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Perspective

Critical overview of the implications of a global protein transition in the face of climate change: Key unknowns and research imperatives

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SUMMARY

Current dietary protein production and consumption are depleting resources, degrading the environment, and fueling chronic diseases. These human and environmental impacts ignite intense debate on how to shift away from resource-intensive animal-based proteins. While there is significant research across disciplines on shifting supply-demand aspects, knowledge gaps remain in how to transition to optimize nutrition while reducing bidirectional climate change effects. These gaps stymy incentives and policy change to make bold food systems transformations and determine levers to invest in. Here we present a transdisciplinary overview of evidence on proteins' environmental impacts and vulnerability of crop, livestock, and aquatic proteins to climate change. We identify critical unknowns fueling concerns surrounding transitions and propose research directions to increase the likelihood transitions will be environmentally sound and healthy, harnessing genetic crop diversity, managing agricultural landscapes sustainably, and considering cell-based alternatives and pro-equity policies that facilitate healthy choices. Implementing changes requires nuanced, regionally tailored approaches incorporating socio-behavioral, public health, nutrition, and climate science fostering effective debate and solutions promoting sustainability and health.

INTRODUCTION

Transitioning food systems and human protein consumption away from carbon- and resource-intensive animal-based proteins to more sustainable, climate-friendlier sources has become a popular topic of analysis and debate. Myriad discussions and publications have been generated—from multiple viewpoints—on shifting protein consumption as a means to promote environmental sustainability and human health.

Such interest has arisen from increasing recognition of the high contribution of food systems to global greenhouse gas (GHG) emissions, particularly those providing animal-based proteins. Food systems currently contribute approximately one-third of total global GHG emissions, with animal-sourced foods a primary driver accounting for two-thirds of food-related GHGs.[1–3] Economic and population growth to 2050 without any transition to alternative protein sources is projected to lead to a 21% increase in *per capita* meat consumption and a 63% increase in total consumption and GHG emissions.[4] This impact on GHGs, coupled with the increasing global burden of diet-related non-communicable diseases (NCDs; e.g., obesity, type II diabetes, cardiovascular disease), heightens the urgency to assist populations in adopting dietary patterns and practices that support human and environmental health.

Conversely, there are also substantial unknowns regarding various protein transitions within food systems. Recommendations put forward to improve health and environmental outcomes often fail to address the complexity of protein transitions, the challenges faced by populations to make those changes, and the interdependent nature of their anticipated effects. Proposed solutions are frequently limited in scope regionally and by population impacted, reflect the narrow financial or mission-specific interests of individual groups, and promote overly simplistic resolutions.[5]

Given the dynamic bidirectional relationship between climate change and food systems, and that animal-based protein sources are major contributors to GHG emissions, use excessive resources (land, water), accelerate biodiversity loss, and can lead to diet-related NCDs, there is a merited focus on altering dietary protein sources and consumption to simultaneously improve planetary and human health outcomes. Moreover, because such a shift in human protein consumption may yield variable impacts across populations on nutritional status and agricultural production, careful consideration of the potential to exacerbate existing inequities as well as the opportunity to effectuate meaningful change to advance sustainability goals must be carefully considered.

The EAT-*Lancet* Commission sought to overcome these concerns by leveraging the expertise of a multidisciplinary group of

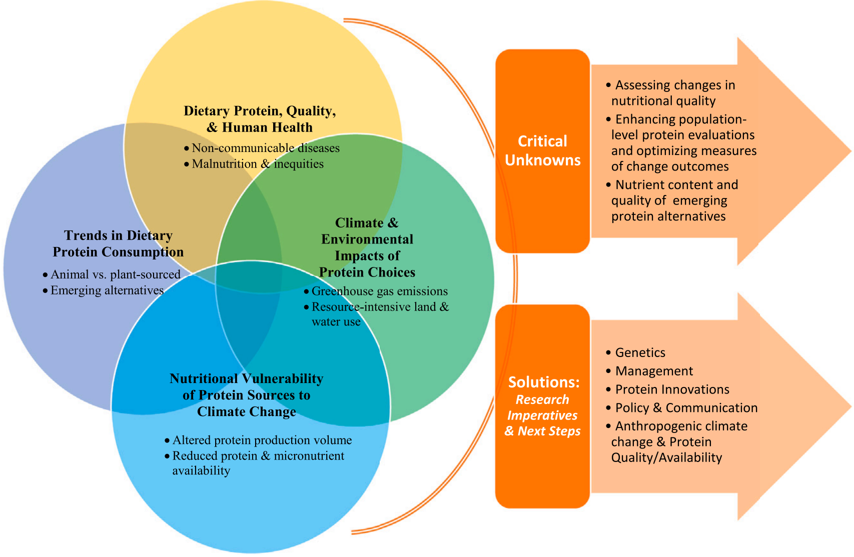

Figure 1. Multidirectional relationship between dietary proteins, human health, and environmental health

This synthesis figure highlights key factors in the multidirectional, interconnected relationships between human consumption of dietary proteins, their impact on human health, the impact of protein production on climate and environmental health, and the vulnerability of dietary proteins to climate change, as well as key critical unknowns of these synergistic relationships and proposed pathways forward toward optimizing health and sustainability.

scientists to incorporate diverse perspectives into a comprehensive report on healthy diets from environmentally sustainable food systems. The EAT-*Lancet* report connected human health and environmental sustainability through food consumption, production, and storage choices[6] and proclaimed food the "single strongest lever to optimize human health and environmental sustainability on earth."

The EAT-*Lancet* report presented the "planetary health diet" (PHD), protective against a set of disease burdens, and calculated its global environmental impact projecting out to 2050. The report has served as a broad-stroke blueprint for food systems transformation and dietary change. The PHD provided guidance for translation into practice, proposing scientific targets for human health and sustainable food production in an uncertain climate.[7] Although not its sole focus, the report made specific recommendations regarding protein, concluding that healthy diets should consist largely of diverse *plant-based* foods with *low* amounts of animal-sourced protein.[7]

However, shifting global protein consumption to meet the PHD would require a sustained move away from consumption of carbon-intensive animal-based proteins (e.g., beef, pork, processed red meats, dairy) toward plant-based alternative options, less energy-intensive seafood (e.g., small fish, bivalves), and cultivated meat.[8] Such a global transition could have variable impacts on the nutritional status of population groups and associated agriculture production systems but could provide a key climate solution by simultaneously reducing emissions and advancing climate change adaptation, as highlighted by the recent UN Intergovernmental Panel on Climate Change (IPCC) Sixth Assessment Report (Working Group II).[9]

Previous assessments have concluded that it is possible to provide 10 billion people with a healthy and sustainable diet within the Planetary Boundaries of climate change, freshwater and land usage, and fertilizer application[2,10]; however, approaches to accomplishing this goal run contrary to deep-rooted and fundamental drivers of food choices and current cultural and societal paradigms on how humanity grows, distributes, processes, and accesses food. What is not known are the various, and widespread, implications of such a dietary transition in regards to nutrition (e.g., protein adequacy, quality, accessibility, equity) and climate change (e.g., bidirectional impact of food systems, production, resource use, environmental effects). These "unknowns" in evidence across various contexts can result in the inability for policymakers and private sector actors to know where to act and how, which technologies and policy instruments could achieve multiple goals, and where there are potential trade-offs if they do act. Without evidence and clear research imperatives articulated, policymakers are navigating in the dark.

The aim of this paper is thus to simultaneously provide an expert view of the nutritional and climatic benefits and challenges of transitioning human consumption away from carbon-intensive protein sources toward more sustainable and healthful alternatives. To address the present knowledge gap and enhance understanding of the implications of shifting dietary intake toward alternative proteins, a review and synthesis of current knowledge was conducted. Following this review, key areas in which additional scientific knowledge is needed were identified, enabling various research imperatives toward more environmentally sound and healthful protein choices in an uncertain climate to be proposed in the present paper (summarized in Figure 1). Our review revealed that various research directions should be taken that consider how demand and supply of protein is being altered. However, the world is ever evolving and, while we have advanced scientific knowledge, shifts in the climate, shifts among consumer demand, and shifts in our ability to produce protein are dynamic with future uncertainties. We identify the following critical unknowns. We propose that there needs to be more research on genetic variation and management of agriculture systems in a changing climate, the role and scale of cell-based alternative proteins, and policies that address a changing consumer base. We conclude that, while there is significant evidence on various disciplinary aspects related to the protein transition, there is a need for research on conventional and new technologies and policies that could clarify unknown scenarios for the future of protein transitions. As the food systems evolve in the context of climate change, so must research. While it is challenging to capture the dynamism of this change, it is critical to do so to ensure that future protein transitions are equitable, just, and sustainable for everyone.

Dietary protein, quality, and human health

Protein is an essential macronutrient for human health, enabling growth, development, maintenance, and repair of bodily structures and systems. Currently, dietary proteins are primarily obtained from animal-sourced (e.g., meat, fish, poultry, dairy, eggs) and plant-based foods (e.g., grains, legumes, nuts, beans). Alternative sources of protein, however, such as plant-based meat substitutes (derived from pulses, grains, oils, and/or fungi to mimic the texture, flavor, and/or nutrient profile of animal-sourced meats), mycoprotein (derived from fungus), insect-sourced proteins, and cell-based meats (i.e., cultured, *in vitro*, cultivated, or lab grown) are gaining increased attention.[11] Given the multidirectional relationship between consumption, health, environmental impacts, and climate change, the emergence of these alternatives holds potential to mitigate the negative human and environmental health effects of traditionally sourced dietary proteins (Figure 1).

At a basic level, proteins consist of amino acids, of which nine are unable to be synthesized by the human body and are thus deemed essential, necessitating intake from dietary sources. Animal-sourced proteins contain sufficient quantities of all nine essential amino acids, serving as complete proteins enabling efficient digestion and utilization. They are considered high-quality dietary protein sources. In contrast, many plant-based proteins are considered *in*complete, providing an insufficient amount or limited bioavailability (the proportion able to be absorbed and utilized by the body) of essential amino acids.

Although several complete plant-based proteins exist (e.g., quinoa, soy-based products), most must be consumed in combination to form complete complementary proteins. An oft-cited example is consuming rice with beans. Complementary proteins are particularly important in populations for which staple grains, rice, and starches constitute the bulk of the diet, with relatively little intake of animal-sourced foods. Such combinations not only provide complete proteins in the diet but also yield supplementary health benefits (e.g., reductions in cardiovascular disease and cholesterol) relative to animal proteins (e.g., beef).[12,13] A recent analysis assessed complementarity of protein quality for binary combinations from a variety of foods, including maize, rice, peas, soy flour, pork belly, and skim-milk powder.[14] Findings confirmed the ability of various combinations to create adequate amounts of high-quality dietary protein. Combining foods containing an excess of one essential amino acid with foods deficient in that amino acid yields a net positive balance, creating a high-quality complementary dietary protein source. For example, mixtures of peas, rice, and maize (incomplete proteins individually) with pork belly, skim-milk powder, or soy flour (complete proteins that contain excess amounts of select essential amino acids) were found to create a complete complementary protein with sufficient amounts of all nine essential amino acids. However, the ratios within such combinations affect the ability to form complete proteins, emphasizing the importance of evaluating consumption within the context of overall dietary and meal patterns.[14] This highlights the complex nature of human diets and the need to consider the totality of dietary exposures, including variety of foods consumed, combinations, and proportions. Examining the influence of single sources of protein can hinder humanity's ability to understand the true impact on human health.

Dietary proteins vary widely in composition, micronutrient content, and digestibility of their constituent parts, making protein quality variable. Dietary protein quality is often estimated using formulas to calculate ratios of weight gain, total protein consumed, type and amount of amino acids present, and ileal or fecal digestibility, among other factors.[14] Commonly employed protein quality assessment methods include the protein digestibility corrected amino acid score (PDCAAS), its successor, the digestible indispensable amino acid score (DIAAS), net protein utilization (NPU), and biologic value (BV). Such protein quality assessments reflect three key characteristics: (1) amino acid composition, (2) digestibility of essential amino acids present, and (3) essential amino acid requirements of a given target population (e.g., infants, children, adolescents and adults, pregnant women).[14] Beyond such physiological considerations, however, protein quality assessment methods do not account for variability in production systems and associated environmental impacts. These characteristics arguably contribute to the overall quality of a protein-rich food, in a manner inclusive of sustainability. Novel measures of protein quality have been proposed that extend current assessments to include both human and environmental health implications.[15] Support for such new metrics includes the potential to inform dietary guidelines (region/country-specific recommendations for intake) and drive improvements in dietary behaviors relative to carbon intensification and environmental concerns.[15,16]

It should also be noted that numerous individual-level factors influence protein utilization, limiting the translation of protein quality assessments to population-level human health implications. Important qualifying factors include the complexity of dietary intake (related to and affected by cultural and regional influences, combination and complementary foods, daily and seasonal variability, etc.), health and disease status, and life stage. Additionally, because the human body does not store excess amino acids as it does calories or micronutrients, temporality of protein consumption is another important consideration. Changes in temporality can be exacerbated by variations in daily protein intake.[14] Protein bioavailability is also influenced by food processing and preparation (e.g., fermentation, baking, frying, roasting), which can decrease digestibility of some amino acids, as well as personal characteristics (e.g., life stage, lifestyle, malnutrition, illness, or infection). Moreover, the presence of other nutrients in the diet, including vitamins and minerals, can also affect protein bioavailability.

Protein-rich foods not only provide amino acids but also deliver a host of other health-sustaining compounds, such as fats, carbohydrates, micronutrients including vitamins and minerals, and bioactives in plants.[12,17] Table 1 provides a snapshot of global nutrient profile estimates of several key protein food sources and average intakes (grams/person/day) across countries for which data are available. Notably, there is considerable variability across commonly consumed plant- and animal-based proteins in the average amount consumed daily, the caloric proportion of protein each provide, the estimated protein quality (based on DIAAS), saturated fat and micronutrients available (specifically, iron, calcium, and zinc). Relative to plant-based sources, animal-derived proteins provide highly bioavailable forms of iron, folate, selenium, zinc, and vitamins A, D, and B_{12}.[17,18] Seafood from fisheries and aquaculture, for example,

Table 1. Global mean estimates of nutrient content across select dietary proteins

Food (g/person/day)[d]	%[a] Protein	Iron[b] (mg)	Calcium[b] (mg)	Zinc[b] (mg)	%[a] Fat	%[a] Saturated fat	kcal[b]	DIAAS[c]
Plant-sourced proteins								
Legumes (34.37)	23.95	6.79	108.51	3.33	11.69	2.9	384.26	98
Wheat (39.73)	11.56	3.05	32.97	1.73	1.67	0.3	344.32	54.1
Maize (31.02)	7.46	2.18	12.91	1.36	2.81	0.39	313.49	37.5
Rice (74.96)	7.08	2.20	13.01	1.25	0.84	0.1	355.05	54.1
Roots/tubers (205.09)	1.80	0.92	17.33	0.35	0.37	0.1	102.49	100
Animal-sourced proteins								
Bovine meat (18.49)	18.95	2.30	8.48	4.97	15.47	9.8	217.75	104.3
Poultry meat (36.04)	18.95	1.60	12.48	1.56	13.78	6.7	202.08	108
Mutton/goat meat (6.4)	18.13	2.51	18.95	3.64	12.64	6.84	191.00	104.33
Pig meat (25.85)	15.94	1.14	14.19	2.28	26.28	12.4	297.26	124.9
Aquatic animals/seafood (24.76)	15.39	5.41	240.15	5.60	1.43	0.1	84.98	103
Eggs (17.81)	13.10	2.92	67.86	2.50	12.63	3.5	176.27	111.5
Bovine milk (304.59)	3.42	217.75	217.75	217.75	217.75	2.9	64.28	101
Non-bovine milk (80.88)	3.93	0.15	152.03	0.36	4.89	3.31	79.72	101
Alternative protein products[b]								
Cultivated meats	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
Plant-based meats average	17.3	3.7	N/A	N/A	14.2	14.2	216.8	216.8
Mycoprotein	11.3	0.5	N/A	N/A	2.9	2.9	85	85
Dry insects average	N/A	12.2	178.8	15	N/A	N/A	N/A	N/A

Source: food composition tables for Global Expanded Nutrient Supply (GENuS).[20] N/A, information is not available.

[a] Percentage per 100 g of protein product.

[b] Amounts per 100 g (mg/100 g, kcal/100 g).

[c] DIAAS is a measure of protein quality based on the ratio of essential amino acids present in a dietary protein source compared to a reference protein and corrected for ileal digestibility.

[d] Average intake across 152 countries with available data on edible food by country in 2011.[21]

provide vitamins (A, B, and D) and minerals (calcium, phosphorus, iodine, zinc, iron, and selenium) that are often not sufficiently available from plant-based foods. These micronutrients play an important role in health, especially during periods of rapid growth and development when nutrient needs are elevated (e.g., fetal development, puberty, pregnancy). Recent estimates suggest that deficiencies in iron, zinc, and vitamin A are rampant globally, particularly among young children and women of reproductive age, for whom suboptimal intake poses significant risks: 56% of preschoolers (372 million) and 69% of non-pregnant women of reproductive age (1.2 billion) are deficient in at least one micronutrient.[19]

Historically, the prevalence of adverse childhood outcomes linked to malnutrition, including stunting and Kwashiorkor disease (a severe form of malnutrition recognized for its distinctive abdominal distention), were believed to stem from general inadequacy of dietary protein, prompting global initiatives to increase protein availability in developing countries.[22] Later evaluations directly measuring protein intake in affected populations indicated that overall dietary protein quantity was sufficient, leading to declarations of a “protein fiasco” centered on false assumptions.[23] However, recent evidence highlights the nuanced nature of the protein adequacy issue; i.e., quality protein availability with sufficient amounts of essential amino acids may be missing in the diet of affected children, resulting in these adverse consequences for growth and stunting.[22–24] Amino acid quality, including digestibility and utilization, aside from availability, is a key constraint to meeting protein demands in some parts of the world.[24] Protein is often one of many nutrients inadequate in the diets of those suffering with undernutrition; thus, protein quantity should be considered in concert with other measures of dietary sufficiency.[5]

Nutrients are not consumed in isolation but instead are ingested as part of complex dietary patterns with daily, weekly, and seasonal variability. Moreover, increases in one food group or nutrient (e.g., proteins) can offset consumption of others (e.g., affecting total intake of saturated fats, carbohydrates, fiber, etc.). As a result, assessments of protein quality and utilization at the population level (versus individual level) are limited. It is therefore challenging to infer the true impact of protein quality from regional or national population-level shifts in protein consumption. This is clearly an area where more cutting-edge science is shedding light on the role of protein in growth and other health outcomes in the context of modern-day challenges and exposure.

Dietary protein is therefore essential to sustaining human health. The quality, quantity, and sufficiency of proteins must all be considered when evaluating consumption and impacts on health outcomes. Nuanced metrics inclusive of these various factors are needed to provide a more robust, comprehensive evaluation of the true implications of shifting dietary intake toward alternative proteins on human and environmental health, at the individual, regional, and global levels.

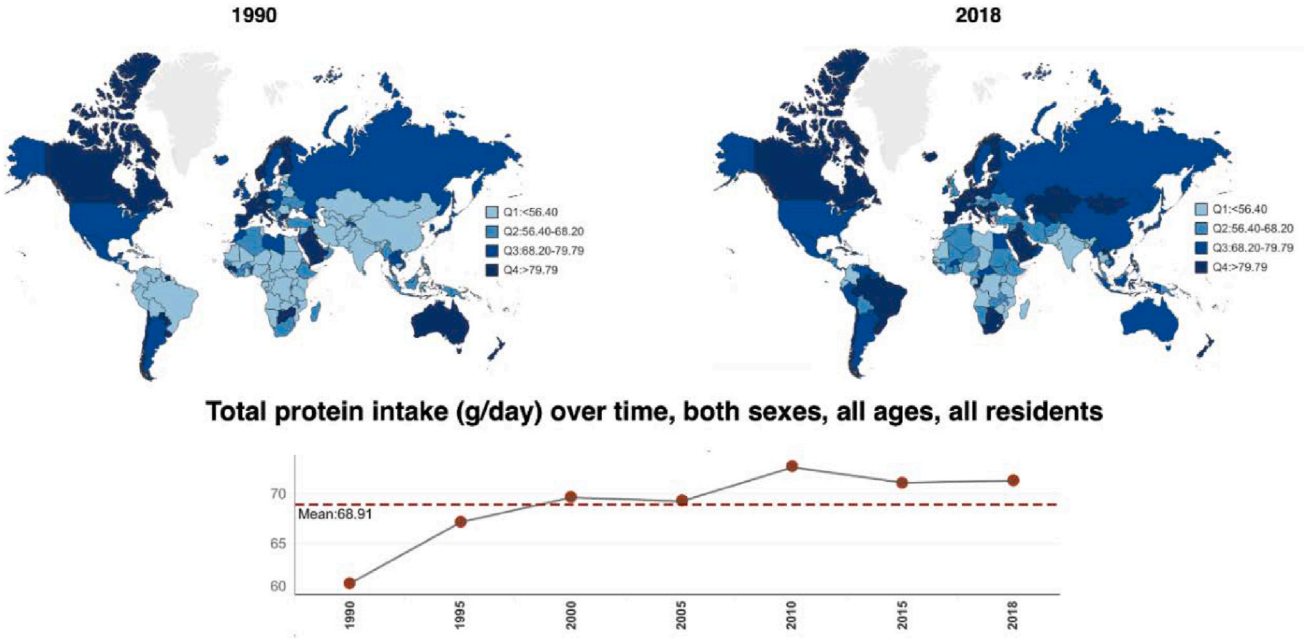

Figure 2. National total protein intake over time for both sexes, all ages, and all residents
National-level total dietary intake of protein in grams/day for both sexes, across all ages and all residents, is presented by country between 1990 and 2018. Source: Global Dietary Database, 2022.[28]

Trends in dietary protein consumption

Historical shifts in protein consumption provide a foundation for understanding future changes in human health and environmental sustainability. Changes in diet and food production systems, including increases in consumption of animal products and decreases in staple grains and cereals, have historically accompanied population growth and rising income.[25,26] These changes characterize the "nutrition transition"—a shift from traditional toward more varied Western-style diets—and the agriculture and development economics of Bennett's law (as incomes rise, people eat fewer calorie-dense starchy staple foods and more nutrient-dense meats, oils, sweeteners, fruits, and vegetables).[25] Shifting societal views and cultural factors also influence changes in consumption. For example, China experienced a recent nutrition transition from a traditional vegetable- and carbohydrate-rich diet toward one characterized by higher intake of animal-sourced foods (e.g., poultry, beef, pork, eggs, milk).[27] This transition was largely driven by rapid economic change, technological innovations in the food sector, and marketing, leading to dietary Westernization with concomitant increases in obesity and NCDs.[27] Such transitions have significant implications for human health, production systems, and environmental costs.[26]

Food consumption has increased over time, accompanied by a rise in protein consumption from an average of 61 g per day *per capita* in 1990 to 72 g in 2018 (Figure 2).[28] Despite recent increases, median intake (68 g *per capita*) remains within the norms of estimated protein requirements (approximately 50 g/day). Estimated requirements for dietary protein sufficiency range from 10% to 35% of daily caloric intake (e.g., based on 2,000 calories/day, 200–700 calories, or 50–175 g, should be derived from protein). The recommended dietary allowance to prevent deficiency for an average sedentary adult is 0.8 g per kilogram of body weight; therefore, based on a global average weight of 62 kg, approximately 50 g of protein are needed per day. There is, however, considerable global variation in consumption and estimates of adequacy relative to physiological demands.[24] The lowest consumption, consistent with food intake, is observed in central and east Africa and South Asia. In an analysis by Ranganathan et al. of protein consumption across 205 countries, it is evident that average protein consumption exceeds estimated dietary requirements in the vast majority of countries analyzed (Figure 3).[29] Notable, however, is the considerable variability observed in the proportion of dietary protein derived from plant and animal sources, with many countries heavily reliant on plants to meet estimated physiological requirements, consuming more than half to three-quarters of protein from plant sources, highlighting the importance of crops in meeting human dietary protein needs.[29] Similarly, it should be noted that crops also play an essential role in the production of animal-sourced proteins as they provide fodder necessary for raising livestock and other feed animals.

Globally, plants and animals constitute 65% and 35% of dietary protein, respectively. Their relative contribution is related to gross domestic product (GDP) (e.g., in the US, plants and animals contribute 32% and 68% of dietary protein, respectively) (Figure 4).[30] As GDP increases and economies improve, average meat consumption *per capita* is expected to rise from 40 kg per year to 52 kg per year by 2050,[31] with a concomitant increase in meat production from 288 million to 494 million tons.[30] Such projected increases will pose additional risks for production of carbon-intensive foods (e.g., beef) with considerable environmental consequences, including concurrent increases in human-edible crops to meet protein needs (a 119% increase by 2050).[32]

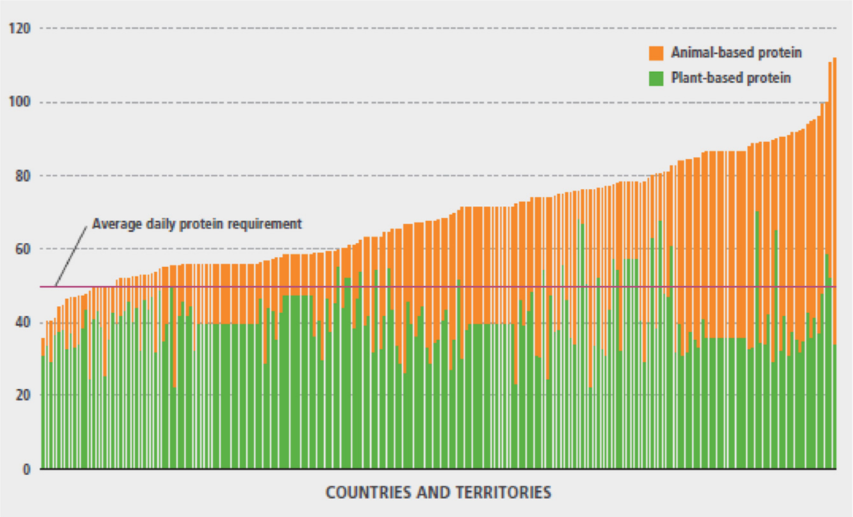

Figure 3. Average daily *per capita* protein consumption relative to requirements
Average daily *per capita* dietary intake of animal- and plant-based proteins are presented with average daily *per capita* protein requirement for countries and territories in grams of protein/capita/day, 2009. Source: Global Food Policy Report, 2016.[29] Note: 205 unnamed countries and territories are included; the average daily protein requirement represented is 50 g/day.

Changing trends in consumption of animal-sourced protein have also been observed in recent decades, including increases in unprocessed red meat, eggs, milk, processed meats, seafood, cheese, and yogurt from 1990 to 2018.[28] Geographic variation in animal sources is also notable. For example, comparing world averages and high-income country averages (with the assumption that high-income countries have increased access to animal-sourced protein), unprocessed red meat intake has decreased in central Europe and Asia as well as in the Middle East and North Africa (24 countries were included in the high-income country category in this analysis, including Australasia [*N* = 2: Australia and New Zealand]; Western Europe [*N* = 20: Austria, Belgium, Cyprus, Denmark, Finland, France, Germany, Greece, Iceland, Ireland, Italy, Luxembourg, Malta, Netherlands, Norway, Portugal, Spain, Sweden, Switzerland, and United Kingdom]; and North America [*N* = 2: Canada and the United States of America). In sub-Saharan Africa, seafood intake has decreased; Southeast Asia has seen some of the highest increases in intake of unprocessed red meat and eggs, whereas lower intake of animal-sourced foods is noted for South Asia and sub-Saharan Africa relative to other global regions.[28] Temporal shifts in animal proteins have also occurred in India and China, with recent increases in chicken consumption.[27,33]

Emerging trends in protein consumption include an increasing focus on plant-based meat substitutes (derived from pulses, grains, oils, and/or fungi to mimic the texture, flavor, and/or nutrient profile of animal-sourced meats) and cultured meat products (i.e., cell-based, *in vitro*, cultivated, or lab grown), driven by rapid market expansion of alternative proteins. Rising popularity and accessibility of commercially produced plant-based meat substitutes have created opportunities for widespread marketing that promotes enhanced health and environmental benefits over traditional protein sources. Such substitutes are often purported to be designed to contain comparable amounts of calories and protein compared to animal-based equivalents[11,34] or have higher levels of micronutrients and vitamins.[35] Seafood substitutes can, theoretically, be fortified with omega-3 fatty acids to mimic the healthful amounts found in fatty fish, but it is unclear if the health benefits would be comparable to unprocessed fish equivalents.[11] Likewise, the nutritional profile of alternative and cell-based meats could, potentially, be enhanced over that of farmed meat (e.g., control fat content, or add vitamin C and omega 3 fatty acids) to confer additional health benefits, adding to the promise and potential of the human health implications of these alternatives.[36] At present, little is known about the precise nutritional characteristics of these emerging alternatives relative to traditional plant- or livestock-based protein sources. Rubio et al. showed that Impossible Beef has similar protein contents as animal-sourced beef, pork, and chicken but substantially higher vitamin B_{12}, iron, and zinc contents.[35] However, the applicability of these results to other alternative protein sources is unclear.

It is also important to note that many of these animal-source protein alternatives are ultra-processed foods that contain (when nutrition information is available and not proprietary) high amounts of sodium, ingredients, and additives, including flavoring, coloring, and binding agents.[34,35,37] There is increasing concern about the negative impact of ultra-processed foods on human health, emphasizing the need for better clarity about the nutrient profiles and ingredients in these alternative protein products. Overall, the potential implications of the trade-offs in processing level and additives as compared with whole-food sources of protein remain unclear. Nevertheless, these emerging alternatives will likely have limited initial impact outside of wealthy countries, for which market demand by high-resource populations may drive availability.

Understanding these historical trends in protein consumption provides a basis for estimating the potential impact of future dietary shifts. In sum, it is clear that dietary intake of protein-rich foods, particularly those sourced from animals, tends to follow economic development, is associated with adoption of Western-style diets, is linked to increased diet-related NCDs, and is associated with resource-intensive and environmentally deleterious production methods. These factors thus pose considerable challenges for low- and moderate-income countries as development progresses. The trends now emerging—mostly among higher-income countries—toward alternative protein sources hold promise as novel solutions to mitigating the negative human and environmental health impacts largely linked to animal-sourced proteins; however, much remains unknown regarding their true potential, as nutrient and production details are not yet widely available.

GHG emissions of protein choices

Animal-sourced foods are responsible for the bulk of food-related GHG emissions and a significant portion (nearly one-third)

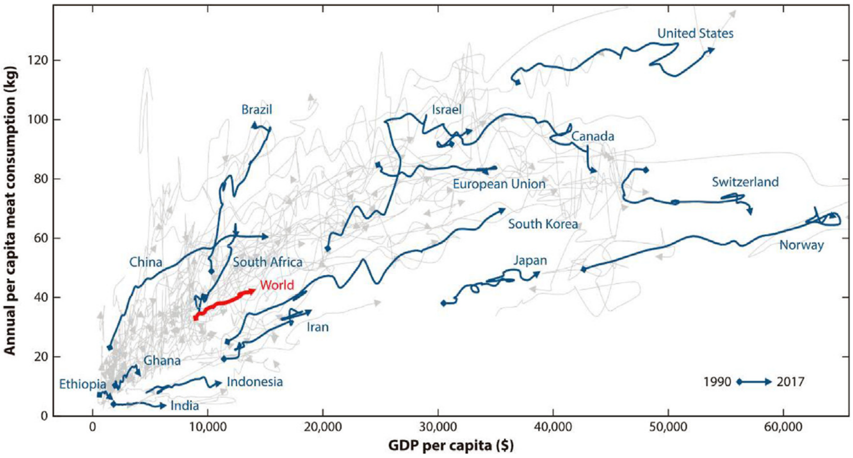

Figure 4. Development of national annual meat consumption *per capita* and GDP over time (1990–2017)

Each arrow reflects the development of *per capita* meat consumption and *per capita* GDP (in constant international dollars) for a particular country. Selected countries are highlighted with blue arrows. All other countries with populations above 1 million people are shown with light gray arrows in the background. Data from the World Development Indicators (https://databank.worldbank.org/source/world-development-indicators) and FAO Food Balance Sheets (https://www.fao.org/faostat/en/#data/FBS), source: Parlasca and Qaim.[18]

of the total agricultural water footprint.[2,3,38,39] However, environmental impact varies considerably by protein source and production method; e.g., GHG emissions and land use are considerably lower for plant-based, aquatic, and insect-based proteins relative to beef (Figure 5).[11] However, water use is a more complicated picture, with particularly high water demand for some farmed seafoods (Figure 5C). Such variability is an important consideration relative to sustainability measures with projected climatic change and ecosystem integrity.

Approximately 20% of global nitrogen and phosphorus applications are attributable to animal-sourced foods, a significant source of pollution for terrestrial and aquatic systems.[2] Meat production is also considered one of the core drivers of global deforestation and biodiversity loss.[40,41] Ruminants such as cattle, sheep, and goats have a far greater GHG footprint than nongrazers such as pigs and chickens (Figure 5). The increased footprint is related to the methane production of ruminants and the inefficient feed-to-biomass conversion. For example, chickens need about 2 pounds, pigs about 3–5 pounds, and cattle 6–10 pounds of feed relative to production of 1 pound of body weight.[11] However, there are means to adopt production methods that can also reduce GHG production for cattle and other ruminants.[42] In addition, consumer choices with respect to ruminant animal consumption can also provide a personally directed, widely available means for individuals to contribute to climate change mitigation by reducing market demand for high-GHG-emission foods.[32,35]

Given that climate change and food systems are interlinked, and that animal-based protein sources are major contributors to GHG emissions, use excessive resources (land and water), accelerate biodiversity loss, and can lead to diet-related NCDs, there is a merited focus on altering dietary protein consumption as a means of influencing both planetary and human health (Figure 1). Hence, solutions to mitigating climate change and environmental

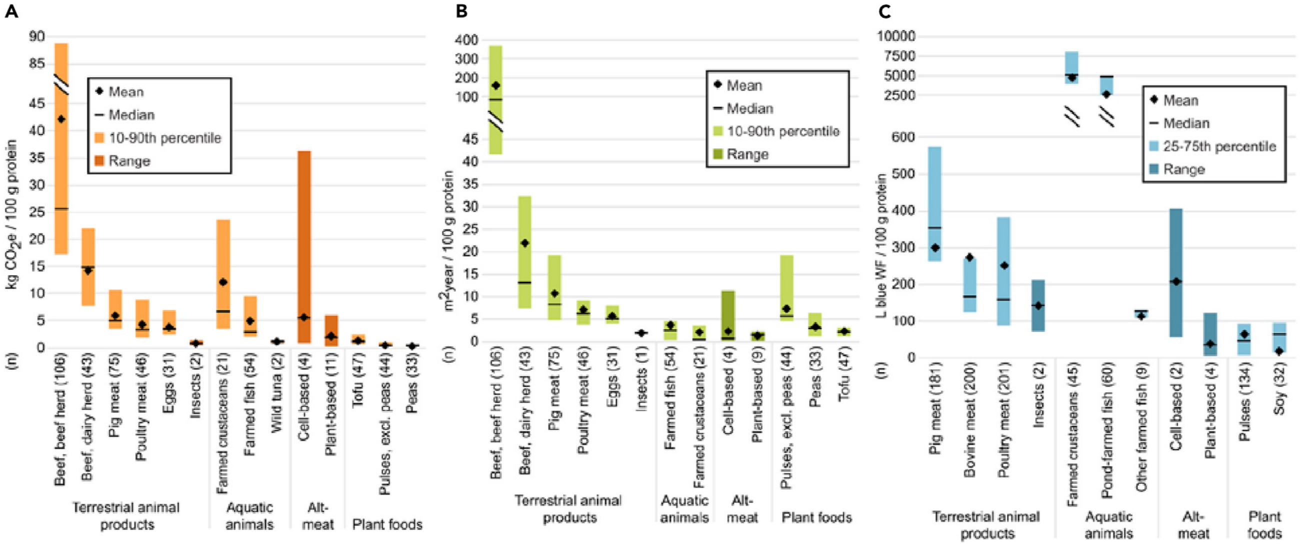

Figure 5. Greenhouse gas, land use, and blue-water footprints of dietary protein sources

The (A) greenhouse gas (GHG) footprint, (B) land use requirements for production, and (C) blue-water footprints of select terrestrial and aquatic animal sources; alternative meat and plant-food sources of dietary protein are presented per 100 g of protein. For details and data sources behind this meta-analysis; see Santo et al.[11]

degradation while promoting economic sustainability and human health outcomes are inexorably linked with food system transitions and protein sources. Overall, in view of climate change and the 2030 Agenda of Sustainable Development Goals (SDGs), it is clear that a profound transformation of the food system is needed to feed a growing world population with a healthy and sustainable diet while safeguarding environmental services.[10]

Nutritional vulnerability of protein to climate Change

Not only do food systems impact climate change but they are also impacted by climate change (Figure 1). Such impacts may influence the nutrient and protein composition and bioavailability of crops and animal-source foods with implications for human health. The vulnerability of current food systems to climate change thus warrants careful consideration in any discussion of food system transition.

Climate change and carbon dioxide impacts crop protein and nutritional quality

Climate change is expected to affect crop productivity across all breadbasket regions globally.[43] The most recent multi-model ensemble estimates suggest that the climate signal emerges earlier than previously thought, negatively affecting staple crops in the global south and in particular maize even at higher latitudes.[44] On the other hand, there is evidence accumulating that moderate warming can create opportunities that may benefit wheat production, which is particularly sensitive to increases in atmospheric carbon dioxide concentration ([CO_2]).[45–47]

Elevated [CO_2], while recognized as a primary GHG, not only stimulates plant growth, it can also affect plant chemistry and the protein content of numerous crop species.[44] Today there is growing evidence that increasing [CO_2] reduces protein and mineral concentrations of major staple crops, especially those with a specific photosynthetic pathway called "C3," including wheat and rice.[48–50] Any effect of [CO_2] on reducing nutritional value of staple crops can, in turn, affect protein and nutritional profiles globally, further exacerbating hidden hunger and chronic malnutrition.[48–51]

However, the mechanisms of crop nutrient uptake in concurrence with changes in [CO_2], temperature, and precipitation and resulting global net effects under unabated climate change remain largely uncertain.[44,51] Crop protein concentrations depend on a complex set of factors including genotype, soil conditions, farm management, weather conditions, and [CO_2].[52,53] In addition to the CO_2 effect on crop protein content, breeding of modern hybrid lines and other factors enhancing crop yield, including increased fertilizer application and irrigation, further reduce the protein content of faster-growing and larger crops.[53] Many studies look at effects of elevated atmospheric [CO_2] on plant growth and protein content, but the effects of warming are often neglected.[50,52–54] Warming and drought stress, however, can increase nitrogen allocations, offsetting some of the [CO_2] effects on the carbon-to-nitrogen ratio (C:N ratio),[52,55,56] although there is evidence that this offset does not always occur.[57]

Open-field experimental trials in which crops are grown under both ambient (~420 ppm) and elevated [CO_2] indicate that concentrations of protein, iron, and zinc of many major crops declines by 3%–17% when grown under elevated [CO_2] levels of ~550 ppm (corresponding to mid-century in a RCP7 scenario, which is a medium-to-high end scenario).[48,54,58] In general, declines in protein content are found to be much smaller in crops with a "C4" photosynthetic pathway and leguminous plants such as soybean. For C3 crops, including wheat, barley, rice, and potato, protein concentrations are found to decline by 10%–15% under elevated [CO_2], equivalent to a high-emission scenario by the end of the century. These declines in protein content and micronutrients represent concerning alterations that may yield considerable impacts on human health outcomes, particularly among vulnerable populations in developing countries in which access to a diverse and varied diet to offset these imbalances may be limited.[49] This is especially important in light of recent evidence that suggests free-air CO_2 enrichment (FACE) data may be seriously underestimating crop responses to [CO_2], further exacerbating observed nutrient reductions.[59]

Process-based modeling can help disentangle some of the underlying processes of N/protein dynamics leading to imbalanced plant stoichiometry. Crop models can provide first-order estimates of the net effects across different crops and heterogeneous landscapes. Asseng et al. provided the first modeling study across various test sites globally for wheat.[46] However, the larger picture of how unabated climate change will affect the total protein yield on a quantitative basis across various major crops and agroecosystems at a global level still remains largely unknown.

A recent study using ensembles of process-based modeling for several major crops indicates that total protein yield might decline under a high-emission climate change scenario for maize, rice, and soybean. Decline in maize and soybean protein yield are associated with crop yield losses rather than changes in protein content (Figure 6). Wheat and rice show substantial decreases in protein content driven by the CO_2 effect, resulting in protein yield losses especially across the major breadbasket regions. These results are based on five bias-adjusted and downscaled CMIP6 climate models and seven leading global process-based crop models (for more details on the simulation protocol of the Global Gridded Crop Model Intercomparison (see Jägermeyr et al.[47]).

Beach et al. use an economic model to leverage observational effects of elevated [CO_2] on crops' nutrient and protein content to evaluate future *per capita* availability.[50] While this approach neglects process interactions between [CO_2], temperature, and growing season length, and other factors, the results indicate that higher [CO_2] levels decrease the global availability of dietary protein in all world regions.[50] Asseng et al. use a multi-model ensemble of process-based wheat models to evaluate protein concentration under climate change and under management adaptation at 60 sites globally, which highlights important disparities between regions.[46] Future protein yields are found to decline especially in low-rainfall regions and, even when using genotypes adapted to a future climate, protein concentrations are shown to decline across most regions. Smith and Myers observed decreases in protein and micronutrient content under elevated [CO_2] for major food commodities and estimate that, by 2050, an additional 175 million people will be deficient in zinc, an important micronutrient for growth and immunity, and an additional 122 million people will be protein deficient.[49]

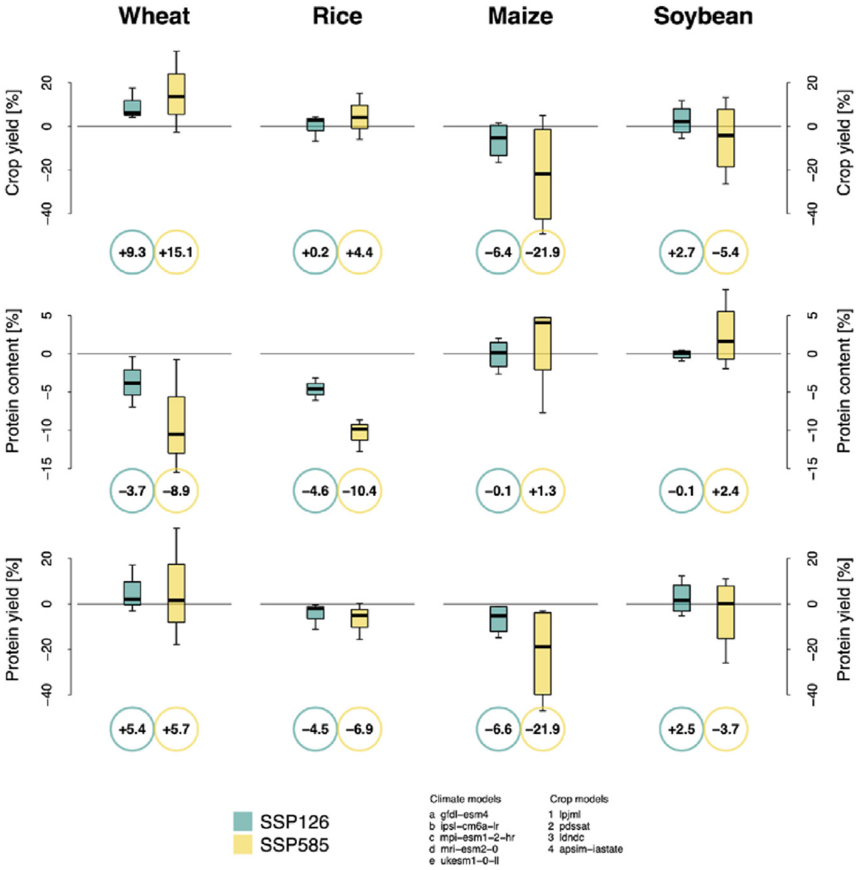

Figure 6. Global crop model estimates of yield, protein content, and protein yield

Boxplots show relative changes in crop yield (first row), crop protein content using the inverted C/N ratio (middle row), and total protein yield (bottom row) for wheat, rice, maize, and soybean between end of century (2069–2099) and current (1983–2013) under the SSP126 and SSP585 scenario. Bullets underneath the boxplots highlight the mean across the multi-model ensemble, the horizontal bar in the boxplot indicates the median response. Multi-model ensemble simulations are taken from the Global Gridded Crop Model Intercomparison (GGCMI) based on five CMIP6 gridded crop models (GCMs) (details on the simulation protocol of the GGCMI; see Jägermeyr et al.[47]).

Further, 1.4 billion women of child-bearing age and children under 5 years old would lose >4% of dietary iron, exacerbating current deficiencies.[44] Regions at highest risk are South and Southeast Asia, Africa, and the Middle East.

Taken together, current reports and analyses raise concerns about estimated reductions in protein availability and micronutrient content of staple crops in the context of rising [CO_2] and climate change. As such, there is concern regarding accessibility of dietary protein, particularly in developing countries where such alterations may yield significant adverse health impacts and worsen existing health inequities.

Climate change impact on nutritional availability from livestock and aquatic systems

Currently, terrestrial animal sources (meat, milk, and eggs) and aquatic animal sources supply 77 and 15 kt of crude protein globally[60]; however, the percentage animal vs. plant protein intake reflects *per capita* income.[61] Climate change has direct adverse effects on livestock systems through the impact of heat stress on mortality and productivity, and indirect impacts through feed and rangeland quality, spread of diseases, and water availability.[43,62,63]

Domestic livestock are found to eat 3%–5% less per additional degree of temperature, reducing their productivity and fertility.[43] Heat stress suppresses the immune and endocrine system, enhancing disease susceptibility,[64] and milk yields are increasingly compromised by the exposure to extreme heat.[65] The direct effects of higher temperatures are found to be more severe for cattle than for goats and sheep,[66] but the growing body of literature highlights the emergence of multiple pressures on current livestock systems.

While higher temperatures and [CO_2] may increase herbaceous growth,[43] potential reductions in nutritional value or increased toxicity of forage species have been observed under elevated [CO_2], with consequences for milk production and weight gain of ruminants.[67,68] The nutritional values of maize and soybean, two common feed crops, are shown to be less sensitive to elevated [CO_2],[48] but there is substantial uncertainty regarding nutritional quality relative to other crops.[55] Crop rotation, including legumes and other forage, can help mitigate farm-level risk and ecosystem buffering in mixed crop and livestock systems.[69]

Boone et al. found that forage productivity declines under 2°C warming by 2050, which results in 7%–10% declines in global livestock numbers—larger than the direct climate change effects on global staple crop productivity.[43,55,70] In addition, climate-driven declines in forage quality for ruminants[71] may also result in increased methane generation overall, and climate change is expected to impact the entire livestock supply chain, from farm production to human consumption; however, the character and magnitude of the impacts remain largely uncertain.[43,63]

Climate change is also expected to reduce maritime protein sources, including marine and freshwater fisheries, as well as aquaculture production.[72–74] Multi-model ensemble estimates indicate declines in global marine fish catch potential of 5.3%–7% by 2050 and mean global animal biomass declines of 17% by 2100 under RCP8.5 (a high end scenario).[43,75] Tropical and subtropical systems are particularly vulnerable, where organisms are closer to approaching their thermal physiological limits than in higher latitudes. Conversely, polar ocean basins are expected to see substantial increases in marine animal biomass with additional warming, creating new fishing opportunities.[76] Contrasting findings suggests that ocean warming and acidification may alter the nutritional quality of commercial mollusks, primarily by reducing healthy fatty acids content, but additional data are needed.[77,78]

Similar to the alterations in protein content anticipated in staple crops, those estimated to occur in animal-sourced proteins, including livestock and seafood, hold potential to significantly impact human health. While there is limited evidence and thus substantial remaining uncertainties associated with climate change and [CO_2]-related impacts on animal-sourced proteins, lower availability of high-quality animal proteins, micronutrients, antioxidants, and healthful polyunsaturated fats from seafood may influence the nutritional status of populations reliant on these dietary sources.

Critical unknowns

Global concerns surrounding a transition in protein-based food systems in an uncertain climate are dynamic, evolving in response to advances in scientific knowledge, shifts in consumer attitudes and perspectives, and innovations in production methods and food products. As such, the critical unknowns that may be addressed through targeted research and the future directions and emerging trends provided here are suggestive but not exhaustive.

There is a vital need to elucidate the basis for changes in nutritional quality. While there is consensus on the role of increasing [CO_2] relative to decreasing protein (nitrogen) and some micronutrients (e.g., Fe and Zn), scientific understanding of these metabolic outcomes is tentative. For example, while nutrient dilution resulting from [CO_2] stimulation of plant growth is often cited,[79,80] there are other reports of nutrient declines even if no [CO_2] biomass stimulation was reported.[81] Changes in nutrient concentrations related to greater Rubisco efficiency, or changes in transpirational flow, need additional enquiry. There is also a critical need to expand understanding of the extent of stoichiometric changes in nutrition beyond protein. Every chemical element necessary for plants is also necessary for humans, but the converse is not true.[82] Humans require key elements (e.g., sodium, iodine, and lithium) that are not provided by plants, and, simultaneously, face additional plant-based toxicological threats from other elements, such as lead and arsenic. Knowledge regarding climate-induced changes in these elements is, at present, very limited; however, it is clear that in some instances, such as rising temperature and arsenic in rice,[83] they may pose a major threat to food systems, independent of production changes. Lastly, while there is a merited focus on protein and climate, there is sufficient evidence to suggest that numerous other qualitative aspects of plant chemistry are likely to be altered by rising [CO_2] and temperature, including changes in carotenoids,[84] changes in B vitamins,[85] as well as more complex secondary compounds (e.g., opioids[86]). Any solution regarding qualitative plant changes related to climate must consider a wider biochemical net.

In addition, available data represent primarily major grain staples, with little information regarding subsistence crops such as cassava, yams, or fruits and vegetables.[84] Similarly, for animal-based protein sources, little is known as to the link between climate/[CO_2] reductions in protein content of feed and livestock protein quality (meat and dairy). Likewise, the role of rising temperature and acidity in aquatic protein sources and quality is not fully characterized. Global aquaculture has shown strong increases in production in the last 40 years and now provides more seafood for human consumption than wild-capture fisheries.[43] As such, it may represent a shift in protein availability that is both more environmentally sustainable while providing significant human health benefits over some land-animal-sourced proteins.

There is also a call for greater information related to the nutrient content, availability, and production demands of emerging protein alternatives, including cell-based protein sources. Cell-based meats and fungi- and insect-based products represent such alternatives to animal-based proteins, but, as they are not yet commercially available, there is little information regarding their nutritional content and bioavailability of nutrients. Similarly, there is an urgent need to understand the role of precision fermentation in the context of advances in genome-based technologies that can be applied to food production systems.[87] Questions remain about the technological feasibility of achieving comparable nutritional profiles *in vitro*, particularly with regard to the quality and composition of proteins, amino acids, vitamins, minerals, fatty acids, and compounds such as taurine and creatine.[88]

In addition to a biological perspective, there is a need to integrate both the cultural and social consequences of protein transitions in an economic context. For example, if rising CO_2 levels reduce protein concentration in rice, then those countries, with low GDP, that rely on rice as a primary food source will be affected to a greater extent.[85] Market forces, policies, and political influences must also be carefully considered, as these factors yield a significant impact on availability, perception, and consumer trends. The cost of consuming a healthy and sustainable diet is also out of reach for many and is thus an essential concern for adoption of dietary recommendations, particularly in low- and moderate-income countries. The Food and Agriculture Organization (FAO) reported that 3 billion people cannot afford what is considered a healthy diet and a recent study found that 1.6 billion people cannot afford the EAT-Lancet PHD.[89,90] Cultural aspects, such as cooking techniques and proportionality among family members also require additional clarification to assess protein and nutrition consequences. Other cultural aspects include varietal preferences and changes in economic status relative to nutritional profiles of food consumed. There is a need for evidence-based regional recommendations and guidance, inclusive of geographic, cultural, socioeconomic, and population-specific needs, norms, and anticipated impacts to inform and drive proposed transitions. Plant-based alternative protein products (e.g., meat, milk, and egg substitutes) are also currently priced at a premium compared to the product they intend to replace (on average, 43% higher).[91] Economies of scale will bring down the price in the future, but it is currently a barrier to wider adoption. Finally, there is an ongoing need to improve understanding of multiple protein sources relative to public health, beyond quality or bioavailability. An essential component will be incorporation of environmental impact metrics as a component of defining quality.

Protein consumption occurs within a complex dietary milieu. Dietary intake is influenced by a number of socio-cultural, economic, behavioral, environmental, biological, and geographic factors. Understanding regional differences in, and the drivers of, dietary variability and complexity will be essential to advance adoption of dietary changes nationally or internationally. Tailored approaches to identify requisite region-specific changes in protein availability to elicit the greatest effect on human and environmental health will therefore be necessary to elicit sustainable and effective change across populations.

Solutions: Research imperatives and next steps

We would caution that any ''one-size-fits-all'' solution to climate change and protein or nutritional quality is unlikely; rather, we would advocate addressing critical unknowns, to integrate and communicate all information to diverse stakeholders (e.g., academia, business, and policymakers), and to provide the necessary public support to address a fundamental and underappreciated aspect of food security. We would also emphasize that the suggestions offered here are not, by any means, exclusive; rather, they represent a starting point for additional interpretation and progress.

Solutions: Genetics

For studies to date that have documented [CO_2]-induced changes in nutritional concentration, it is of interest to note the extent of [CO_2] × cultivar interaction. For example, for, Zhu et al. show significant variation in both Zn and Fe relative to elevated [CO_2], suggesting inherent genetic variability and potential via selection to maintain micronutrient levels as [CO_2] increases.[85] High-throughput screening could, potentially, provide a means to determine stability of nutritional traits in a CO_2/climate context; however, to our knowledge, such an approach to maintain nutritional integrity has not been attempted. We would argue that any long-term solution to nutritional vulnerability will require greater genetic insight of intra-specific variation and GMO development in response to [CO_2] and climate.

Solutions: Management

Overall, in wealthy countries with less labor and greater mechanization, there is a greater emphasis on economic crop production and not nutritional metrics. However, in addition to genetic efforts to increase biofortification, the use and temporal application of select fertilizers can add to micronutrient concentration (e.g., the addition of Zn in rice fields).[92] In addition, phytoremediation can serve as a useful tool to remove excess metals, alter soil pH, and increase nutrient availability.[93]

Land management may also play a critical role in sustainable livestock practices. Changes in temperature can affect feeding behaviors and meat quality.[94] To meet this challenge, some livestock farmers are integrating forestry and pasturelands to enhance sustainability and reduce climate vulnerability. Such a silvopasture approach can provide a range of benefits, including heat reduction and enhanced forage diversity as well as carbon sequestration.[95] Innovative approaches to decreasing environmental and climate risks associated with protein-intensive food systems are also needed. Livestock feeds, for example, can adopt less environmentally perilous protein sources, such as insects, cultivated seaweed, or precision fermentation products, with a subsequent lowering of land requirements and crop expansion. Such alternative sources, if produced with renewable energy, may also offer substantial GHG benefits.[96–98]

Solutions: Protein innovation

Cell-based alternative protein sources represent actual animal meat that is manufactured by directly cultivating animal stem cells. As such, this approach has potential for considerable reductions in land use and plant-based animal feeds.[99–101] An estimate by the consulting firm Kearney in Chicago, Illinois, suggests that 35% of all meat consumed globally by 2040 will be cultured.[99] A more recent life-cycle assessment based on primary data from 15 cultivated meat companies confirmed transitioning from beef to cultivated beef could avoid about 90% of the associated emissions in [CO_2] equivalents.[102] Although promising, at present, the cost of such meat is prohibitive, and additional research and investment are necessary to determine long-term viability and trade-offs associated with necessary production inputs. The environmental footprint and mitigation potential of cell-based approaches need to be better understood, and further life-cycle assessments of cell-based meat are needed.[103]

Solutions: Policy and communication

At present there is widespread governmental concern regarding climate and food supply; however, other aspects, especially related to nutrition and diet, receive little attention. Policies that could provide economic incentives for nutritionally enhanced food, or to encourage production of more diverse, minimally processed foods high in nutrient value, are needed. Such incentives should be considered at multiple levels, from food production systems to offset costs incurred by sustainable, healthy food production methods to individual end consumers to relieve the financial burden of purchasing healthful, sustainably produced foods. There is also a fundamental need to communicate these approaches and estimates to a public that is growing increasingly aware of the carbon costs of foods. For example, in an innovative approach by Wolfson et al.,[104] when customers were provided with carbon (GHGe) information on a fast-food menu, 23% more participants ordered a sustainable (non-red meat) item. This suggests that carbon information on food choices could be an effective means to promote sustainability and promote GHG reduction. Dissemination of such information alone, however, is insufficient to effectuate wide-reaching and sustained dietary behaviors. Additional efforts to support and facilitate dietary choices that promote both planetary and human health would be necessary, including tailored public health and nutrition education campaigns, financial subsidies, and updates to dietary guidelines inclusive of sustainability measures.

Greater attention regarding the dynamic between anthropogenic climate change and protein quality and availability is also needed. At present, there are few resources available to assess the global outcomes of CO_2, climate change, and nutrition. We are unaware of any RFAs at the National Institute of Health (NIH) or the National Science Foundation (NSF) that specifically address the interconnected role of [CO_2] and/or climate change on nutrition and public health.

Finally, there is a need to recognize and address the underlying drivers of inequities in protein consumption and associated environmental and human health implications that disproportionately burden low-resource and socially vulnerable populations globally. Existing food systems, power structures, and failures in governance that promote and perpetuate inequitable access to foods that optimize health and minimize negative climatic impacts must be thoughtfully evaluated and effectively addressed to avoid replicating historical faults with future dietary protein shifts to come. Additional research into socioeconomic and political factors that may serve to drive inequitable human and environmental health outcomes is needed to identify effective, scalable solutions.

Conclusions

The precise impact of unabated climate change on protein yield and availability across various crops and agroecosystems globally still remains largely unknown; however, modeling shows higher [CO_2] levels decrease the global availability of dietary protein in all world regions. The growing evidence that increasing [CO_2] reduces protein and mineral concentrations of major staple crops (e.g., maize, rice, and soybean) is a concerning alteration that may negatively impact human health, particularly among vulnerable populations. Similar alterations are anticipated to occur in animal-sourced proteins, including livestock and seafood. Lower availability of high-quality proteins, micronutrients, antioxidants, and healthful polyunsaturated fats may influence the nutritional status of populations reliant on these dietary sources.

Despite anticipated health and environmental benefits of shifting dietary intake toward plant-based proteins, acceptability of such a shift must be recognized both with respect to human nutritional needs and as an existential means to address climatic change. Evidence-based regional recommendations and guidance, inclusive of geographic, cultural, socioeconomic, and population-specific needs, norms, and anticipated impacts, are needed to inform and drive protein transitions while not exacerbating existing economic disparities and inequities in disease burden. Population-specific approaches to protein transition should therefore be developed to equitably address the differential prevalence of undernutrition and diet-related NCDs across regions.

The complex interdependent nature of food systems should be acknowledged alongside the dynamic socio-environmental, cultural, political, and financial influences surrounding protein production, access, and consumption. Implementing necessary changes and navigating the myriad obstacles likely to impede the path forward will require informed, nuanced, and regionally tailored research that incorporates insight from socio-behavioral, public health, nutrition education, and climate science. Encompassing multiple scientific disciplines could foster a more effective debate and facilitate identification of solutions that optimize uptake and widespread adoption of changes and outcomes that promote both environmental sustainability and human health.

There is a clear need for the scientific community to define and address critical unknowns and potential solutions regarding protein sources and climate vulnerabilities. Such a need must be considered through a sustainable agricultural lens, relative to socio-cultural and economic factors that ensure dietary health. In so doing, it is imperative that the research community conveys the urgency of dietary vulnerability to a range of stakeholders, from business to policy makers and community leaders.

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AUTHOR CONTRIBUTIONS

Conceptualization, C.L.L., J.J., and L.Z.; investigation, C.L.L, J.J., and J.F.; writing – original draft, C.L.L., J.J., J.F., and L.Z.; writing – review & editing, C.L.L., J.J., and L.Z.; supervision, C.L.L. and J.J.

DECLARATION OF INTERESTS

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