plant proteins alone often lack some nutrients and require extensive post-processing steps to improve their flavor. Therefore, previous studies have targeted the partial incorporation of animal meats during the extrusion of plant proteins. This has also been considered as an opportunity to add value to the side streams from the meat or poultry processing industry, which often have low market value and face low consumer acceptance due to poor texture and product formation capacity. For most consumers, replacing meat with plant-based ingredients is acceptable if the meat content is no less than 50 % (Grasso, Ascoli, & Smith, 2022). This range allows for a significant reduction in meat content while maintaining the sensory qualities desired by consumers (van Dijk et al., 2023). However, animal meat or their side streams often contain high moisture and fat content, which makes their incorporation into the extrusion process challenging. To address these challenges, Lawrie and Ledward (1983) conducted foundational studies on the extrusion of hybrid meat analogues using dry protein powders derived from meat side streams. The protein powders were blended with soy grits in up to 90 % of the mixture and extruded using a single-screw extruder at 140–190 °C and 35–40 % moisture content. The extrudates, containing

approximately 20 % water, were subsequently dried at 65 °C to achieve a moisture content of ~6–8 %. The resulting products exhibited adequate expansion ratios, a laminar structure, and firm textural attributes, including hardness and chewiness, upon rehydration. This method closely resembles the production of textured vegetable proteins, with the expanded structures attributed to maintaining water and fat content within optimal levels during extrusion, not exceeding 40 % and 5 %, respectively (see Table 1).

Later, the concept was expanded to HMEs to directly mix wet mechanically deboned chicken meat (MDM) with plant proteins (Mégard et al., 1985). The restructuring of MDM in combination with 10–20 % wheat flour or pregelatinized corn starch, while adding 25 % soy protein isolate using twin-screw extrusion under high-moisture conditions (50–80 %) and elevated temperatures (~150 °C) resulted in products resembling meat loaf with a solid gel matrix with dispersed meat particles. This process was introduced as a pathway for producing simulated meat chunks or slices from poultry side streams for canned or frozen applications. Also, hybrid products incorporating pork, despite challenges posed by its high fat content using HME, has been also proven (Liu et al., 2005), by using lean pork and controlling the fat content. Using a twin-screw extruder, with careful optimization of extrusion temperature (60–100–120–150–110 °C) screw speed (60–80 rpm) and moisture content (50 %) and 12–16 % oil content, the authors managed to incorporate 30 % lean pork into a mixture of defatted soy flour, isolated soy protein, and corn starch and achieve high-quality hybrid extrudates. Their results showed the importance of precise formulation and process optimization in producing high-quality hybrid soy-pork analogues with desirable sensory attributes.

As explained, increasing fat content during HME to levels above 6 % decreases shear and, consequently, the fiber formation in the extruded meat analogues. Recently, Pöri et al. (2023) showed that an increase in fat content from 6 % to 16 % did not affect the quality of hybrid products made of minced beef and pea protein at 1:1 ratio developed with HME (Fig. 2a). However, they found that the type of pea protein ingredients (i.e. pea protein isolate (PPI) vs pre-texturized protein concentrate (TPC)) plays a significant role in the structural and textural properties of the hybrid products as well as their sensorial attributes. Hybrids containing PPI exhibited a softer, layered structure with a dominant pea-like taste and odor. While those made with beef and TPC displayed a harder, more fibrous structure, a meat-like odor, and umami flavor. The pre-texturization of TPC reduced volatile compounds, contributing to its enhanced meat-like characteristics. Both PPI and TPC were deemed suitable for hybrid meat analogues due to their high protein content, low solubility, and high water-binding capacity (WBC). However, the starch in TPC likely promoted phase separation and fibrous structure formation during extrusion, suggesting its potential for producing hybrid products with superior textural and sensory attributes.

Another interesting approach opening a new window for the development of plant-based hybrid products with better taste was targeted by Chiang, Hardacre, and Parker (2020a, b) to benefit from the chemical reactions and high temperature during the co-extrusion process. They incorporated Maillard-reacted beef bone hydrolysate (MRP), at 10–40 % to soy protein concentrate and wheat gluten during HME. They found increasing MRP concentrations reduced fibrous structure formation, with 40 % MRP exhibiting the lowest degree of texturization and a microstructure characterized by segmented layers and limited fibrousness (Fig. 2b and c). However, hybrid extrudates with 20 % MRP scored highest for sensory attributes, including appearance, meaty aroma, and taste (Fig. 2d). They also showed that there is a threshold of 49 % for moisture content on which the hybrid products could mimic the textural and microstructural properties of the reference sample, boiled chicken breast (Chiang et al., 2020b).

In conclusion, the incorporation of animal-derived ingredients, including meat side streams, into plant protein matrices during extrusion offers a promising pathway for developing hybrid meat analogues with improved texture, structural, and sensory attributes. While

Table 1

A summary of hybrid plant-based foods developed using extrusion technology, the used sources and their key findings.

Hybrid source	Plant-based protein	Main Purpose	Extrusion max temperature/ moisture	Key findings	Reference
Deboned Chicken	Soy protein isolate (SPI)	Texturization of recovered chicken meat after mechanical deboning.	150 °C/80 %	<ul style="list-style-type: none"> Addition of 10–20 % wheat flour or pregelatinized corn starch are necessary to resemble the texture and techno-functionality of meat loaf. Incorporation of 25 % soy protein isolate gives a solid gel matrix. The extrusion-texturized samples withstand freeze-thaw treatments or heat processing up to 120 °C for 20 min. 	Mégard et al. (1985)
Lean pork	Defatted soy flour	Enhance flavor, sensory texture and nutritional values of TVP by adding animal protein.	140–150 °C/50 %	<ul style="list-style-type: none"> The optimal sensory texture and energy consumption were obtained with a rectangular die, lean pork content of 30–50 %, and oil content of 12–16 %. 	Liu et al. (2005)
Meat bone hydrolysate	Soy protein concentrate (SPC) and wheat gluten (WG)	Ensure the sustainability of the meat industry and improve the sensory aspect of extruded food products <i>i.e.</i> , contributing to their appearance, texture, flavor, and aroma	170 °C/45–60 %	<ul style="list-style-type: none"> Meat alternatives at 49 % moisture were the closest in terms of both textural and microstructural properties to boiled chicken breast. Moisture content is important in the formation of fibrous structure in extruded meat alternatives. Meat alternatives containing 20 % Maillard-reacted beef bone hydrolysate obtained highest sensory scores for appearance, meaty aroma, meaty taste, and overall acceptability. 	(Chiang et al., 2020a, Chiang et al., 2020b)
Minced beef (with 7 or 17 % fat)	Milled texturized pea protein (TPC) and pea protein isolate (PPI)	Enhance flavor, sensory texture and nutritional values of TVP by adding animal protein	150–160 °C/NE	<ul style="list-style-type: none"> Extrudates with beef and PI were softer and layered, while extrudates with beef and TPC were harder and had smaller fibres. The fat content did not significantly affect the textural properties. TPC conveys meat-like odor and umami taste, while PT mainly conveys pea taste. 	Pöri et al. (2023)
Whole/gutted Herring mince	Commercial pea protein isolate	Avoid the need for extensive pre-processing of undervalued fish species	150 °C/55 %	<ul style="list-style-type: none"> The structure of the whole fish extrudate was weaker than the gutted fish and pea protein isolate. Whole fish and gutted fish extrudates showed uniform flavor- and odor-related sensory profiles. 	Nisov et al. (2020)
Fish Surimi	SPI	Analyze nutritional changes in extrudates, varying SPI–surimi ratios and extrusion parameters. Likewise, examine how hydrothermal parameters affect the nutritional aspects	145 °C/75 %	<ul style="list-style-type: none"> More surimi improved the amino acid and fatty acids content, while lowering the n-6/n-3 ratio Higher moisture and temperature increased the fatty acid content Digestibility was highest at SPI–surimi ratio of 90:10, in the stomach and 70:30 in the intestine. 	Hu et al. (2024)
		Analyze the gelling properties, texture and structure of mixed proteins to establish relationships between gelling properties, fibrous degree, hardness, chewiness, gel strength, and specific mechanical energy.	135 °C/70 %	<ul style="list-style-type: none"> At SPI–surimi ratio 80:20, the extrudate showed the higher hardness, while more than 40 % surimi hinder the fibrous-oriented structure formation. SPI may act as the continuous phase that is dispersed by surimi during the extrusion processing. The gel strength of SPI–surimi blends was nonlinearly correlated with the specific mechanical energy and product textural properties 	Zhang et al., 2022a,b
<i>Insect (Alphitobius diaperinus)</i>	Soy protein concentrate	Developing meat substitutes that resemble the taste and physical properties of meat	170 °C/NR	<ul style="list-style-type: none"> Inclusion of 15–40 % of insect protein concentrates imitates the meat texture. Extruder barrel temperature and soy–insect ratio affect the physical properties of the extrudates. Increasing the temperature or decreasing the water input improved the hardness of the intermediates. 	Smetana et al. (2019)
<i>Insect- Cricket (Acheta domesticus)</i>	Soy protein isolate	Creating appealing meat-like products to vehicle insects as foods and enhance consumer acceptance	160 °C/10 mL min ⁻¹	<ul style="list-style-type: none"> Cooking temperature and insect flour inclusion had a significant effect on the physical aspect, while water rate was not significant. 	Kiiru et al. (2020)

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Table 1 (continued)

Hybrid source	Plant-based protein	Main Purpose	Extrusion max temperature/ moisture	Key findings	Reference
				<ul style="list-style-type: none"> Insect inclusion caused a shift from a tough multilayered structure to a more homogenous fibrous structure. SPI-cricket flour blend having 30 % low-fat CF content showed best anisotropic structure. 	
<i>Insect-Black soldier fly (Hermetia illucens)</i>		To characterize cricket flour its incorporation into high moisture extrudates together with soy protein	140 °C/50 %	<ul style="list-style-type: none"> Addition of cricket flour enhanced anisotropic structure formation, while higher concentrations reduced mechanical strength and coherence Cricket contributed pyrazines and ethers, imparting a desirable burnt and baked flavor 	Wang et al., 2024a,b,c
		To examine how black soldier fly protein affects the texture of meat analogues made via high-moisture extrusion and compare it with plant-based and animal-based products.	100 °C/55 %	<ul style="list-style-type: none"> Black soldier fly larvae protein decreased the textural characteristics of meat analogues as its amount in the formulation increased. The interaction of black soldier fly larvae protein with soy protein affected the hardness and chewiness of meat analogues. 	Miron et al. (2023)
<i>Insect (Tenebrio molitor)</i>	Defatted soy flour, isolated soy protein, and corn starch	To investigate the effects of die temperature and moisture content on physicochemical properties of meat analog extruded with mealworm	150 °C/30 %	<ul style="list-style-type: none"> Integrity index, texture profile analysis, and oxidation activity decreased with increased mealworm larva content. Water holding capacity, nitrogen solubility index, protein digestibility, and DPPH radical scavenging activity increased alongside mealworm content. Lower die temperature and higher moisture content reduced protein digestibility. Extrusion cooking reduced, the total amino acid levels but increased the sulfur-containing amino acids and glutamic acid. 	S. Y. Cho and Ryu (2021)
<i>Microalgae (Spirulina platensis)</i>	Lupin protein	To evaluate the effect of <i>Spirulina platensis</i> flour addition and extrusion parameters on texture, bioactive composition, <i>in vitro</i> digestibility and molecular changes changes of lupin protein-based meat analogues was studied.	170 °C/60 %	<ul style="list-style-type: none"> <i>Spirulina</i> increased the bioactive content but decreased the digestibility of the extrudates. β-sheets decreased, whereas α-helix, β-turn and antiparallel β-sheets were increased compared to the raw extrusion mixtures. 	Palanisamy et al. (2019)
<i>Microalgae-Spirulina (Arthrospira platensis)</i>	Functional soy protein concentrate	To investigate the sensory properties of <i>Arthrospira platensis</i> and soy-based meat alternatives	180 °C/77 %	<ul style="list-style-type: none"> High spirulina content caused a black color, an intense flavor with earthy notes and an algae odor. A higher share of spirulina resulted in lower elasticity, fibrousness and firmness. High moisture content resulted in products evoking a juicy and soft mouthfeel plus a moist appearance. 	Grahl et al. (2018)
<i>Microalgae (Haematococcus pluvialis)</i>	Soybean meal and soybean protein isolate	To evaluate the potential of <i>Haematococcus pluvialis</i> as a colorant for meat analogues and its impact on the quality and color stability during post-processing and storage.	160 °C/50 %	<ul style="list-style-type: none"> Algae addition reduced the extruded elasticity but increased hardness, chewiness, and resilience. 1 % algae resulted in a beef-like color, while 0.25 % resembled pork. Excessive HP hindered protein cross-linking. Light exposure caused the most color loss, while frozen storage in darkness preserved color effectively. 	Huang et al. (2024)
	Pea protein powder	To prepare pea protein-based meat analogues with <i>Haematococcus pluvialis</i> residue by high moisture extrusion	150 °C/50 %	<ul style="list-style-type: none"> Algae residue improved the textural properties by the increased free water content and β-Sheet structure of extrudates. 	Xia et al. (2022)
Yeast (<i>Saccharomyces cerevisiae</i> protein)	Soy and pea protein isolate	To formulate meat analogues via mixing pea or soy with <i>Saccharomyces cerevisiae</i> protein	160 °C/55 %	<ul style="list-style-type: none"> Addition of yeast protein increased the lightness of the extruded product 30–40 % enhance the fibrous structure, hardness and chewiness. Yeast protein addition resulted in the formation of protein aggregates. 	(Xia, Shen, Ma, et al., 2023; Xia, Shen, Song, et al., 2023)
	Soy protein isolate	To investigate the fiber formation mechanism of yeast-soy protein extrudates and their digestive properties.	140 °C/50 %	<ul style="list-style-type: none"> Extrudates containing 40 % yeast protein had the most abundant fiber structures. 	Zhao et al. (2023)

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Table 1 (continued)

Hybrid source	Plant-based protein	Main Purpose	Extrusion max temperature/ moisture	Key findings	Reference
Fungi (<i>Penicillium limosum</i>)/mycelial protein	Pea protein isolate	To evaluate one fungal strain with high protein content, essential amino acids and non-toxic as protein source for meat analogues	140 °C/60 %	<ul style="list-style-type: none"> Extrudates with high yeast protein content had higher gastric emptying rates and produced digestates with smaller particles. Extrudates containing 30 % yeast protein exhibited the highest essential amino acid index 5 % mycoprotein enhanced the viscosity, gelling properties, chewiness, fibrous degree and <i>in vitro</i> protein digestibility. Oil and water absorption capacities demonstrated inverse trends 	C. Zhang et al. (2024)
Fungi (<i>Pleurotus eryngii</i>)/mycelial protein	Pea protein isolate	To evaluate the effect of mycelial protein in the physicochemical, rehydration, and structural properties of extruded proteins	140 °C/30 %	<ul style="list-style-type: none"> Mycelial protein incorporation changed the color attributes due to Maillard reaction during extrusion. Techno-functional properties increased significantly with mycelial protein addition. 	Mandliya et al. (2022)
Cultured meat tissue (Chicken satellite cells)	Wheat protein and Pea protein isolate	To evaluate the quality characteristics of hybrid cultured chicken breasts by incorporating different concentrations of cultured meat tissue with pea protein using wet spinning.	NR	<ul style="list-style-type: none"> Cultured meat reduced shear force. More cultured meat decreased sourness but increased bitterness and richness. Essential amino acids increased with cultured meat, except phenylalanine. 	Kim et al. (2024)

myofibrillar proteins' functional properties provide a strong foundation for hybrid product development, ensuring compatibility with plant proteins requires careful optimization of formulation and processing conditions. The production of hybrid foods with plant and animal proteins by extrusion requires precise control of process parameters to achieve optimal textures and sensory properties. Among the most critical parameters are temperature, screw rotation speed, moisture content, and pressure, which directly influence the transformation and alignment of proteins. Plant proteins generally require higher temperatures for adequate denaturation and expansion of molecular structures (120–160 °C), while animal proteins require temperatures below 100 °C. Overall, too high a temperature can excessively denature proteins, causing water retention capacity and elasticity loss (Zhao et al., 2024; Zhou et al., 2016). To improve the stability and cohesion of the blend during the extrusion process, emulsifying and stabilizing agents can be added to facilitate the interaction between proteins of different origins (Tan & McClements, 2021). Future research should explore optimizing ingredient combinations, such as varying plant protein types and their pre-treatment processes, to enhance sensory and nutritional profiles. Additionally, addressing challenges related to high-fat content during extrusion and further understanding the physicochemical interactions between animal- and plant-derived components can open new avenues for hybrid product innovation.

4.2. Plant-based hybrids co-extruded with aquatic proteins

The development of hybrid food products combining fish proteins, such as mince or surimi, with plant proteins using co-extrusion technology presents a unique opportunity to diversify and enhance the nutritional and sensory profiles of plant-based alternatives. Fish proteins, with their high-quality amino acid profile, high digestibility, presence of Omega-3 PUFAs, vitamins and unique functional properties, offer significant potential when co-extruded with plant-based proteins to create products that mimic the texture and taste of traditional seafood but impose less pressure on aquatic resources (Arponen, 2012; Zhong et al., 2023). The seafood industry also suffers from unsustainability due to overfishing combined with very low resource efficiency where a large fraction of aquatic resources, such as small pelagic fish and fish processing side streams, end up in animal feed due to difficulty in processing and low consumer acceptance (Yan et al., 2021).

The development of hybrid fish-plant protein products using co-extrusion also provides an opportunity to enhance the texture of products like surimi, which typically lacks the anisotropic and fibrous structures found in traditional seafood or more attractive products from low-value pelagic fish or seafood side streams. Thiébaud et al. (1996), found that the mixture of fish surimi and soy protein concentrate in the ratio of 80/20, was easily texturized into bands with a fibrous layered internal structure. It was found that the barrel temperature and moisture level significantly influenced the color of the extrudates. A study on the possibility of using whole and gutted Baltic herring as a raw material for hybrid plant-fish analogues produced by their co-extrusion with pea protein using HME obtained analogues with high microbial quality and uniform flavor-and odor-related sensory profile. However, the structure of the whole fish extrudate was weaker than the gutted fish, and the color of the whole fish extrudate was darker than the gutted fish as shown in Fig. 3A (top and medium). In addition, the hybrid products showed microstructurally medium to weak fiber alignment compared with meat analogue made of pea protein (Fig. 3A – bottom). It was concluded that Baltic herring has the potential to be used as a base in fish analogue products, thereby minimizing the waste of this highly nutritious small-sized pelagic fish (Nisov et al., 2020).

Achieving the characteristic texture and flavor of fish is a complex task in food technology. Replicating the unique nanoscale fibrous architecture of fish requires mimicking the tissue, cellular, and molecular structures, with particular attention to the intra- and intermolecular connections among protein chains (Kazir & Livney, 2021). Through careful control of extrusion parameters, it is possible to align plant and fish proteins into a cohesive, flaky structure that partly mimics the texture of seafood. However, maintaining the integrity of fish proteins is challenging, as they are sensitive to heat and shear during extrusion, which can lead to denaturation and reduced functionality. Therefore, careful adjustment of fish-to-plant protein ratio and extrusion conditions is essential to preserve the desired gelation properties and sensory qualities. For example, combining soy protein isolate (SPI) with surimi at an 80:20 ratio creates a continuous SPI phase, improving textural integrity and mimicking the flaky texture of traditional fish products using HME (70 %) (Zhang et al., 2022a,b) as shown in Fig. 3D. The authors found that an excessive amount of surimi (more than 40 %) in the hybrid would hinder the fibrous-oriented structure formation during the extrusion process. A delicate balance in the surimi:soy protein ratio

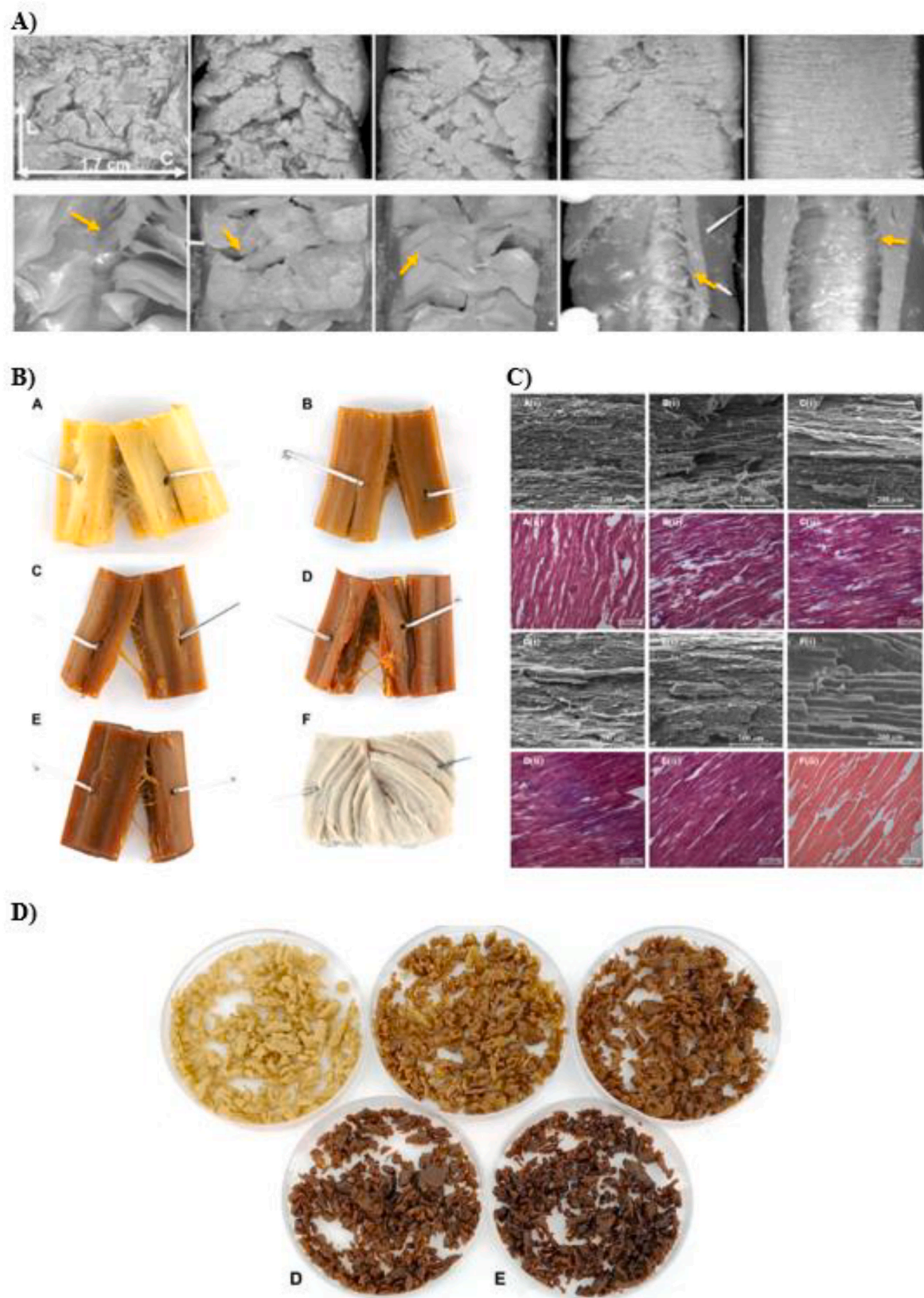
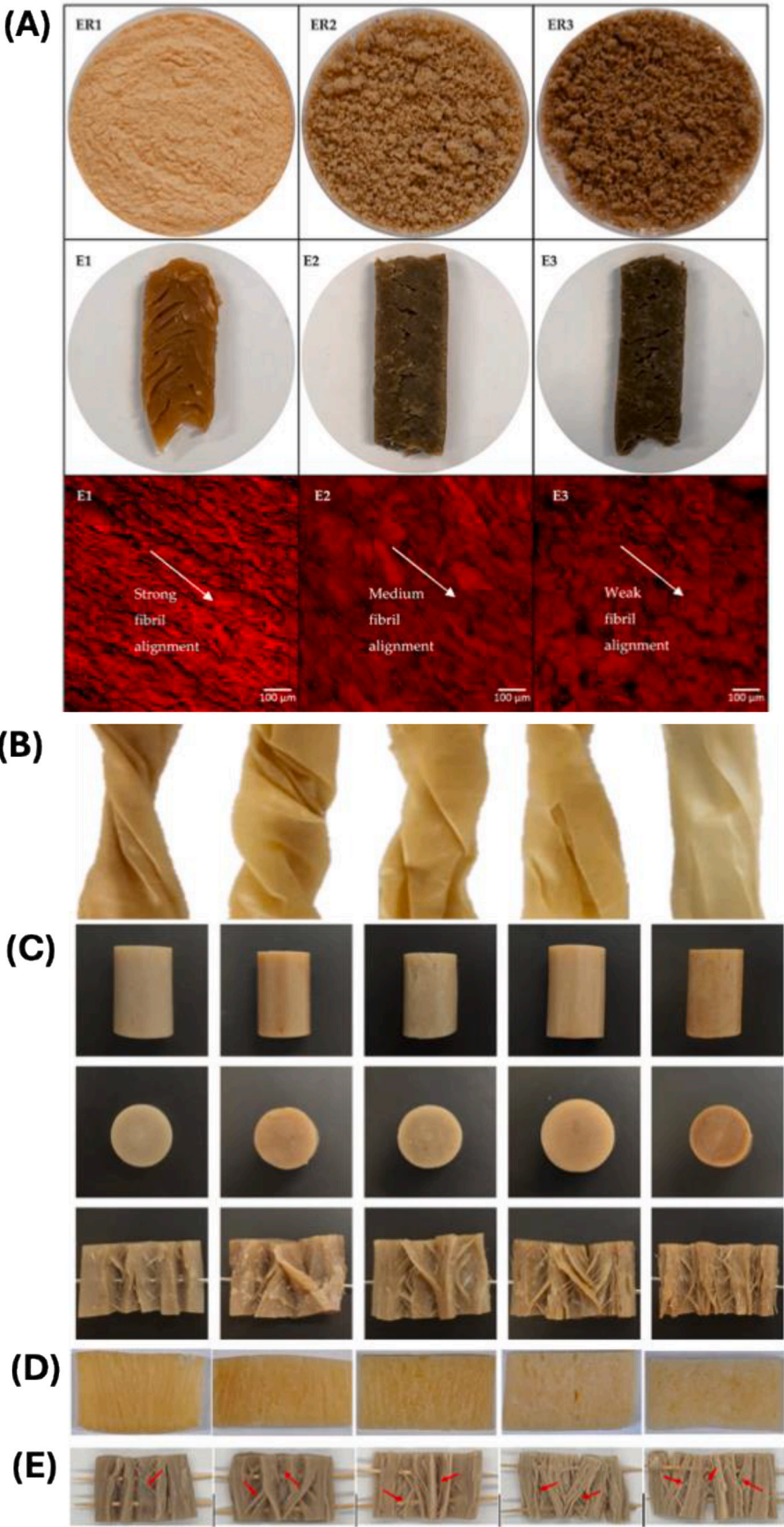


Fig. 2. Hybrid plant protein-based foods co-extruded with animal protein. (A) Stereo images of hybrid extrudates from minced beef and pea protein (Pöri et al., 2023); Extruded (B) and minced meat (D) alternatives at varying concentrations (10–40) of Maillard-reacted beef bone hydrolysate with wheat gluten and starch, shown through macro images, SEM, and light micrographs (C) (Chiang et al., 2020a).



(caption on next page)

Fig. 3. Extruded hybrid fish-plant protein products. The appearance and the color of the extrusion raw materials, extrudates, and microstructure of high moisture extrudates of whole and butted Baltic herring with pea protein (A) (Nisov et al., 2020); Appearances images of extrudates with different surimi to soybean flour ratio (B) (Li et al., 2022); Surface, cross-section, and internal structure of Alaska pollock surimi-based meat analogues prepared with different types of plant-based colloids (C) (Wang et al., 2024a,b,c); Macro- and microstructure of extrudates of the soy protein isolate and surimi blends (D) (Y. Zhang et al., 2022a,b); Macrostructure of Alaska pollock surimi-based meat analogues (E) (Hou et al., 2023). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

was also found during the development of hybrids using low moisture (37 %) extrusion (Li et al., 2022) (Fig. 3B). The excess ratio of surimi and soybean flour (more than 2:8) was detrimental for extrudates' textural properties, microstructural fiber alignment and water distribution. Their sensory evaluation using E-tongue and E-nose analysis suggested that adding surimi significantly increased sweetness and umami taste of TVPs, and an appropriate ratio (2:8 or 3:7) could reduce the beany flavor without an obvious fishy off-flavor. Extrusion offers flexibility in textural customization, making it possible to tailor gel strengths and structural properties to meet specific product characteristics. For example, the addition of different hydrocolloids including konjac glucomannan, curdlan, carrageenan, and sodium alginate during HME of Alaskan pollock surimi and soy protein isolate at a ratio of 7:3 (w/w) resulted in big variations in micro- and meso- and macro-structure of the produced hybrids as shown in Fig. 3C (Wang et al., 2024a,b,c). Meso-structure and microstructure results indicated that 2 % curdlan, carrageenan, or sodium alginate promoted the formation of less tight three-dimensional structures and contributed to the formation of fiber filaments while the best fibrous structure was obtained in hybrids with 2 % sodium alginate. Tuning the ratio of wheat gluten to soy protein was found to be effective on fibrous structure and hardness of the hybrid product of Alaska pollock surimi and plant protein (8:2), where the plant protein consisted of different ratios of soy protein and wheat gluten (9:1, 7:3, 5:5, 3:7 and 1:9) as seen in Fig. 3E (Hou et al., 2023). The hardness of the extrudates decreased, while the fibrous degree, free water ratio and lightness increased with increasing wheat gluten content.

Another significant challenge is the sensitivity of seafood nutrients, particularly omega-3 fatty acids and proteins, to high temperatures. The extrusion process may trigger lipid oxidation, leading to a decline in the nutritional quality and sensory appeal of the final product. However, the addition of fish protein and surimi to plant protein during extrusion has been highlighted as a tool for the improvement of the nutritional value of plant-based extrudates. In this regard, Hu et al. (2024) showed that increasing surimi content from 10 % to 50 % in a hybrid HMEs containing SPI increased the limiting amino acid score from 88.82 to 109.50. Moreover, the levels of docosahexaenoic acid and eicosa-pentaenoic acid in the extrudates significantly increased, concurrently reducing the n-6/n-3 fatty acid ratio. Surimi-to-SPI ratio had a significant effect on the *in vitro* digestibility of the extrudates, but extrusion condition at a constant ratio was also very important. At lower extrusion temperatures (125–135 °C), increasing moisture content led to a notable increase in the small intestinal digestibility of the extrudates while at a constant ratio, the amount of fatty acids was substantially affected by extrusion temperature and moisture content.

Studies have shown that incorporating fish proteins at controlled levels improves sensory profiles, reduces undesirable flavors, and enhances the textural properties of plant-based extrudates (Appiani et al., 2025; Kazir & Livney, 2021). Despite advancements, challenges remain, including the sensitivity of seafood nutrients, particularly omega-3 fatty acids, to high extrusion temperatures imposing lipid oxidation which can compromise the sensory and nutritional quality of the final products (Böttcher et al., 2015). The development of hybrid products from underutilized or low-value aquatic resources, such as small pelagic fish and side streams, presents a significant opportunity to address resource efficiency and waste minimization in the seafood industry while enhancing the nutritional profile of the hybrids, as evidenced by improved amino acid scores, higher digestibility, and favorable fatty acid compositions. Furthermore, advancements in extrusion technology,

coupled with the integration of emerging approaches such as the use of Maillard reactions or enzyme-aided modifications, could open new avenues for tailoring hybrid fish-plant analogues to meet diverse consumer demands for taste, nutrition, and sustainability.

4.3. Plant-based hybrids co-extruded with insect proteins

Historically, insects have been integrated into human diets, with a current global consumption of over 1900 species (Hadi & Brightwell, 2021). Insect farming requires less land, water, and feed than traditional livestock and with minimal greenhouse gas emissions, utilizing vertical farming and organic waste for a circular economy (Kouřimská & Adámková, 2016). Thus, insect farming offers a sustainable protein source for plant-based hybrids. Commonly consumed insects like crickets, mealworms, and grasshoppers are known for their high protein content, often complemented by a rich profile of essential fatty acids, vitamins, minerals, and fiber (Finke, 2002). In many species, especially *Orthoptera*, proteins constitute over 60 % dry matter (DM), offering high digestibility and nutritional value, similar to egg whites, milk, and beef, while being rich in essential amino acids like threonine, valine, and histidine (Sawicka et al., 2020). However, Western societies are reluctant to consume insects, and meals with insects can be rejected and somehow not reach widespread application. Studies indicate that consumers are more receptive to meat substitutes and insects when presented as part of a meal or an ingredient. This typically involves processing insects into fine powder or flour and then combining them with plant-based ingredients. For instance, a study performed in the Netherlands concluded that processed insect protein on pizza was preferred over visible insects in a salad (Grasso et al., 2019).

To overcome this repelling character of insects, co-extrusion allows for the homogeneous mixing of all ingredients, which is crucial to achieving a final product with a uniform texture, an attractive flavor profile, and well-distributed nutrients. When well-integrated into the food matrix, insect protein is almost imperceptible, increasing consumer acceptance by reducing characteristic tastes and odors that may be less familiar or appealing (Santiago et al., 2024). Several studies have evaluated the possibility of incorporating cricket powder, yellow mealworm larvae and black soldier fly larvae into bakery products or hybrid meat analogues by substituting meat and or by direct mixing with plant proteins or TVPs as reviewed elsewhere (Borges et al., 2022), but few studies have also investigated their co-extrusion with plant proteins.

In this line, incorporation level and extrusion conditions have been found to be important for the development of hybrid products with acceptable textural properties. Investigating the ratio of soy protein concentrate to *Alphitobius diaperinus* protein concentrate (68 % protein content DM) at 15–50 % DM revealed that it is possible to achieve fibrous meat analogues with hardness texture and protein composition similar to meat, with maximum 40 % of insect. The microstructural investigation showed that texture of the hybrid extrudates could be further improved by adding 5–10 % of soy fiber. The same group revealed that higher temperatures, or reduced water input during HME, increased the hardness of the intermediates from 6.5 to 8 N (at a barrel temperature of 160 °C) to 8–11 N (at a barrel temperature of 170 °C). Optimal meat-like texture, with the highest inclusion of insect biomass (40 % DM), was attained at a maximal extruder barrel temperature of 170 °C (Smetana et al., 2019).

The type of insect and its composition is also an important factor that will define the behavior of insect protein during co-extrusion but also

their interaction with plant proteins. Fat content in the cricket flour showed a big impact on the fiber formation during HME of hybrid products with SPI when a low fat and full fat cricket flour were compared (Kiiru et al., 2020). Fibrous meat analogues with high anisotropic indices reaching up to 2.80 were achieved, particularly at a water flow rate of 10 mL min^{-1} and with the inclusion of 30 % low-fat cricket flour. In contrast, blends containing 30 % full-fat cricket flour exhibited less distinct fibrous structures. During extrusion, it is hypothesized that lipids form complexes with other macromolecules, which are then distributed on the surface of protein aggregates. These lipid-macromolecule complexes may hinder protein-protein interactions, thereby preventing proper aggregation and stabilization of the fibrous structure. A more recent study showed that incorporating cricket powder with 72 % protein enhanced the formation of anisotropic structures, achieving optimal anisotropy at 10 % cricket powder inclusion (Wang et al., 2024a,b,c). However, higher cricket powder concentrations negatively impacted mechanical strength and microstructural coherence due to the presence of insoluble components and the development of large cracks (Fig. 4). The optimum content of black soldier fly larvae protein (87 % protein) in hybrid meat analogues with SPI and

wheat gluten which mimics textural characteristics of chicken breast and plant-based meat analogues were 6.7 g.100 g^{-1} and $21.5 \text{ g.100 g}^{-1}$, respectively (Miron et al., 2023).

The impact of including insect proteins during the extrusion of plant protein on the nutritional and sensorial properties of hybrid products is another important but less investigated aspect that will define their final success for market penetration. The hybridization of SPI and corn starch with dehydrated mealworm larvae significantly enhanced the nutritional value and flavor profile of the blends (Cho & Ryu, 2021). Protein digestibility and total amino acid content increased with the inclusion of mealworm larvae. However, subsequent denaturation during high-temperature extrusion resulted in a slight decrease. Post-extrusion, glutamic acid—a key flavor-enhancing amino acid—was identified as the most abundant, with the highest levels observed in hybrids containing 30 % mealworm larvae. This inclusion also led to notable improvements in meaty taste, aroma, and overall sensory acceptance. The findings suggest that the elevated glutamic acid content in the 30 % mealworm hybrid synergizes with other flavor compounds, amplifying the overall flavor profile. Flavor profiling demonstrated that cricket powder (CP) significantly contributed to the hybrid system by

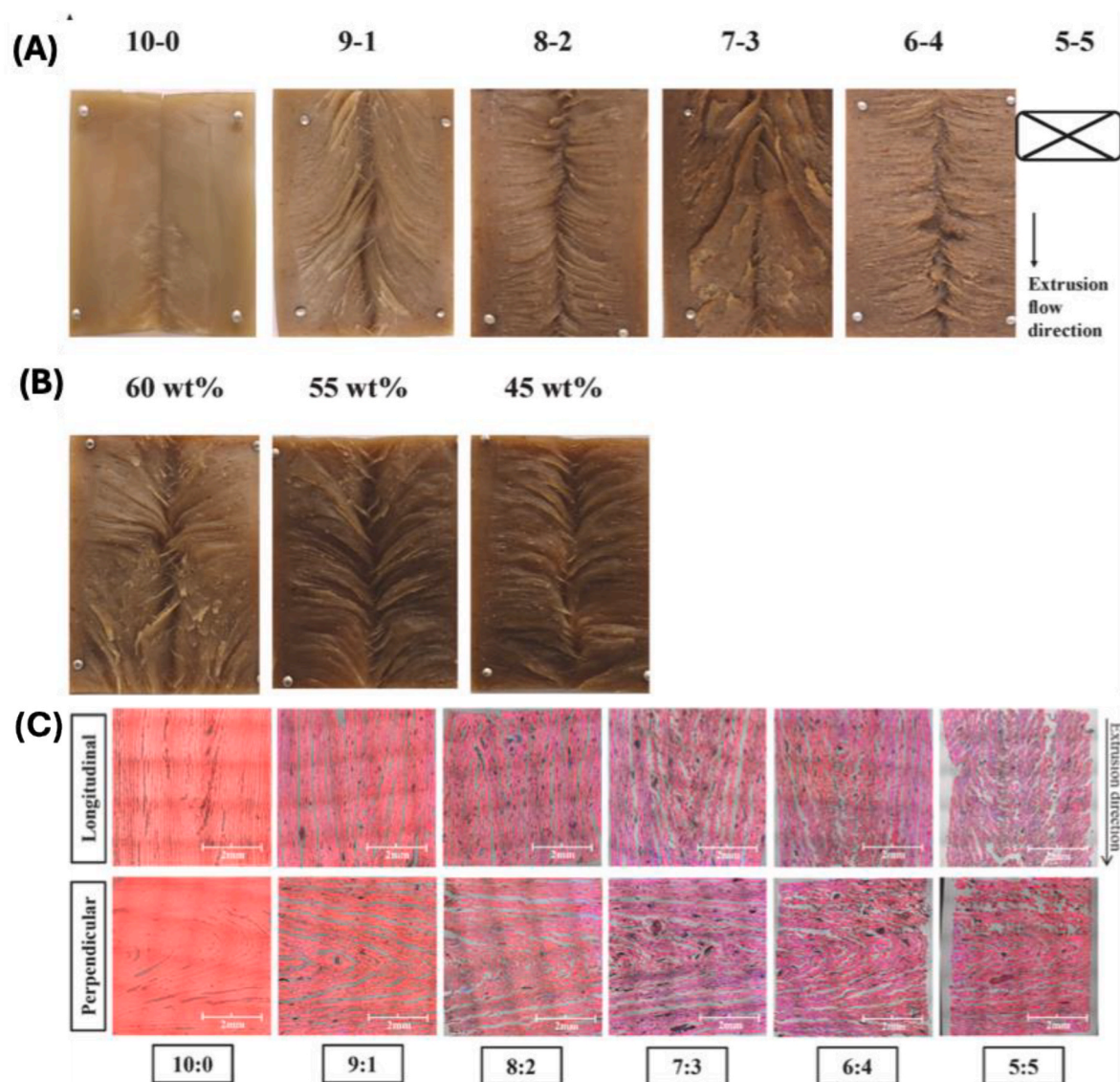


Fig. 4. Microstructural image of soy protein isolate extrudates with cricket powder. Macrostructure of soy protein isolate-cricket powder at 50 % moisture (A) and 10 % cricket powder and varying moisture content (B); confocal laser scanning microscopy images of soy protein isolate-cricket powder extrudates (C) (Wang et al., 2024a,b,c).

introducing pyrazines and ethers, which imparted a desirable burnt and baked flavor to the extrudates (Wang et al., 2024a,b,c). The incorporation of CP into hybrid formulations offers complex and favorable flavor profiles, but its sensory impact requires careful management. While cricket imparts desirable roasted and baked flavors at moderate levels,

its inclusion at higher concentrations can introduce bitter or metallic notes, detracting from the overall sensory appeal. Research suggests that the optimal inclusion level of CP is around 10 % in SPI-based extrudates. At this level, CP enhances flavor without compromising the product's structural integrity or introducing undesirable sensory characteristics.

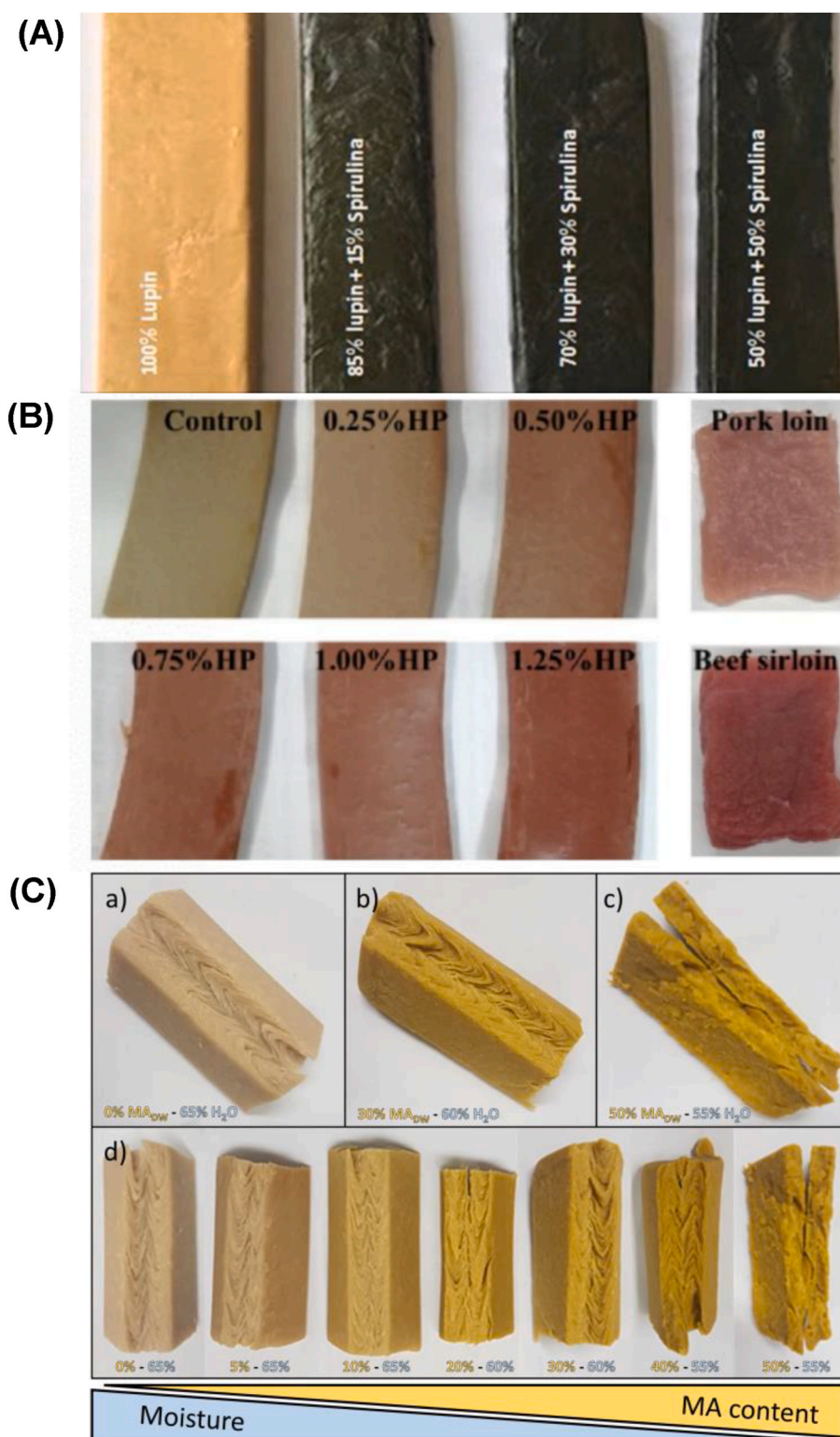


Fig. 5. Plant-based extrudates with microalgae. Blend extrudates of Spirulina/lupin protein mixtures (A) (Palanisamy et al., 2019); Color of high moisture meat analogues with different amount of *Haematococcus pluvialis* and soy protein (B) (Huang et al., 2024); Fibrillary structure in extrudates produced with different proportions of yellow, heterotrophically cultivated *Auxenochlorella protothecoides* microalgae, moisture and soy protein concentrate (C) (Caporgno et al., 2020). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

However, exceeding this threshold can lead to sensory defects, including overly earthy or bitter tastes, due to insoluble components in cricket (Wang et al., 2024a,b,c). These issues may negatively affect consumer acceptance, emphasizing the importance of precise optimization of insect levels to balance flavor enhancement with product quality.

Still, the development of plant-based hybrids with insect proteins presents significant challenges at a general level. To integrate these proteins into large-scale industries, extensive research is necessary to refine processing methods and achieve an optimal balance between cost-effectiveness, functionality, palatability, and sustainability, all while ensuring consumer safety (Gravel & Doyen, 2020). These include food safety risks associated with edible insects, such as bacteria, mycotoxins, parasites, allergens, heavy metals, and anti-nutrients but also the effect of extrusion (Hadi & Brightwell, 2021). The challenges also lie in achieving a harmonious balance between the flavors and textures of insect and plant components during co-extrusion to ensure the end products are both palatable and appealing.

4.4. Plant-based hybrids co-extruded with algae

Algae, comprising microalgae (such as cyanobacteria) and seaweeds (referred to as macroalgae or sea vegetables), have historically played a vital role in Asian food cultures and are currently experiencing an upsurge in European markets, propelled by a growing consumer inclination towards sustainable and health-conscious dietary choices (Mendes et al., 2022). Seaweeds, including varieties like kelps and nori/laver, account for approximately 40 % of global algae consumption in recognizable forms, excluding their widespread use as hydrocolloids (such as agar, alginate, and carrageenan) in food and beverage products for thickening purposes (FAO, 2022; Wells et al., 2017). Regarding microalgae, species such as *Spirulina* and *Chlorella* are increasingly acknowledged for their contribution to plant-based hybrid foods. *Spirulina*, a type of blue-green algae, is esteemed for its substantial protein levels (~63 % DM), antioxidants, and B-group vitamins composition (Sharoba, 2014). *Chlorella*, a green alga, offers a similar nutrient profile (63 % proteins and up to 17 % oil content DM, most of it corresponding to oleic acid) (Tokuşoglu & Ünal, 2003). These algae enhance the nutritional value and sustainability of food products and introduce distinctive flavors and colors, augmenting their culinary appeal (Huang et al., 2024).

Due to their rich chemical composition and content of bioactive substances, algae can be combined with plant-based ingredients to create functional plant-based hybrid foods. However, their application in food formulation is often challenged by their effect on color, sea/fishy flavor and effect on texture which is highly dependent on the algae species, cultivation conditions and addition level. For example, when *Spirulina* flour was co-extruded with lupin protein at levels up to 50 %, it resulted in hybrid HMEs with a significant increase in total phenolic and flavonoid content, and Trolox equivalent antioxidant activity. However, the addition of *Spirulina* at 30 % and above reduced the *in vitro* protein digestibility and negatively affected their textural properties which was to some extent mitigated by adjusting moisture and extrusion conditions (Palanisamy et al., 2019). In addition, *Spirulina* addition strongly affected the color of the extrudates turning it from dark blue to dark (Fig. 5A). High *Spirulina* content caused a black color, an intense flavor with earthy notes and an algae odor that is rather musty (Grahl et al., 2018). The addition of heterotrophically cultivated *Auxenochlorella protothecoides* microalgae with a whitish to yellowish color during HME (55–65 %) to SPI (up to 50 %) improved the extrudate's nutritional profile by incorporating B-group vitamins and E, where over 95 % was retained in the final product with slight discoloration to yellow, as seen in Fig. 5C. To address this, yellow *Chlorella vulgaris* was integrated into pea protein-based meat substitutes. This study, utilizing wet and disrupted *Chlorella vulgaris* biomass, established disrupted *Chlorella vulgaris* as a promising, nutritious, and sustainable ingredient for meat substitutes. The addition of 10 % ($w.w^{-1}$) high-pressure

homogenization-treated *Chlorella vulgaris*, whether in wet or dry form, to pea meat substitutes showed no significant differences in hardness, visual appearance, or the anisotropy index (De Gol et al., 2023). Yet not all algae exhibit undesirable colors. *Haematococcus pluvialis* (HP), a specific algae species abundant in astaxanthin, demonstrates promising outcomes in the production of soy-based high-moisture meat analogues with 50 % humidity content, which is a great bonus for development of hybrid products. Research suggests that HP is a valuable colorant for plant-based hybrids with algae, effectively mimicking the color profile found in animal meat (Huang et al., 2024). Here, a small quantity of microalgae was used as a colorant and an optimal degree of texturization was achieved with 0.75 % HP. Sensory evaluations revealed that hybrid extrudates with 1 % HP had a color similar to fresh beef sirloin, while extrudates with 0.25 % HP had a color closer to fresh pork loin (Fig. 5B). The same concept was proven by adding residue from astaxanthin extraction from SP coextruded with pea protein at 10–40 $g.100^{-1}$ of HME at 50 % moisture (Xia et al., 2022). Interestingly, the addition of SP residue at 10 % increased the fibrous degree of the extrudates by increasing free water content and β -Sheet structure of extrudates.

Despite the successful example proving the incorporation possibility of microalgae biomass to meat analogues by co-extrusion, they are often deficient in forming fibrous structures (Caporgno et al., 2020; Sägeser et al., 2024). Few studies have associated this with the elevated fat content of microalgae biomass, which led to lubrication effects or undisturbed microalgae cells acting as passive fillers and limiting the access of intracellular proteins (Caporgno et al., 2020). However, a recent detailed compositional comparison between microalgal biomass and conventional soy and pea proteins revealed that macro-compositional differences had only a minor effect on fibrous structure formation in hybrid extrudates. Instead, poor structuring performance of microalgae was primarily linked to their protein composition, properties, and the surrounding electrolyte environment. Proteins in the analyzed microalgal biomass were 20 % smaller in molecular weight, exhibited 18–68 % higher solubility, and contained 15–50 % fewer hydrophobic sidechains. These characteristics reduce the potential for protein-protein interactions and hinder network formation, ultimately limiting the ability of microalgal biomass to contribute to fibrous structure development. While further studies are necessary to understand the weak fiber formation capacity of microalgae, various strategies such as employing pH shift, addition of cysteine, transglutaminase and polyvalent cations have been proposed as measures to improve their functionality (Sägeser et al., 2024).

Flavor is another substantial challenge for microalgae in hybrid products aiming to mimic meaty and savory flavors. In contrast, some microalgae impart unpleasant 'fishy' odors from PUFAs, phytosterols, and volatile organic metabolites (Wen et al., 2022). Excessive microalgae fibers or protein debris will decrease the sensory scores for taste and appearance, as well as potential consumer acceptance issues. However, this can be a unique and positive sensory attribute for the development of seafood analogues where fishy and sea flavor are highly appreciated. Despite the existing challenges, purpose-driven incorporation of carefully selected microalgae species in small quantities (up to 10 %) as a functional ingredient to boost meat analogues nutritional value, mimicking meat color or inducing sea flavor for fish analogues remains a very promising strategy for the development of hybrid extruded products containing microalgae.

Overall, the integration of algae, mostly microalgae, into plant-based hybrid foods represents a promising frontier in the development of sustainable and nutritious alternatives to traditional animal-derived products, while macroalgae remains untapped. Algae offer remarkable nutritional and functional attributes, including high protein content, essential fatty acids, antioxidants, and unique coloring capabilities. These qualities make them particularly suitable for enriching hybrid foods, enhancing their sensory appeal, and contributing to sustainable food systems. However, challenges such as undesirable coloration, strong algae-like flavors, and limited fiber formation capacity in HME

systems remain significant barriers to their broader application. The variability in textural properties and sensory acceptance largely depends on algae species, cultivation methods, and incorporation levels, which necessitate targeted formulation strategies. Advances in processing techniques, such as high-pressure homogenization and modifications of protein properties through enzymatic or chemical treatments, show potential to mitigate these challenges and optimize the functional performance of algae in hybrid foods. Future research should focus on refining algae-based formulations to balance nutritional value, sensory characteristics, and functional performance. Investigations into the

synergistic effects of algae with plant proteins, particularly in HME, will be critical for achieving the desired fibrous textures and improving consumer acceptance. Furthermore, the development of tailored algae strains with optimized compositions and minimal undesirable sensory attributes, alongside innovative applications in seafood analogues where marine flavors are desired, offers exciting opportunities for innovation. The purposeful incorporation of algae into hybrid foods underscores their potential as a versatile and sustainable ingredient. With ongoing advancements in processing technologies and a deeper understanding of algae's protein interaction with other food

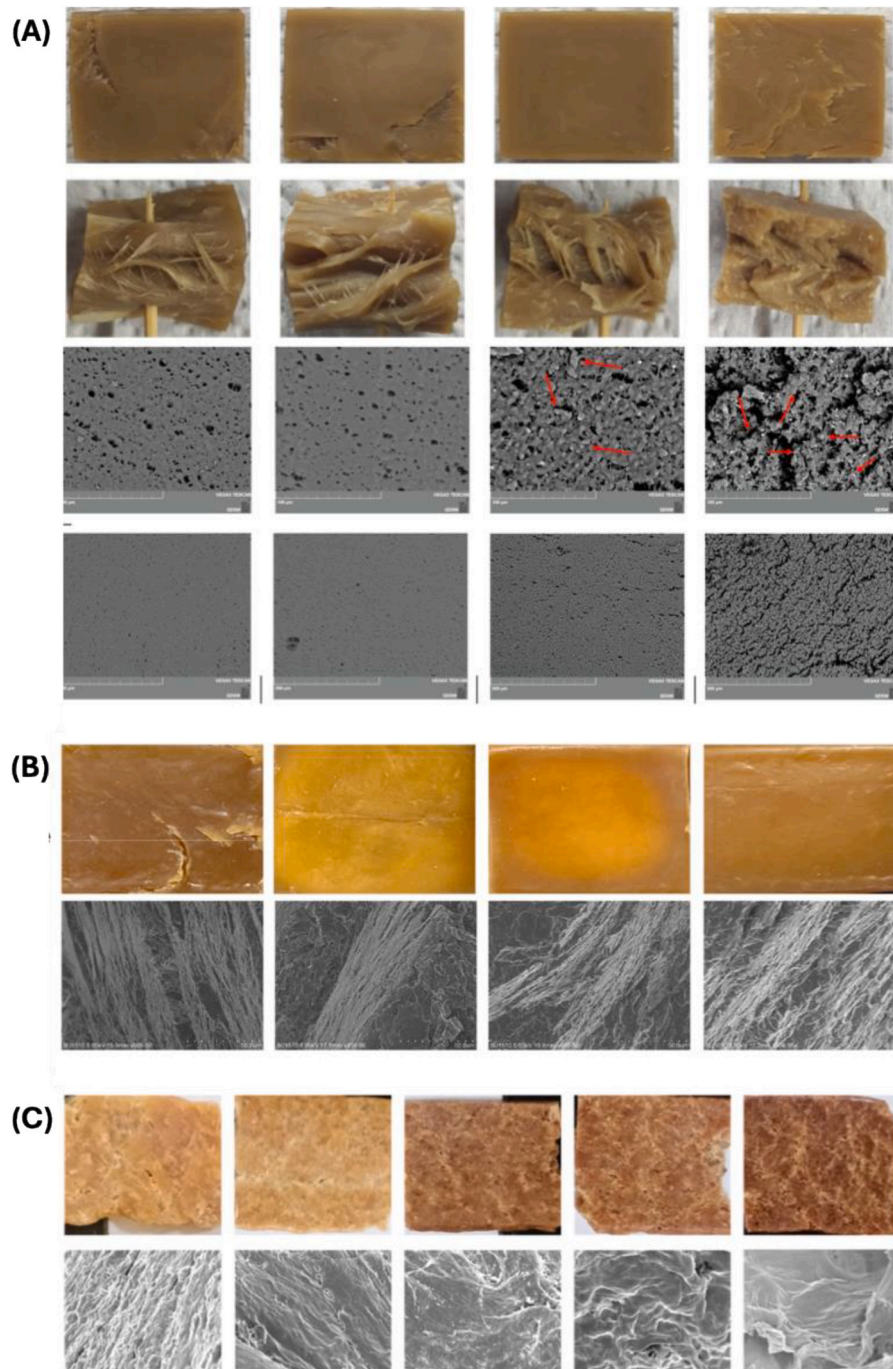


Fig. 6. Plant-based hybrids fueled with microbial ingredients. The visual and SEM images of meat analogues of yeast-pea protein with different formulations (A) (Xia, Shen, Ma, et al., 2023); Surface appearance and microscopic textural analysis of high-moisture meat analogues of *Penicillium limosum* and pea protein isolate (B) (C. Zhang et al., 2024); Surface appearance and microstructure of dried and freeze-dried rehydrated *Pleurotus eryngii* in pea protein-based low moisture meat analogue (C) (Mandliya et al., 2022).

components, these aquatic resources could significantly contribute to the development of more attractive hybrid foods.

4.5. Plant-based hybrids fueled with cellular agriculture ingredients

Cellular agriculture is an emerging and innovative field at the intersection of biotechnology, agriculture, and food science, dedicated to producing animal-like or novel food ingredients through cell-based and microbial processes, eliminating the need for traditional farming. It encompasses three main segments: biomass fermentation, precision fermentation, and cell-cultured meat. Biomass fermentation leverages microorganisms such as fungi, yeast, and bacteria to produce large quantities of protein- or fat-rich biomass, such as mycoproteins and single cells. Precision fermentation involves engineering microbes to produce specific high-value compounds, such as animal proteins (e.g. casein, whey, albumin, collagen, heme protein etc.) enzymes, flavor compounds, vitamins or tailored proteins, to enhance food functionality and nutrition (Cho et al., 2025; Hilgendorf et al., 2024). Cell-cultured meat involves cultivating animal cells directly, creating real meat without the need for raising animals. Among these segments, biomass and precision fermentation offers immense potential for hybrid product development. Ingredients derived from these processes, like mycoproteins and single-cell proteins or food ingredients as flavor coloring or texturizing agents, bring unique nutritional, sensorial and functional benefits to hybrid foods and nicely complement other alternatives (Bajić et al., 2022; Devaere et al., 2022). From a nutritional perspective, microbial biomass could be a rich source of B-group vitamins (Ritala, et al., 2017), antioxidants such as carotenoids (Joshi et al., 2024) and macromolecules like oils (Donot, 2014). The most notable success in this field is the Impossible Burger, a hybrid product that combines texturized plant proteins with leghemoglobin, a key flavor-enhancing ingredient produced in yeast through precision fermentation (Hilgendorf et al., 2024). Biotechnological innovations enable precise control over the composition and properties of these ingredients, including their amino acid profiles, lipid content, and structural features. By utilizing engineered or natural metabolic pathways, fermentation enables the precise production of target ingredients and biomaterials, reducing dependence on chemical additives (Singh et al., 2022). Hybrid products could be also a very effective route to address the challenges these ingredients are facing due to lower consumer acceptance and cost.

4.5.1. Microbial ingredients in the development of hybrid foods

Yeast protein has been recently explored as a microbial protein source for the development of hybrid meat analogues via high moisture (55 %) extrusion together with soy (Xia, Shen, Song, et al., 2023) and pea (Xia, Shen, Ma, et al., 2023) protein isolates (Fig. 6A) for 10–50 % incorporation. The addition of yeast protein during extrusion up to 30–40 % has significantly improved fiber formation, textural properties and whiteness of hybrid extrudates compared with those only made of SPI or PPI. A combination of segmental sampling and a closed cavity rheometer revealed that yeast protein (YP) was dispersed within the SPI network in both the mixing and melting zones. As a distinct phase, YP transformed SPI into a “mushy” state, facilitating the development of intermolecular forces and enhancing the reconstruction of the protein network in the cooling zone (Zhao et al., 2023). Furthermore, *in vitro* dynamic gastrointestinal digestion demonstrated that hybrid extrudates with higher YP content exhibited faster gastric emptying rates and produced digestates with smaller particle sizes. Notably, extrudates containing 30 % YP achieved the highest essential amino acid index (Zhao et al., 2023). However, the effect of YP on the flavor profile and sensorial properties of the hybrid extrudates remains unclear.

Filamentous fungi biomass has also been recently explored in combination with pea protein for development of hybrid meat analogues using both LME and HME. A filamentous fungi biomass of a non-toxic strain, *Penicillium limosum*, with a high biomass yield, protein, and essential amino acid contents, isolated from wheat Qu was blended with

PPI to produce high-moisture meat analogues (Fig. 6B) (Zhang et al., 2024). The inclusion of just 5 % mycoprotein improved the viscosity, gelling properties, chewiness, and fibrous structure of the extrudates compared to 100 % PPI. Additionally, it enhanced *in vitro* protein digestibility (68.65 %), as the high temperature in thermal extrusion method promoted protein denaturation, and increased oil absorption capacity. Incorporation of mycelium *Pleurotus eryngii* to PPI up to 30 % during LME also resulted in a fibrous and porous hybrid low moisture meat analogue with improved functionality and a meaty color induced by Millard reaction (Fig. 6C) (Mandliya et al., 2022).

4.5.2. Plant-based hybrids with cell cultured meat

Cell-cultured meat incorporation as food ingredient remains a relatively unexplored area in food science and especially co-extrusion. Only a few studies have been published, with one notable example being the research of Kim et al. (2024). The authors investigated the impact of cultured meat tissue at concentrations of 10–30 % to PPI on the quality of imitation muscle fiber developed with wet spinning and hybrid cultured chicken meat. Although wet spinning does not specifically refer to HME, it can show the potential and inspiration for application of the same concept in co-extrusion of hybrid products (Cui et al., 2022). For this, chicken satellite cells were isolated and suspended in growth media and incubated at 41 °C and 5 % CO₂. They found that increasing cultured meat, content reduced pH and shear force, as measured by the Warner-Bratzler shear force test using a texture analyzer with a V-shaped shear blade in shear mode. It also improved chewiness at 20 % and enhanced texture attributes, such as hardness at 30 %, as determined by compression and decompression tests with a texture analyzer. Higher cultured meat levels also increased essential amino acid content but altered taste, reducing sourness while increasing bitterness and richness.

In addition, several patents have been registered in this area. Saville et al. (2020) patented a method combining a plant-derived fraction with cultured animal cells to enhance sensory and nutritional characteristics. Specifically, cultured cells contribute to meaty texture, umami taste, and color stability, further improving the sensory profile of the final product. The authors note that the animal cells do not form tissue and constitute less than 30 % of the blended food product. A different type of document, registered by Xin et al. (2022) describes the procedure to extrude food products comprising cultured animal cells, plant proteins, and other ingredients. The extrudate undergoes high-moisture extrusion (50–70 % water) at 100–180 °C with shear forces to develop a fibrous texture. Cultivated cells are injected during or after extrusion, forming scaffolds or 3D printing substrates. A wet cell paste with gelation properties can also be integrated. Similarly, Xin et al. (2016), patent presents a method to produce mixed cell-cultured meat by combining non-animal-derived structural proteins (e.g., protein fibers) with non-human animal cells. The process uses extrusion or spinning techniques to create protein fibers, which are mixed with cells and shaped into a product that mimics the appearance, texture, and flavor of real animal muscle.

Another innovative approach for the development of hybrid cell-based meat has been also introduced by using extruded plant proteins as edible scaffolds (Ben-Arye et al., 2020) as shown in Fig. 7. Textured soy protein, a porous and protein-rich biomaterial, has proven effective in supporting cell attachment, proliferation, and differentiation into 3D-engineered bovine muscle tissue. By optimizing media composition with growth factors and employing co-culture techniques, enhanced myogenesis and extracellular matrix deposition were achieved, improving texture and structure. Taste tests confirmed the meaty flavor and sensory attributes, highlighting the potential of combining plant-based scaffolds with cultured cells to create sustainable and realistic hybrid meat alternatives.

Overall, the integration of cellular agriculture-derived ingredients, such as yeast protein, filamentous fungi biomass, and cultured meat, into hybrid products through extrusion technology demonstrates significant potential to enhance textural, structural, and nutritional

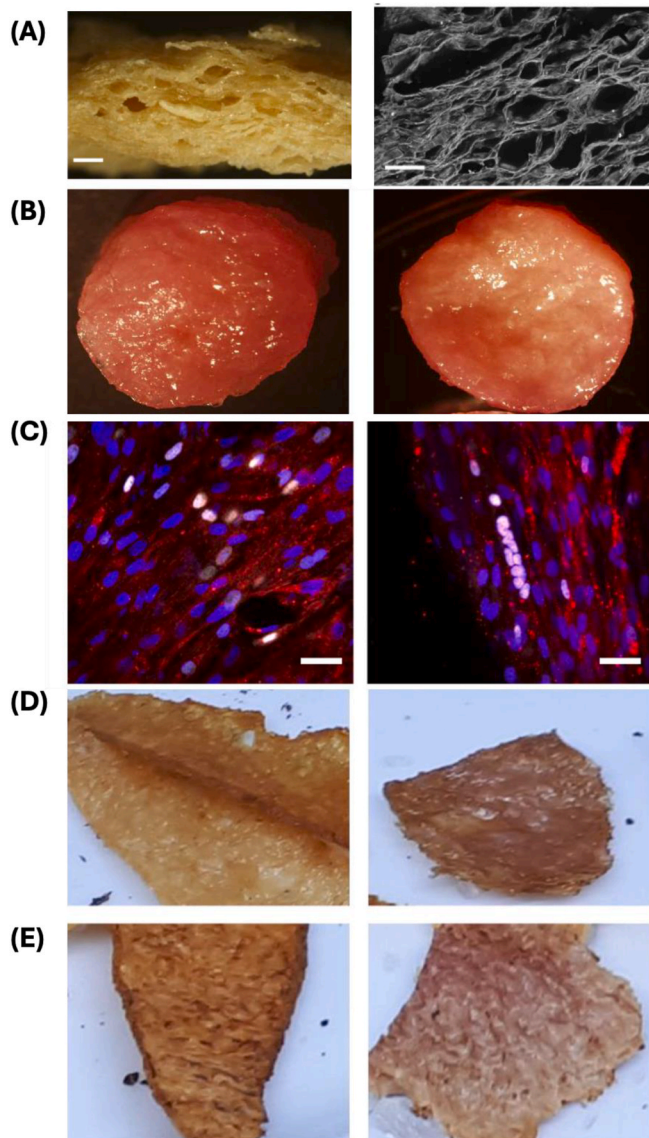


Fig. 7. Plant-based hybrids fueled with cell cultured meat. Extruded soy protein scaffold and scanning electron microscopy image of the basic structure of the textured soy scaffold (A); Cylinder of textured soy scaffolds seeded with bovine satellite cell only or with bovine smooth muscle cells co-culture (B); High-magnification images of bovine satellite cell only or with bovine smooth muscle cells (C); Representative images of fried (D) and baked (E) textured soy scaffolds with and without cells (Ben-Arye et al., 2020).

attributes. Despite significant improvements in the science behind producing food from microbial origin or through their action, the full transformative potential of microbial foods is still poorly appreciated (Linder, 2023). Future research should explore the flavor profile and sensory properties of hybrid extrudates to ensure consumer acceptance. Additionally, optimizing the inclusion levels of different microbial proteins and understanding their interactions with plant proteins during co-extrusion could further enhance product functionality. Furthermore, use of tailored ingredients using precision fermentation as a functional fraction and leveraging patented techniques, such as combining plant-derived fractions with cultured cells or extruding mixed cell-cultured meat and plant proteins, could further enhance the functionality and appeal of hybrid foods. Expanding the application of various cellular agriculture-derived ingredients and combining them with innovative processing techniques offers an exciting pathway for developing next-generation hybrid foods that are nutritionally superior,

functionally versatile, and environmentally sustainable and capable of meeting the demands of modern consumer.

5. Nutritional value and health aspects of hybrid foods

While plant-based meat alternatives made from a single protein source often provide sustainability benefits, they may lack certain essential nutrients—such as B-group vitamins, Omega-3 PUFAs, and key amino acids (e.g., methionine, lysine, tryptophan, and threonine). Although their overall nutritional impact has not properly been thoroughly assessed within the context of a balanced diet, various strategies are targeted to design plant-based meat analogues with optimized macro- and micronutrient profiles. Here, hybrid foods present a logical step towards more nutritious and health-conscious food production (Ayaseh et al., 2022). Hybrid foods offer an enriched and balanced nutritional profile, combining the positive dietary aspects of animal-based proteins and other alternatives e.g. algae and microbial sources with the well-balanced characteristics of plant proteins, creating a synergy that optimizes the biological value of the final product (Baune et al., 2023). For instance, grains and legumes are often rich in amino acids like lysine, while meats provide other essential amino acids, creating products with complete, easily digestible protein (Dasiewicz et al., 2024). These additional nutrients play a crucial role in fighting chronic diseases, such as cardiovascular disease and diabetes, which are common in diets rich in processed red meat (Derbyshire, 2017).

Hybrid foods can offer greater health benefits than pure plant- or animal-based foods. Notably, fiber content can be increased by incorporating high-fiber plants, addressing a standard limitation in animal-based foods. Additionally, animal-derived ingredients can boost protein levels, amino acids, and vitamins more effectively than plant sources alone. Consequently, a hybrid diet that combines the nutritional advantages of both plants and meat may support a balanced diet with higher fiber intake and enhanced levels of protein, vitamins, and other essential nutrients. This approach may promote improved gut health, support muscle growth, and help prevent nutritional deficiencies. However, the nutritional profile of hybrid foods is still a relatively new study area, with various findings and the knowledge about the nutritional value of co-extruded hybrid products is very underdeveloped. This is especially important considering the potential positive and negative effects that extrusion conditions may have on macro and micronutrients in each individual source and the effect of induced interactions.

6. Consumer acceptance of hybrid foods

Meat-plant mixtures, also known as meat hybrids, have been shown to appeal to a broader segment of the population (Tarrega et al., 2020), as compared to entirely plant-based products, as these hybrid products often demonstrate better sensory acceptance (Neville et al., 2017). Research shows that people following flexible diets are open to milk substitutes but tend to resist meat substitutes, perceiving them as overly processed. Hybrid meats are designed to offer a familiar taste and convenience, aligning with consumer preferences without significantly altering dietary habits. At least 50 % of consumers expressed willingness to experiment with hybrid meats, choosing responses such as “would,” “probably would,” or “definitely would try.” However, their willingness to make an actual purchase was relatively low (Grasso & Jaworska, 2020). Hybrid products may facilitate the transition to plant-based alternatives by containing a familiar meat component. Consequently, they offer sensory qualities similar to traditional meat products (Neville et al., 2017), making it easier for consumers to shift from fully meat-based diets to more plant-forward eating habits (Tarrega et al., 2020). As Spencer and Guinard (2018) demonstrate, consumers report satisfaction with plant-based products when substituting 50–80 % of the beef. Regular meat eaters, who rarely aim to reduce meat consumption, often find strict vegetarian or vegan diets challenging but express interest in

healthier eating options (Lang, 2020). Moreover, the format of hybrid products influences their acceptability. For instance, Neville et al. (2017) demonstrated that hybrid sausages tend to receive higher acceptability scores compared to hybrid burgers.

In addition, studies have shown that consumer intentions to purchase hybrid meats are influenced by factors beyond environmental sustainability, such as self-assessed ecological footprints and environmental self-identities (Smart & Pontes, 2023). According to Banovic et al. (2022), the “sensory trade-off effect” explains why environmental self-identity has a limited impact on attitudes toward hybrid meat analogues; consumers with strong environmental self-identities are likelier to prioritize taste over sustainability. Regarding the nutritional aspect, the protein content was deemed as the main driver towards hybrid products (Salgaonkar & Nolden, 2024).

Besides the product itself, several studies have examined consumer acceptance of various alternative protein sources, including plant-based, insect-based, cultured meat, and algae. Overall, plant-based proteins are the most widely accepted alternative protein sources, driven by factors such as familiarity, taste, and perceived health benefits (Onwezen et al., 2021). Plant-based meat alternatives are particularly viewed in a positive light, especially for their environmental benefits and alignment with animal welfare concerns, as discussed throughout this manuscript. In contrast, research on insect-based proteins shows lower levels of acceptance, primarily due to food neophobia and feelings of disgust, despite their well-documented nutritional benefits (Puljić et al., 2025). A similar trend is observed with algae and microalgae: while valued for their nutritional properties and sustainability, consumer acceptance remains limited due to unfamiliarity and sensory challenges (Neville et al., 2017; Onwezen et al., 2021). Finally, cultured meat faces skepticism, mainly due to concerns over its perceived unnaturalness and safety. However, a segment of consumers is open to trying cultured meat, particularly those motivated by ethical concerns related to animal welfare and environmental impact (de Oliveira Padilha, Malek, and Umberger, 2022; Rehman et al., 2024).

Banovic et al. (2022) further argue that companies should focus on enhancing and promoting the sensory qualities of hybrid products rather than emphasizing their environmental and health benefits. Despite the appeal of hybrid products as healthy and sustainable alternatives, consumer acceptance strongly depends on sensory attributes, underscoring the importance of taste and texture in developing successful new products. In a recent study, Grasso, Rondoni et al. (2022) explored the sensory qualities of beef burgers versus hybrid and plant-based alternatives, finding that compositional information significantly influenced consumer acceptability, purchase intent, and willingness to pay across all burger types. Hybrid burgers received positive feedback on acceptability, purchase intent, willingness to pay, and favorable consumer comments. Another study by Profeta et al. (2021) examined a survey of 500 German consumers on their preferences and attitudes toward meat hybrids. The study revealed that over half of consumers sometimes substitute meat with other foods, with nearly half considering sustainability and health in their consumption choices. Health perceptions played the most significant role among the factors influencing the choice between meat hybrids and conventional beef.

In line with consumers' willingness to pay for hybrid meat products, production costs are also an important factor to consider. However, as this is a relatively new area of research, only a few studies have evaluated the economic feasibility of this product category. Notably, studies have demonstrated that 80 % of consumers are not willing to pay more for a hybrid meat product compared to its 100 % meat counterpart. Likewise, 37 % of consumers would pay a higher price for a food product made entirely of meat (Profeta et al., 2020). Nevertheless, willingness to pay can be influenced by the type of information provided about the product, such as health benefits, sensory attributes, and convenience (Asioli et al., 2023). Overall, production costs need to decrease as technology progresses. Additionally, typical consumers who prefer these products are generally well-educated and have high incomes, as

indicated by Chen, Zhou, and Hu (2023). In a novel study, Park et al. (2024), integrated bovine muscle and fat cells into rice grains, estimating a production cost of around \$2.23 per kg—comparable to regular rice (\$2.20/kg) but significantly lower than beef (\$14.88/kg). Similarly, Grasso and Jaworska (2020) evaluated the market for hybrid meat products in the UK. Although there are variations in processing and plant-to-meat ratios, the data show that, on average, each gram of hybrid food may cost up to \$0.011. It is important to highlight that the cost of this food category is highly influenced by the type of plant protein used and the processing methods, particularly texturization (Baune et al., 2023). Considering these factors, increasing consumer awareness and familiarity with hybrid meat products can enhance market acceptance and willingness to pay (Boukid et al., 2024; Salgaonkar & Nolden, 2024). These studies highlight the economic feasibility of hybrid products. However, more research is needed to address scalability and optimize production parameters, as costs tend to decrease with increased production scale.

In summary, findings from the literature suggest that while environmental self-identity and health consciousness can shape attitudes toward hybrid products, sensory perceptions remain a more substantial influence. Further research is needed to fully understand consumer attitudes toward other plant-based hybrid products made via their co-extrusion, especially given that many consumers remain unaware of these alternatives. Building on the findings, the integration of other hybrid food categories, such as algae-enriched plant-based products, fermentation-based ingredients, fish proteins, and insect-derived proteins, could benefit from the existing consumer familiarity with meat hybrids. By leveraging the sensory acceptance and health-driven motivations associated with hybrid meats, these alternative protein sources—whether algae, insects, or fermentation-based—may more effectively bridge the gap between traditional animal-derived products and fully plant-based or other alternatives. Consumers already open to hybrid meat products may be more inclined to experiment with similar hybrids, allowing for a smoother transition into alternative protein sources, which can be introduced gradually.

Moreover, the consumer acceptance of hybrid products can encourage a broader shift in dietary habits, facilitating the adoption of other novel food technologies, such as cultured meat and fermented plant proteins. By strategically emphasizing sensory qualities like taste, texture, and nutritional benefits rather than solely focusing on environmental sustainability, companies can enhance the market appeal of hybrids made from algae, fermentation-based proteins, fish, or insects. This approach could also help consumers feel more comfortable incorporating alternative protein sources into their diets, thus contributing to broader sustainability goals. Ultimately, these hybrid products, whether they contain algae, fermentation-based ingredients, fish proteins, or insect-derived proteins, may serve as an entry point for consumers to explore more sustainable food options.

7. Conclusions and future perspectives

Hybrid foods represent an innovative solution to today's environmental and nutritional challenges. These products can play a vital role in the transition towards more sustainable and diversified diets, offering a viable and attractive alternative for those looking to reduce their meat consumption without giving it up completely or looking for alternatives with similar sensorial and nutritional value but with less environmental impact. Co-extrusion can be a promising and scalable approach for the integration of different conventional and emerging alternatives as hybrid products into the meat alternatives mimicking the textural attributes of animal products while different sources are uniformly and homogeneously dispersed in the food and are not recognizable as their original form but the interaction of various sources during co-extrusion remains less understood. This is particularly interesting for incorporating underutilized side streams from animal protein production and insects in the food chain combined with plant proteins, yielding

nutritious and flavorful hybrid products that satisfy flexitarian consumers' demand for alternatives with improved nutritional value and taste. Further investigations and technological improvements to maintain the integrity of the nutritional content, particularly heat-sensitive nutrients such as omega-3 fatty acids and heat-sensitive vitamins are essential for the successful expansion of this approach.

With a more purposeful selection of the sources and careful optimization of the extrusion process and replacement levels (often below 40 %), co-extrusion of emerging alternative sources with plant proteins can mitigate their counterpart shortcomings such as color, texture, flavor and cost. Co-extrusion of insect proteins with plant-based ingredients leads to homogenous textures, minimizing the consumer acceptance challenges associated with visible insects. However, balancing inclusion levels of insect proteins to optimize both texture and flavor remains a key challenge, as higher concentrations may introduce off-flavors or affect the structural integrity of the final product. Insect proteins also offer a unique opportunity to enrich the amino acid profile and improve flavor profiles, contributing to the meaty taste and aroma often sought in plant-based analogues. It is still crucial to optimize the inclusion levels to avoid undesirable tastes, such as bitterness or earthiness, and address safety concerns that could deter consumers.

Microalgae's high nutritional value make them excellent candidates for enhancing the nutritional profile of hybrid foods but challenges such as undesirable coloration, strong algae-like flavors, and limited fiber formation in co-extrusion systems remain. Tailored processing techniques, including pH adjustments, enzymatic modifications, and the addition of functional additives, could mitigate these issues. Future research should prioritize the development of tailored algae strains with optimized compositions and minimal undesirable sensory attributes. Moreover, the purposeful incorporation of algae into seafood analogues, where marine flavors and meat-like colors are desirable, presents another promising direction. The exploration of ingredients made with cellular agriculture, especially those tailor-made via precision fermentation as functional, colorant, nutritional or flavor agents or in the development of plant-based hybrid foods and their interactions with plant-based proteins during co-extrusion, remains a big gap but presents an exciting frontier. Finally, technological advancement in extrusion, consumer acceptance, sustainability, stability and cost-effective production will be critical for the widespread adoption of co-extruded hybrid foods, necessitating transparent communication about their benefits and rigorous safety testing.

Declaration of competing interest

The authors declare no conflicts of interest.

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Nomenclature

BSG	Brewer's Spent Grain
CP	cricket powder
DM	dry matter
HMB	hybrid meat burgers
HME	high-moisture extrusion
HP	<i>Haematococcus pluvialis</i>
IF	insect flour
LME	low moisture extrusion
MDM	mechanically deboned chicken meat
MRP	Maillard-reacted beef bone hydrolysate
PPI	pea protein isolate

TPC	texturized protein concentrate
TVP	Textures vegetable proteins
SP	soy protein
SPI	soy protein isolate
WBC	water-binding capacity
YP	yeast protein

Data availability

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

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