frontiers | Frontiers in Science

TYPE Frontiers in Science Lead Article
PUBLISHED 31 July 2025
DOI 10.3389/fsci.2025.1575468

Harnessing agri-food system microbiomes for sustainability and human health

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RECEIVED 12 February 2025
ACCEPTED 02 June 2025
PUBLISHED 31 July 2025

CITATION
Fernández-Gómez P, Leong D, Berg G, Brennan F, Caruso T, Charles TC, Cocolin LS, Lange L, McAuliffe O, Maguin E, O'Sullivan O, Sanz Y, Sarand I, Sessitsch A, Smidt H, Brereton N, Candela M, Kenny J, Kostic T, Mahony J, Wagner M and Cotter PD. Harnessing agri-food system microbiomes for sustainability and human health. *Front Sci* (2025) 3:1575468. doi: 10.3389/fsci.2025.1575468

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Abstract

Food system microbiomes include complex microbial networks that range from soil and marine environments to primary agriculture, farming, food processing, and distribution, and which influence human and environmental health. Advances in "omics" technologies, such as metagenomics, metatranscriptomics, metaproteomics, metabolomics, and culturomics, and their integration have deepened our understanding of microbiome dynamics and interactions. This growing knowledge is being leveraged to develop microbiome-based solutions enabling more sustainable food systems. This review explores microbiome interconnections along the food system and how this and other knowledge relating to microbiomes can be harnessed to, among other things, enhance crop resilience and productivity, improve animal health and performance, refine management practices in fishing and aquaculture, or prolong shelf life and reduce food spoilage during distribution. The often-overlooked role of bacteriophages on shaping microbiomes is discussed, as is the impact of diet on the human gut microbiota and, in turn, health. Despite advances, knowledge remains incomplete in particular areas and targeted experimental approaches are necessary to fill these gaps—going beyond merely predicting microbiome functionality. Ultimately, the ideal development of microbiome-based innovations in food systems will require collaboration between stakeholders and regulators to ensure safety, efficacy, and widespread adoption, unlocking its full potential to improve the health of animals, humans and the environment globally.

KEYWORDS

meta-omic approaches, microbiome mapping, high-throughput sequencing, food-omics, microbiome interconnection, bacteriophages, agri-food system

Key points

- Food system microbiomes form a complex, dynamic, and interconnected network that can be traced across soil and marine environments to primary agriculture, farming, and food processing sectors, ultimately influencing human gastrointestinal niches. These microbiomes impact both human and environmental health.
- Meta-omic technologies are valuable tools that contribute to advancing our understanding of the composition, functionality, and interactions of food system microbiomes within and across ecosystems to fully leverage the potential of microbiomes.
- Advances in microbiome-characterization technologies have helped to highlight the deterioration of specific microbiome networks, including decreased microbial diversity and the spread of antimicrobial resistance, and also to design positive microbiome modulation interventions.
- Microbiome-based innovations and applications have the potential to improve the resilience and sustainability of agri-food systems, and the global health of animals, humans, and the environment.
- An integrated approach involving all relevant stakeholders is vital for protecting existing microbiomes and restoring damaged microbial networks.

Introduction

Agri-food systems are crucial for society. They consist of multiple integrated sectors that provide nourishment while also contributing significantly to employment, trade, and innovation (1, 2). In 2021, the global annual value of agriculture, forestry, and fishing reached US$3.7 trillion and the sector was estimated to provide a livelihood for around one billion people, accounting for 27% of the global workforce (3). In addition, agriculture can have a variety of positive and negative impacts on environmental health, including various aspects of nutrient cycling, water purification, landscape conservation, as well the emission of ammonia and methane.

The 21st century has brought a wide spectrum of climate-related challenges, including prolonged droughts, extreme flooding episodes, and biodiversity loss, which test the resilience of agri-food systems. Moreover, (intense) agriculture is one of the most important anthropogenic drivers of these crises, contributing to six of nine planetary boundaries already being crossed. The planetary boundaries concept defines safe limits for nine critical processes that maintain a stable and resilient Earth. The boundaries “climate change”, “biosphere integrity”, “biogeochemical flows”, “land-system change”, and “freshwater use” are those that are already outside what has been defined as a safe operating space for humanity (4).

An estimated one-fifth of food produced globally for human consumption is lost or wasted (5), which highlights the necessity to reduce food losses along production and supply chains as well as at retail and consumer levels. Indeed, the targets associated with United Nations (UN) 2030 Sustainable Development Goals (SDGs) include reducing by 50% food losses per capita along production and supply chains, doubling agricultural productivity, ensuring sustainable and resilient food production systems, increasing water-use efficiency, and reducing land degradation (6). Ultimately, innovation is critical to ensure food availability, accessibility and affordability while addressing the need to reduce greenhouse gas emissions, energy demand and waste, increase productivity, and preserve environments and biodiversity (7).

In recent decades, there has been a notable increase in research dedicated to understanding microbiomes along the food system. A microbiome is defined as a characteristic microbial community occupying a well-defined habitat that has distinct physio-chemical properties. This term refers not only to the microorganisms involved but also includes their theatre of activity (8). Microbiomes, including those in food systems, are dynamic and interactive micro-ecosystems that are susceptible to changes over time and scale, including processes of coalescence among microbiomes that come into contact (9).

Agri-food-related environments—soil, water, air, plant, food-processing industries, food products, and animals, including humans—contain microbiomes that are often linked to form complex interacting networks. Indeed, microbiomes can influence each other directly, by the inter-microbiome dispersion of microorganisms able to colonize different ecosystems, or indirectly, through the exchange of different molecular mediators (10). This trans-microbiome molecular crosstalk is mediated by the microbiome secretome, which includes proteins and metabolites, which can control, in many cases selectively, the growth of certain taxa. Other mechanisms of microbiome interaction depend on predatory dynamics, involving inter-microbiome exchanges of bacterial, protist, and/or viral predators, such as phages (11). The rhizosphere microbiome offers an example of such a complex trans-microbiome interaction dynamic. Closely connected to soil and aquatic ecosystems, this microbiome can regulate the content of complex polysaccharides or secondary metabolites (e.g., polyphenols or tannins) produced by edible plants; moreover, once ingested by herbivores or omnivores (including humans), these plant foods can shape the composition and functional layout of their respective gut microbiomes.

This concept of interconnected environments is encompassed within the One Health approach, which aims to balance and optimize the health of people, animals, and ecosystems (12), with microbiomes playing a pivotal role (13). More specifically, microbial communities along the food system influence and shape the nutritional, quality, safety, and sensory attributes of food products. Conversely, human activities can modify those microbiomes, with both positive and negative outcomes for global health (Figure 1).

The rapid development of omics technologies has allowed us to analyze the structural and functional dynamics of these microbiomes at unprecedented spatiotemporal resolution, as well as the complex, interdependent networks that microbes and their host form in ecosystems. This has included the use of complementary approaches, such as metagenomics, metatranscriptomics, metaproteomics, metaproteomics, metabolomics, and culturomics,

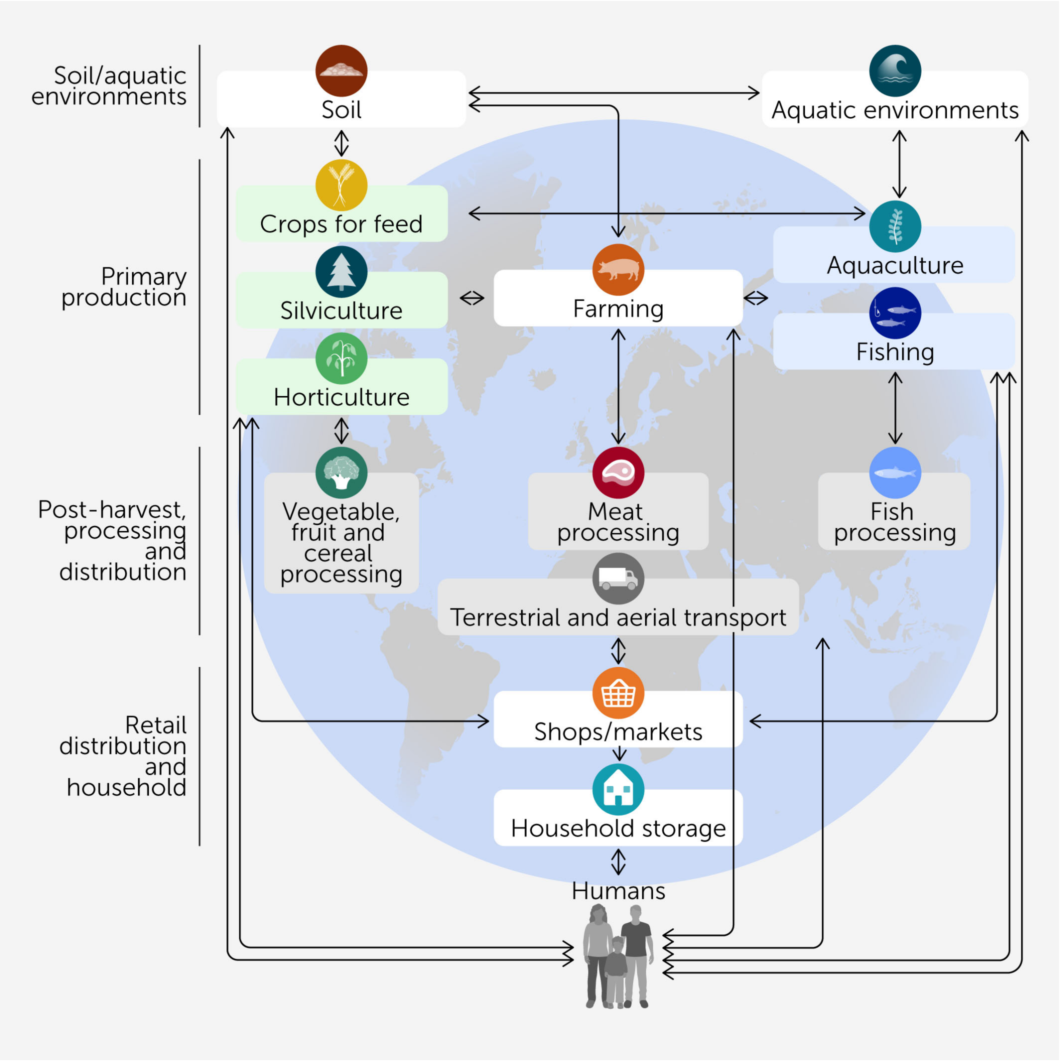

FIGURE 1
Microbiome connections. General microbiome interconnections map in agri-food systems and their potential to impact human health. The arrows represent the bidirectional influences between the most relevant food system environments, which have been grouped into broader categories (left-hand side labels) that correspond to the different sections of the review.

to provide valuable insights into the composition, functional capacity, and biochemical activity of microbial communities and specific components thereof (14, 15). It has also involved the development and use of large data modelling techniques, such as those from network science (16, 17). These advancements have led to several applications for sustainable food systems, as previously reviewed (18–23).

Figure 2 depicts the general pathway followed for the development of microbiome-based agri-food solutions. High-throughput DNA sequencing technologies have been particularly useful to help track the movement of specific strains into and through different ecological niches, thanks to the downstream analysis of these data through bioinformatic pipelines. Whole genome sequencing has been used for strain tracking during outbreak investigations, using well-defined thresholds of single nucleotide polymorphisms (SNPs) between genomes to differentiate strains, and allowing the identification of contamination routes in food processing facilities (24). Whole metagenome sequencing has also been used to characterize microbial networks and track strain movement through the reconstruction of metagenome-assembled genomes (MAGs), as in the case of the tracking of individual *Bifidobacterium* strains between mothers and infants (25, 26).

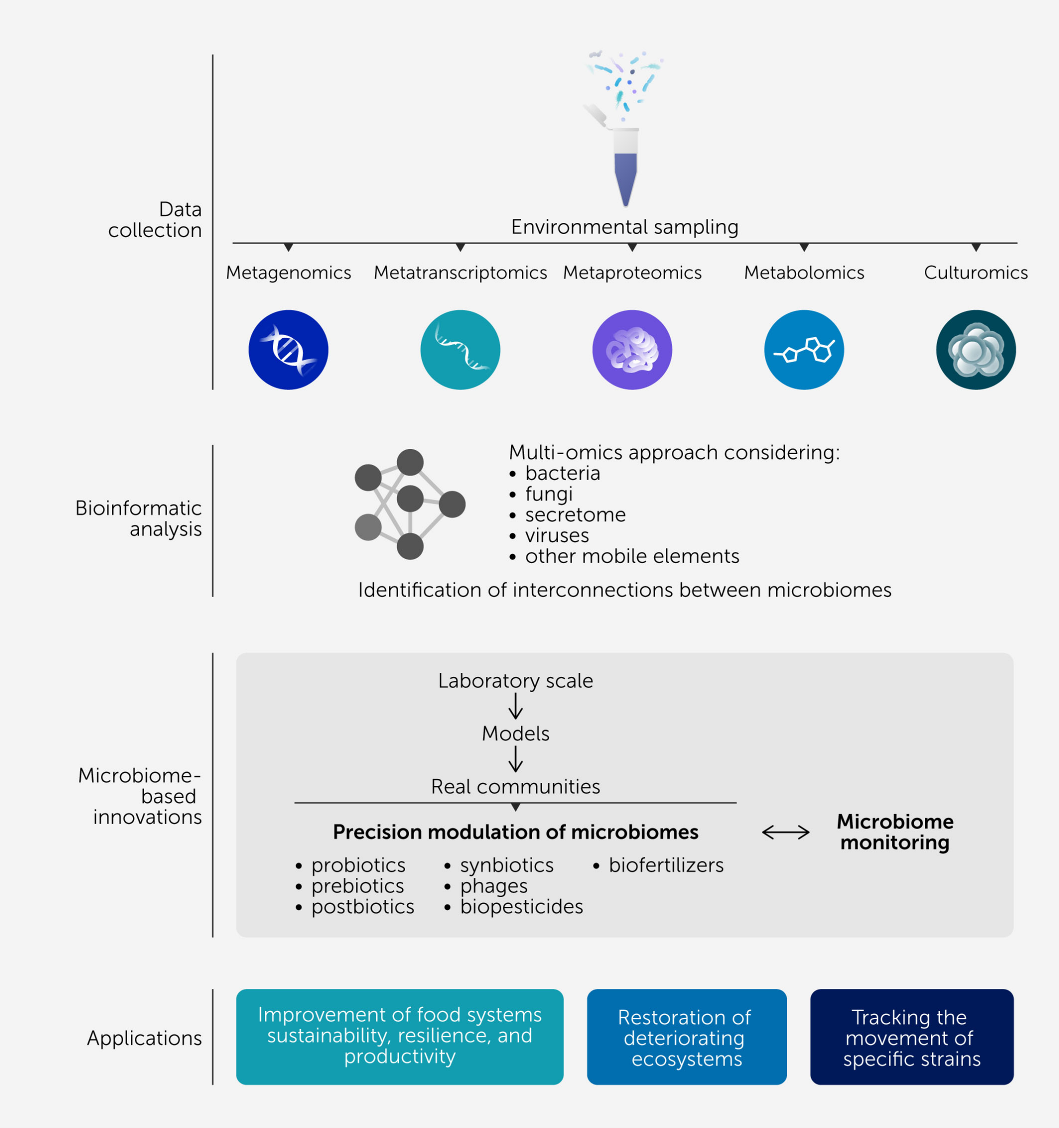

FIGURE 2
Multi-omics for microbiome interconnections research. Pathway for microbiome exploration using diverse omics methodologies and for the development of novel solutions leveraging microbiome interconnectedness. The importance of considering the different components of the microbiome and the functional capacity of the secretome (proteins and metabolites) is highlighted. The interconnections between microbiomes can be studied at different levels, from laboratory scale (increasing the systems complexity), followed by models of real environments (using *ex vivo* models, animal studies, greenhouses tests, etc.) and finally real-world communities (including field studies, studies with humans and livestock, and studies on rivers, oceans, soils or food processing facilities). Microbiome modification strategies can be designed by harnessing the knowledge relating to microbiome interconnectedness and information derived from microbiome monitoring.

These examples demonstrate how alterations in one microbiome can subsequently affect other microbiomes and how this knowledge can be harnessed to develop microbiome modulation strategies.

Influencing microbial communities through intervention has the potential to alter human and environmental health and improve our understanding of microbial niches. Efforts to influence the microbiome in a persistent manner have taken many forms, including the use of probiotics, prebiotics, starter cultures, protective cultures and other biotics (27, 28). While pro- and prebiotics initially came to prominence as supplements for human health, they are now also widely used in agriculture, where they can also be referred to as biostimulants and biofertilizers, and aquaculture with a view to protecting farm animals and fish against disease or to enhance health. Some examples of microbes being used in agri- and aquaculture in this way include the application of bacterial communities to desert crops to protect against abiotic stress (29), the use of yeast to decrease postharvest disease in strawberry production (30, 31), bioprotective lactic acid bacteria treatments used to prevent spoilage in food production (30, 32), and targeted vaccination against the louse microbiome to reduce salmon infections (33). Microbial modulation approaches can also be employed to control a microbial population, and as such, decrease the use of antibiotics, which should be limited to strictly therapeutic purposes due to the potential spread of antibiotic resistance as well as collateral damage that can be inflicted on desirable microorganisms. Microbiome-targeted interventions also have the potential to restore deteriorating biodiversity and increase the resilience of entire (agricultural) ecosystems (34). While such interventions have proven to be successful in specific circumstances, there are also many examples of failures, with challenges including difficulties in translating research in laboratories or on a pilot scale to a real-world setting.

This review aims to highlight the importance of food system microbiomes in the context of environmental and societal health through a series of examples. More specifically, we highlight how the interconnectedness of microbiomes can be apparent through continuous links from soil and marine environments, to primary agriculture, farming and food processing sectors, and ultimately influencing the human gastrointestinal niches and, in the process, impacting both human and environmental health.

Microbiome interconnections and interventions throughout the food system

Primary production environments

Land used for agriculture

The implementation of agricultural practices that promote soil health is key in order to achieve the One Health objective, i.e., accomplishing the best health outcomes for people, animals, plants, and our environment (35, 36). The soil microbiome is closely interconnected with the microbial communities found within above- and below-ground plant microbiomes (Figure 3A). These short- and long-term associations are influenced by various abiotic and biotic factors. Ultimately, they play a crucial role in crop growth and health (37, 38), and can be harnessed to, for example, improve the yields, quality, and resilience of agricultural crops (39). In this regard, abiotic factors, such as soil type and salinity, water, and nutrient availability or photoperiod, have traditionally been the focus of strategies such as irrigation and fertilization.

Some soil–plant interactions with potential applications in agriculture have been observed in non-managed field environments where plants are exposed to extreme conditions. The current knowledge regarding the role of plant-associated microbiomes on abiotic stress protection has been described in multiple review articles on drought stress (40), flooding stress (41), and salt tolerance (42, 43). Moreover, the influence of plant microbiomes on nitrogen fixation (44–46) and the mobilization of other minerals (47) have been well documented. Even host-associated microbiomes, such as those of soil nematodes, can be important for the decontamination of a polluted soil and the release of important macro- and micronutrients for soil fertilization (48). There are also studies that address the influence of microbiomes in mitigating the effects of other limiting abiotic factors on plant fitness, including cold stress (49), freezing stress (50), and other extreme conditions, such as the presence of heavy metals or acidic and alkaline soils (51). Additionally, co-cultivation and intercropping strategies have been widely adopted to increase production and quality by improving soil fertility. To this end, understanding the role of microbial communities in this response has greatly benefited from the application of omics-based technologies (52–54).

Extensive research has focused on how the composition and activities of soil microbiomes, the plant genome, and environmental characteristics combine to impact plant health (38, 55, 56). This approach is based on the so-called "microbiome-associated phenotype" models that consider the contributions of the host genotype, environmental factors, and microbiome to the final host phenotype (57). However, even more interesting is the possibility of intentionally modifying soil microbiomes to replicate similar benefits (58–63). Some successful applications include the engineering of soils with plant-associated bacteria consortia to protect different crops against abiotic stresses such as high salinity, to preserve stable wheat yields under drought, to improve phosphorus solubilization and nitrogen fixation, and to inhibit pathogen invasion (64–67). The last of these is particularly important as plant pathogens can result in substantial losses for producers, and these novel mitigation approaches might offer an alternative to the traditional use of phytosanitary products that can be toxic to soils, water bodies, and even consumers. However, more detailed information about the effectiveness of microbial consortia, including potentially synergistic and antagonistic/competitive interactions between strains, under operational conditions is essential for future implementation (68).

As noted above, the interaction between soil–plant microbiomes is not limited only to the below-ground niches. In fact, colonization occurs primarily at three distinct levels, i.e.,

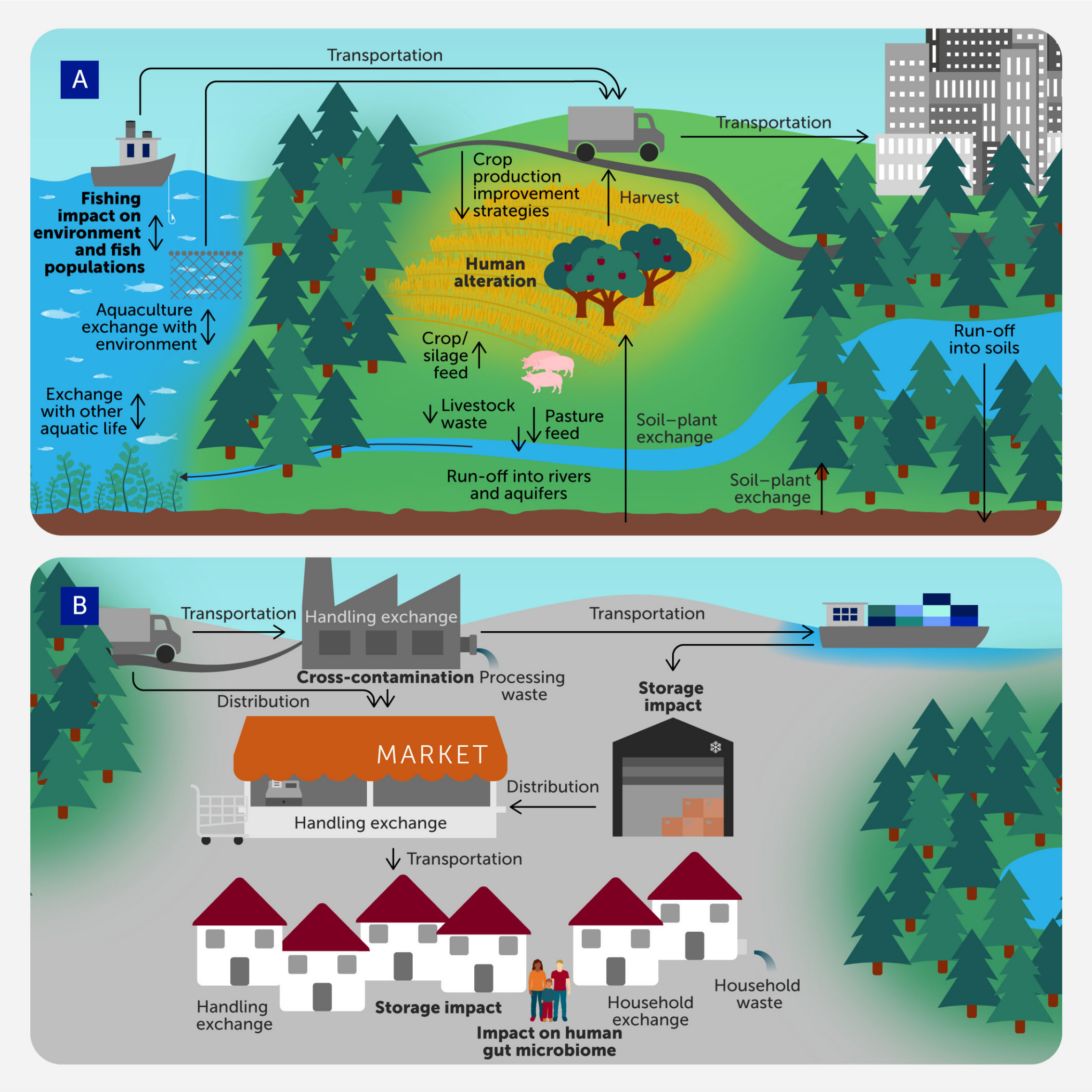

FIGURE 3
Microbiome interconnectedness in agri-food environments **(A)** in horticulture and silviculture cropping, livestock farming and aquatic environments, and **(B)** in distribution, processing, transport to retail, storage, markets, and household handling before reaching the consumer.

the rhizosphere (zone of influence of root exudates), endosphere (internal plant compartments), and phyllosphere (aerial plant surfaces) (37, 69). Changes in climate and agricultural management also impact the phyllosphere microbiome, which is involved in diverse functions such as pathogen suppression, tolerance to extreme temperatures, and nitrogen fixation (70, 71). For example, water stress, fertilization, and arbuscular mycorrhizal colonization can affect the plant phyllosphere (72) and, a large proportion of leaf bacterial species are shared with those in the soil, thereby representing an example of microbiome transmission with implications for foodborne pathogen transmission (73). These findings provide evidence that below-ground microbial interactions and abiotic conditions can shape above-ground microbial communities and show the importance of understanding the whole plant microbiome in the context of developing sustainable agriculture solutions.

There are also strong connections between soil, food crops, and animal microbiomes (13, 74). Ruminant livestock are a very important component of agriculture due to their ability to feed on grass, crops, or fiber-rich crop residues not digestible by humans—often utilizing land not suitable for human food production (75). The common practice of companion cropping in pasture, such as the inclusion of clover, results in distinctive soil microbiome profiles and can increase yields by improving the efficiency of nitrogen fixation (76). As a result, a lower usage of fertilizers is needed, which in turn improves water quality in surrounding water bodies owing to reduced nitrogen runoff. Also, the re-inoculation of endophyte isolates can enhance drought tolerance and improve the growth of pasture and forage crops (77, 78). The application of animal manure instead of chemical fertilizers can also improve fodder crop yields and the nutrient efficiency of the system. However, this practice presents several risks that have led to increasingly restrictive regulations on its use. More specifically, while soil microbial communities decompose manure to release nutrients for plant and microbes, and this process temporarily alters the composition of these communities (79), the introduction of microorganisms through manure treatments on the grass phyllosphere and soil microbiome can have other implications of even greater concern, such as the spread of antimicrobial resistance between livestock and grassland. Manure application can introduce bacteria harboring antimicrobial resistance genes (ARGs) into soil and grass microbiomes, increasing also the risk of horizontal gene transfer within these microbial communities. These ARGs can ultimately be transmitted back to livestock through grazing or other interactions with the contaminated environment, highlighting the importance of understanding microbiome interconnections in order to mitigate biological risks (80, 81). Additionally, manure application can cause an excessive nitrogen input and, if not well managed, increased nutrient levels in run-off waters from the field that end up in the aquatic environment, seriously damaging biodiversity. Indeed, it has been estimated that, in 2018, manure contributed to around 55 million tonnes of nitrogen, either being dispersed in the air, mostly as ammonia gas, or leached in water bodies. Also of importance, nitrous oxide emissions from livestock manure left on pasture are the largest source of greenhouse gas emissions after methane from enteric fermentation (82).

A final example relates to green foliage crops that are commonly preserved as silage through fermentation for use as animal feed. Even though this is a traditional practice worldwide, there is potential to improve the nutritional and functional quality of silage using specific lactic acid bacteria, with consequent benefits for animal health and welfare (83). An important component within this process is the microbial community within the associated phyllospheres, which have been shown repeatedly to influence silage fermentation processes and final product characteristics (84, 85). Unsurprisingly, the introduction of silage into the diet of cattle has an effect on growth performance and the rumen microbiome (86). There remains considerable room for further optimization of these processes through the identification of effective strains, consortia, and/or modes of delivery that could provide persistent benefits across a range of crops and environments.

Aquatic environments

When looking at the effect that primary agricultural production can have on the environment, it is important to include potential impacts on both terrestrial and marine aquatic environments (Figure 3A). Recent technological advancements have allowed scientists to gain a better insight into bioprocesses performed by the marine microbiome that are essential to the health of the planet, such as oxygen production and global biogeochemical cycles (87). Moreover, host-mediated microbiome interactions can also be important for the restoration of degraded marine ecosystems. For example, the microbiomes associated with filter feeders, such as mussels, sponges or cnidarians, can nurture and contribute to the recovery (and protection) of damaged marine habitats (88).

As noted above, fertilizer use is particularly important to the effect of primary food production on the aquatic environment. Fertilizers can have a considerable effect on aquatic environments, especially in rivers and lakes where fertilizer run-off is more concentrated than at sea. The unintended effect of inappropriate fertilizer use can be severe disruption to the existing aquatic microbiome by the spread of pathogens (89, 90), as well as the dissemination of antimicrobial resistance genes (91). Fertilizer spread can also cause the overgrowth of particular species at the expense of others and can change nitrogen and phosphorus cycling, potentially causing severe alterations to aquatic microbiomes (92). Due to the risk of these damaging effects, both direct and indirect, fertilizer use must be monitored, well managed, and clearly regulated.

Aside from the study of unintended impacts on aquatic microbiomes, these communities have been the focus of ever-greater interest due to the growth of the aquaculture production industry. Notably, over the last 50 years, aquaculture-based production of fish and seafood has increased four-fold, overtaking the wild fish catch biomass, and so reducing the pressure on wild fish catches to support the growing population (93). This is important, as excessive fishing of wild fish can cause substantial harm to aquatic ecosystems by disrupting ecological balances. Regulations such as protected areas, types of fishing equipment allowed, fish catch limits, and size exclusion criteria are essential to ensuring population stability and biomass protection (94, 95). However, despite the benefits of aquaculture, associated practices can also have multiple noteworthy effects on marine waters and on the general microbiome of waters as a result of temperature and pH changes, nutrient availability, microplastics, or pest proliferation (96–98). This type of human activity has been shown to increase microbial load in water and lead to algal blooms that cause oxygen depletion and large-scale fish kills, thereby ruining entire ecosystems (99).

Other factors polluting aquatic environments include direct microbial contamination, resulting in an increase in microbial numbers (100, 101), and indirect contamination, such as by microplastics, pharmaceuticals, pesticides, and fertilizers—as next-generation pollutants (96, 102). The use of antimicrobials in agriculture, aquaculture, and clinical applications—especially when not necessarily needed—all contributes to an increase in the antimicrobial stress on aquatic system bacteria (103). Disruption of the aquatic microbiome can result in changes to the overall balance of aquatic species, including changes to plant-microbiome associations, which are essential for the general health of the aquatic ecosystem (104). One clear marker of aquatic disruption is coral decline. Although corals occupy a relatively small area of the ocean, they are a vital part of the marine ecosystem and their decline is of particular concern (105). The special sensitivity of corals to environmental changes is related to their nutritional dependency on a symbiotic association with populations of photosynthetic dinoflagellates. In this context, the identification of a possible pathway to recover damaged coral microbiome after the removal of algal stress shows the potential of microbiome-based studies in developing strategies to restore previously damaged ecosystems (106). In parallel, being able to monitor the bacterial communities of coral can allow a better understanding of the microbial shifts that have happened in response to human activity—including global temperature shifts, increasing ocean acidity, and higher aquatic microbial loads—and hopefully enable human intervention to help preserve these delicate bionetworks (107).

In this regard, the use of beneficial microorganisms is a promising strategy to help corals and sponges to respond to anthropogenic stressors (108).

Technological advances offer considerable opportunities to monitor aquatic microbiomes, including modelling shifts in fish communities (109) and using the skin and gill microbiota as indicators of fish gut health (110). One particularly interesting example is the application of novel sequencing technologies in the Continuous Plankton Recorder (CPR) survey, a major sampling programme implemented in 1931 and one of the oldest in the world (111). The use of molecular technologies for analysis in the CPR offers a significant opportunity to majorly advance our knowledge of global marine ecosystems. Indeed, pico- and nano-plankton, which could not be studied until recent decades, can be used as general indicators of marine health and provide a basis for the formation of marine policy (112). Although the insights from such surveys are not always immediately translatable to aquaculture settings, it is to be hoped that an ever-greater understanding of marine microbiomes will ultimately be valuable in a broad variety of ways. Thus, as nations worldwide prioritize sustainable environmental practices, integrating metagenome-based solutions into public policies regarding the health of aquatic ecosystems has the potential to improve the outcomes of conservation and restoration efforts.

Post-harvest, processing, and distribution environments

Fruit, vegetable, and cereal production

Continuing our overview of the interconnectedness between specific microbiomes in the food system (Figure 1), we now shift the focus from primary production to the interactions occurring during the distribution, transformation, and commercialization of produce.

Fruits and vegetables can have quite direct routes from the field to the consumer (Figure 3B). These types of food are often minimally processed and, if they are not subjected to microbial decontamination methods, can retain much of the microbiome present during harvest (113, 114). Indeed, the term "edible plant microbiome" has been used to describe these communities (115, 116). However, these microbiomes can be impacted by a variety of factors such as storage conditions, transportation, and/or packaging. These are particularly important in light of the increased demand from consumers for products that are out of season and/or not available locally due to the climate of a given region (117–119). Despite advances in the storage and distribution of these products, it has been estimated that globally between 25 and 50% of fruits and vegetables are lost post-harvest (120), emphasizing the importance of spoilage prevention to achieve a more sustainable food system. Improved strategies to monitor spoilage microbiota and food safety verification systems, such as strain-resolved metagenomics, have the ability to provide information regarding, for example, the presence of spoilage and pathogenic microbes, source attribution, temporal, and geographic distribution and cross contamination (121). This knowledge can then be harnessed to improve post-harvest storage practices. For example, using a biological control approach (122–124) technological advances in high-throughput sequencing methods can facilitate a more targeted identification of antagonistic bacteria and fungi for disease and spoilage postharvest control based on a deeper understanding of microbial interactions on epiphytic microbiomes (125, 126). Some specific recent examples have included the identification and successful application of biocontrol agents to decrease postharvest problems with strawberries and peaches (31, 127). This highlights the importance of collaborative efforts between academic research and industry stakeholders in order to translate metagenomic research into real-world applications. The practical experience and insights provided by the industries can help identify the main challenges in the sector and the best ways to apply the knowledge and cutting-edge technology necessary to successfully implement novel microbiome-based solutions.

Not all fruits and vegetables are consumed directly—some are prepared/processed in multiples ways, for example to produce juices, ready-to-eat salads, or fermented foods. Storage time and transportation between harvest and processing/fermentation can affect the final microbiome diversity and microbial load of the product, as shown for example in a tracking study developed on romaine lettuce (128). Often, and particularly for more complex produce distribution chains, a decontamination step is typically included to ensure the safety of the final product that arrives to the consumer. In this context, microbial distribution and interactions inside vegetable processing plants become relevant and the recent application of microbiome mapping as part of routine monitoring programs in food industries has shown potential as a way to decrease spoilage-related issues and ensure food safety (129). In the case of fermented products, the microbiota of the substrate and processing environment can become especially relevant if a spontaneous fermentation is involved (130).

Terrestrial farm animal production

It has been estimated that the terrestrial animal biomass (Figure 3) needs to almost double by 2050 in order to meet the global demand predicted by the UN Food and Agricultural Organisation (131). Farm animal microbiome research and its applications will be of key importance in the move towards more environmentally friendly intensification of animal husbandry on Earth. An increased understanding of microbial interactions in the digestive tract of production animals could allow for the development of diet-based modulation strategies to improve their metabolism, immune system, and overall feed efficiency (132). Notably, the application of omics technologies to the investigation of cattle rumen microbial composition and functionality patterns has greatly helped to unravel its role in the relationship between nutrition, nitrogen excretion, and methane emission (133–138), with a view to the development of new intervention products and strategies. For example, in beef cattle and lambs, diet has a direct effect on the rumen microbiome, with the abundance of certain genera of bacteria and archaea being a potential predictor of growth performance (139, 140). Interventions based on diet supplementation with prebiotics, probiotics, or a combination of both have been developed for different types of livestock, including dairy calves, bulls, sheep, and camels, generally showing positive effects on the rumen microbiome and improving general feed efficiency and other health markers (141–145). Diet can also affect the production of the greenhouse gas methane, a by-product of the fermentation of complex carbohydrates by methanogenic archaea in the rumen, with considerable implications for global warming (146–148). Notably, greenhouse gas emission intensities show geographic differences being lower in areas with a high level of specialization and productivity and higher in regions with lower quality of feed, reproduction efficiency, herd management practices, and animal genetics (149).

Microbiome interconnections are not unidirectional, and livestock grazing has been shown to influence the microbiome and productivity of soil. Grazing livestock species (cattle, sheep, swine, or multi-species) can impact soil microbial community structure and antibiotic resistance gene profiles in a variety of ways (150) and, over the long-term, intense grazing can detrimentally decrease soil carbon and nitrogen mineralization rates (151, 152).

As for plant-based foods, high-throughput sequencing technologies have also provided a better understanding of contamination routes in foods of animal origin (153–156). In the dairy sector, for example, microbiome-based studies have shown the influence of the grazing system on the microbiota of cow teat skin, which can be a reservoir of many microorganisms found in raw milk (157). Similarly, the microbial exchange between feed, bedding material, and cow teat skin was shown by the detection of live yeast provided as a supplement in a grass-diet system (158). Given the importance of the teat canal and the udder surface as a source of milk contamination and intramammary infections by mastitis pathogens, the effectiveness of different disinfection protocols has been extensively evaluated (159, 160). There is growing agreement that a better understanding of the mammary microbiota can lead to the identification of improved therapeutic products and disinfection protocols that favour beneficial microorganisms (161, 162). Importantly, while this review focuses on non-pathogenic microorganisms, microbial transfer is also critically important to the transmission of zoonotic pathogens such as *Listeria monocytogenes*, *Salmonella*, and Shiga-toxin producing *Escherichia coli* from plant or animal sources, as reviewed elsewhere (163).

Microorganisms can end up within the microbiome of food products via the raw ingredients or the food processing environment (Figure 3B). An example of the former relates to cheese production, whereby some non-starter lactic acid bacteria (lactic acid bacteria that do not form part of the added starter culture) originating from the milk became part of the cheese microbiome, being associated with positive or negative quality outcomes after cheese ripening (164). The pathways of microbial transfer along the cheese-making process have been described on several occasions, gaining special importance in the case of traditional raw milk cheeses where non-starter bacteria can shape the fermentation and ripening processes (165, 166).

Similarly, the routes of microbial transmission into and inside processing facilities have also been studied using next-generation sequencing approaches, for example, in the meat industry (167–169). In this way, facility-specific transmission maps can be created, helping to predict previously unidentified sources of bacterial contamination (170). Other successful applications of this approach include the longitudinal tracking of the divergence and spread of foodborne pathogens (171) and studies of the microbial colonization of newly open facilities identifying routes of entrance of pathogens and antibiotic-resistant microorganisms (172, 173). Despite these advances, investigations into the transmission of foodborne pathogen outbreaks continue to draw conclusions based on culture-dependent approaches combined with whole genome sequencing (24). Once again, academia–industry partnerships encourage knowledge exchange and contribute to research whose outcomes address critical issues in food production and are effectively integrated into industry practices, accelerating the adoption of metagenome-based innovations in the food system (174).

Aquaculture

In aquaculture (Figure 3), the microbiomes of fish can have a major impact on health and growth rates and should thus be of upmost concern for the associated production industry to prevent losses and maximise production. Modern sequencing technologies can greatly advance aquaculture microbiome monitoring (175), as the identification of a core microbiome can be essential in understanding the health of an aquaculture population and the bidirectional interactions between aquatic microbiomes and aquaculture (176). Importantly, while pathogens can be a natural part of an ecosystem they can also be extremely damaging to aquaculture and so need to be carefully observed, with interventions made when appropriate to prevent infection and production loss. Careful monitoring of multiple factors is vital to aquaculture, as the microbiota can be affected by numerous factors, including diet, disease, oxygenation, pH, and temperature (177, 178). The use of aquafeed needs to be carefully examined to ensure that it is providing the necessary nutrients for its intended recipients but is also free from contaminants, including fungal contamination and mycotoxins, which can spread beyond the aquaculture environment to the wild aquatic environment (179). Aquaculture can also damage aquatic environments via algal blooms derived from changes in water conditions and nutrient availability, and because intensive fish farms are vulnerable to infections that can spread into the wild (90). Probiotics are commonly used in aquaculture, especially particular strains of bacilli (180, 181), lactobacilli (182), and bifidobacteria (183). Certain strains have been shown to protect against disease and infection, and to improve the general health of the aquaculture fish and seafood (184). Antimicrobial use is sometimes necessary to prevent infections becoming pervasive but, as in other environments, their use can have unintended but severe consequences, including the increase of antimicrobial resistance in the environment (185–187).

Moving to fish processing, food safety and spoilage can be a major issue, especially considering the short shelf life of seafood. Although the shelf life of fish and shellfish has been significantly improved with advances in refrigeration and freezing technologies, fish losses are still estimated at 27% between landing and consumption (188). The addition of microorganisms can prevent spoilage through multiple mechanisms. Microorganisms can be added directly to act as a bioprotectants against foodborne pathogens (30), while bacteriocins (189) and bacteriophages can also be used to help control unwanted pathogens and spoilage organisms (190).

The improved understanding of aquaculture microbiomes is also being applied to develop novel monitoring and mitigation strategies. These include: investigations of the potential of gut microbiomes to mitigate disease in aquaculture (191); harnessing knowledge relating to the skin microbiome of fish to predict population collapse (192); using machine learning models to predict fish kills and toxic blooms in intensive aquaculture (193); and using seawater transfer to improve microbiome diversity (194) and the removal of ammonium and nitrite (195). While microbiome-informed practices and innovations can help to protect natural microbiomes, they can also offer advantages to the aquaculture industry itself. Indeed, such studies have shown that common practices in aquaculture, such as the use of bleaching powder to disinfect marine water, may not have the previously presumed effect as aquatic microbiomes treated in this way have been seen to recover quickly (196). Ideally, advances in our understanding of aquatic microbiomes can be leveraged towards a more efficient production system while, at the same time, reducing damage to the wider ecosystem.

The future growth of the aquaculture sector will be sustainable only if the industry transitions to more eco-friendly approaches that minimise environmental impacts, particularly in terms of reducing eutrophication in marine water. Integrated multi-trophic aquaculture (IMTA) provides one concrete solution, as a sustainable approach to intensive aquaculture. IMTA combines fish farming with the growth of lower-trophic species that can recycle/adsorb organic and inorganic nutrients to increase the eco-compatibility of the aquaculture practice. Crucial to its success is the selection of the appropriate combination of productive and nutrient-extractive species that complement each other from a trophic perspective. This enables novel eco-designed solutions that also integrate marine microbiomes as an innovation in the IMTA design. The selected species contribute to an overall holobiont solution to nutrient cycling. Indeed, many microbiomes —environmental and host-associated—can exert a primary role in the recirculation of organic matter in marine ecosystems, and their targeted integration at the metacommunity level in IMTA systems has the potential to lead to even more efficient reductions of ecological footprints (197).

Retail and household environments

Food uptake impacts all levels of physical and, in higher organisms, mental health. Access to a reliable food supply facilitates the development of societies and stabilizes political systems. The corollary is also true with disturbance of the food supply system frequently leading to major human crises, including, as an extreme, famine and mass starvation. Although enough food is produced on earth to feed the entire population, the biggest challenge in modern food production remains the logistics behind the food distribution system that largely determines whether food is consumed or discarded (198, 199). In developing countries, which lose up to 50% of their primary production due to spoilage and mismanagement, major distribution failures result from a lack of power and storage capacity during and after harvesting campaigns. In developed countries, food is discarded primarily due to shelf life issues and inappropriate buying patterns (200). At the retail level, food storage is the most essential economic parameter, especially for perishable food, and most of the costs of a supermarket or retail premise go into the energy supply for food cooling and presentation (Figure 3B). Understanding the microbial dynamics during cold storage of intermediate and final products is of utmost importance to lower the levels of foods that are discarded to an acceptable level. A special advantage for microbiome-based interventions lies in the enhanced capacity to detect fastidious growing spoilage-associated microbes that are usually difficult to detect by culture-based technology (201).

The issues raised above also pertain to households (Figure 3B). More and more households store food for an extended period of time due to the conditions of the modern working world. Knowledge relating to spoilage processes and control of the cooling processes in household refrigerators is still surprisingly scarce, even though a link between microbial communities found in the kitchen and the skin microbiome of humans has been described (202). Microbiome tracking strategies can also be used to detect routes of contamination in consumer households to, for example, show the importance of refrigerated storage of products that could limit the proliferation of opportunistic human pathogens (203). These approaches have also been taken even further to track the movement of lactic acid bacteria, such as *Weissella* and *Leuconostoc* species, from ready-to-eat salads to the human gut after their consumption (204, 205). Although microbiome tracking approaches continue to be applied predominantly for academic research, as costs and other barriers are reduced, it is expected that these approaches will be used more widely by industry and, eventually, consumers.

The role of bacteriophages in shaping microbial communities

While the bacterial and fungal components of food production systems and food products have been widely studied, the viral component of these ecosystems is less well defined. Bacteriophages (or phages) are bacterial viruses that typically infect strains of a given bacterial species. Phages may be considered beneficial in certain situations, for example, in the elimination or reduction of human or animal pathogens, or spoilage bacterial numbers (206). Conversely, phages that infect starter bacterial cultures are a major threat to food fermentations as they may compromise the acidification or flavor development of the product. In recent decades, studies have focused on defining the phage populations in food fermentation facilities relating to lactic acid bacteria such as *Lactococcus lactis/cremoris* and *Streptococcus thermophilus* (207–209). These studies initially used culture-based approaches to tease apart the interactions of phages and their hosts. In the context of phages, this requires the ability to perform plaque assays. More recently, high-throughput DNA sequencing has allowed a more unbiased examination of the viral component of the microbiome. The role of the virome, and more specifically the “phageome”, in influencing bacterial compositional changes in microbiomes has garnered increasing research attention (210–212). From an evolutionary perspective, the phages and their bacterial hosts have been in conflict for millennia, and recent studies have allowed us to question the mode of these interactions and their impact on microbiome maintenance, modulation, and functionality, including through horizontal gene transfer across food system niches (213–216).

One such example is the initial interaction between a phage and its host, dictated by the presence of a suitable receptor on the cell surface of the host bacterium, which may be a carbohydrate, protein, or (lipo)teichoic acid. These early interactions are exceptionally well studied in a small number of bacterial host systems, including specific spoilage and pathogenic species such as *E. coli* (217), *L. monocytogenes* (218, 219) and beneficial starter bacterial culture species such as *Lactococcus lactis/cremoris* (220) and *Streptococcus thermophilus* (221). These foundational studies have provided insights into generalized and specialized modes of host recognition and subsequent infection by phages of these species, and which may be applied to the development of tools to improve the consistency, sustainability, and safety along the food production chain. Combining these studies with developments in sequencing, computer-assisted prediction of the folding and functionality of structural proteins, and imaging is allowing further elucidation of these interactions and serves as a blueprint to studying the interactions of players within a microbiome.

The impact of microbiome interconnections and interventions on human health

One major area greatly enhanced by recent advances in multi-omics approaches is the study of the human gut microbiota and its contribution to human health. Many factors can influence the human gut microbiota, including genetics, geography, socioeconomic status, age, and health status. Notably with respect to this article, diet is a key modulator and diet–microbiome interactions are often at the forefront of microbiome research.

Having a diverse gut microbiome is frequently associated with health, potentially through protection against pathogens and disease (222, 223). However, this diversity can be affected by multiple factors. There is evidence that a modern, Western diet (high in simple carbohydrates, saturated fats and salt, but low in fiber, complex carbohydrates, and micronutrients) has a damaging effect on the gut microbiome and can contribute to multiple health problems including cancer, obesity, gastrointestinal and gut–brain-related issues (224, 225). Specific ultra-processed foods that are high in fat, sugar and/or salt are of particular note as an issue in a modern, Western diet. These foods often lack microorganisms, complex nutrients, prebiotics, and fiber, can contribute to decreased gut microbiome diversity and, in turn, various health issues (226).

There is growing evidence of the occurrence of food-to-gut microorganism transmission (116, 227). Although necessary to ensure food safety in large-scale production, many food processing techniques remove most or all naturally occurring microorganisms, thus contributing to an altered human gut microbiome and an increase in non-communicable diseases (228). Historically, food was sourced from the local area and was subject to seasonal variation. Some of this food would have been completely unprocessed and consumed quickly so microorganisms naturally present in the food were introduced to the consumer gut microbiota. Advances in processing, refrigeration, storage, and transport techniques have allowed for more food to be sourced from further afield and have allowed for foods not to be restricted to a particular season. However, these advantages in food availability are also contributing to the decrease in diversity in human gut microbiota as many of these foods now need to have a longer shelf life and many techniques to prevent spoilage and pathogenic activity also decrease or completely remove the indigenous microbiota of the foods. Similarly, the higher demand for convenience foods, for example, a pre-packaged, pre-washed salad in contrast to unprocessed salad, has further distanced the consumer from food’s naturally occurring microbiota. In any case, the safety of the food that reaches the consumer is of utmost importance. While the emphasis of this review is on the broader microbiome interconnections between food and the human gut, it is important to acknowledge that the food system also serves as a route of transmission of opportunistic human pathogens (229, 230).

In addition to live microorganisms, prebiotics and bioactive compounds are other components in food that can alter the gut microbiota. Prebiotics, such as certain fermentable fibers, polyphenols, and oligosaccharides, can promote positive effects on health through gut microbiota alteration (231–233). However, modern Western diets are often deficient in fiber and contain an overabundance of fat and sugar (234). The high proportion of meat in the modern Western diet has also been seen to decrease gut microbiota diversity, while plant-based diets have been shown to be advantageous to human health (235). Nevertheless, it is important not to overlook the possible nutrient inadequacies that can be associated with different dietary patterns, including vegan, vegetarian, and meat-based diets (236, 237). Bioactive compounds can contribute to human health, including via antioxidant and anti-inflammatory effects, and can come from a variety of sources, including marine algae-sourced bioactive compounds (238, 239). A relatively underutilized source of bioactive compounds are those resulting from food wastes and by-products, which could offer benefits without the need for further alterations to natural microbiomes through additional production streams (240).

Another diet-based approach that can beneficially impact gut microbiome diversity and function is through the consumption of fermented foods. Fermented foods have been widely shown to be advantageous to the gut microbiota through the promotion of a

TABLE 1 Potential microbiome-based solutions for different sectors across the global agri-food system and the private and/or public stakeholders involved.

Agri-food ecosystems and system components	Microbiome-based solutions	Agri-food system stakeholders	Relevant references
Soils and crops	Plant-associated microbial consortia to: - protect crops against high salinity and drought - improve crops phosphorus solubilization and nitrogen fixation - inhibit pathogen invasion	Private sector - crop production Policymakers	(65–67)
Soil and pasture	Inclusion of clover as companion cropping in pasture to increase yields and improve nitrogen fixation efficiency Re-inoculation of endophyte isolates on pasture and forage crops to enhance drought tolerance and to improve the growth	Private sector - crop and animal production Policymakers	(76–78)
Pasture and farms	Use of specific lactic acid bacteria to improve the nutritional and functional quality of silage Livestock diet supplementation with prebiotics, probiotics or a combination of both to improve the general feed efficiency and other health markers	Private sector - crop and animal production Policymakers	(83, 141–145)
Aquaculture	Monitoring fish skin microbiome as an indicator of fish gut health and to predict population collapse Improvement of microbiome diversity through seawater transfer and removal of ammonium and nitrite Fish diet supplementation with probiotics to protect against disease and infection, as well as improving the general health	Private sector - aquaculture Policymakers	(110, 180–184, 192, 194, 195)
Marine environments (coral reefs)	Use of beneficial microorganisms to help corals and sponges to respond to anthropogenic stressors	Public sector - environmental protection initiatives Policymakers	(108)
Processing plants and distribution	Application of biocontrol agents to decrease postharvest problems with strawberries and peaches Microbiome mapping of food processing industries to predict sources of bacterial contamination and decrease microbial spoilage and foodborne pathogen-related issues Use of starter cultures and protective cultures to improve food product characteristics and shelf live	Private sector - fruit production - vegetable, meat and dairy products processing Policymakers	(31, 127, 129, 170–173)
Foods	Consumption of probiotics, prebiotics, bio-active compounds and fermented foods to promote positive effects on human health through gut microbiota alteration	Private sector - producers - consumers - media Policymakers	(231–233, 238, 239, 241, 249–252)

diverse microbiota and the potential to simultaneously provide prebiotics, probiotics, and bioactive compounds (241). Indeed, the European Food Safety Authority (EFSA) has approved the claim that live yoghurt cultures improve yoghurt lactose digestion in individuals with lactose maldigestion (242). Although some fermented foods have been produced over hundreds or thousands of years, many are not yet well characterized (243). Foods and feeds produced by spontaneous fermentation have been shown to typically result in products that contain very similar microbial taxa and applying ecological and evolutionary frameworks can be valuable with respect to understanding the assembly of fermented foods microbiomes (244, 245). Indeed, establishing a better understanding of such microbiomes, and the strains present therein, may offer advantages to human health that have not yet discovered. Some of these benefits may relate to the consumption of live microbes specifically (246–248). In addition, the consumption of specific probiotic strains, added to foods or taken as supplements, can contribute to reducing the incidence of particular human diseases (249–252).

Conclusions

Food system microbiomes form complicated and connected networks that can be very difficult to disentangle. Advances in technologies, especially in high-throughput sequencing technologies, have enhanced our understanding of these networks. Developments, especially in soil, plant, animal and marine microbiome research, have been instrumental in the recent progress of agriculture and aquaculture practices, including practical management strategies and interventions for more sustainable and resilient food systems (Table 1). However, understanding is only one step in the process of protecting and promoting the health and diversity of our microbiomes. Advances of knowledge, facilitated by new technologies, have illuminated many issues in microbiome networks, including reductions in microbial diversity and the spread of antimicrobial resistance.

In addition to ensuring continuous advances in the understanding of food system microbiomes, developing a greater understanding of their composition, functionality, and interactions within and across ecosystems and the development of microbiome-based applications is necessary to fully leverage microbiome potential. In this regard, it is also essential to ensure that other framework conditions are met, e.g., societal awareness and understanding, and the establishment of a suitable regulatory landscape. Further promoting microbiology and microbiome education among different stakeholder groups would enable them to make well-informed decisions about microbiome-related products (21, 253). This is not only important for the end-users but also for the industry developing new microbiome-based products/applications and for the regulators who must assess them. The challenges faced by regulators are multifaceted. On the one hand, there is an absence of explicit legal requirements to account for microbiome-related effects when risks/benefits are considered (254). On the other hand, the roadmap for the approval of microbiome-based innovations is particularly complex because microbiome science has been generated in the absence of standards and validated methodologies (255). The implementation of a systemic approach involving all relevant stakeholders is vital to aid in protecting existing microbiomes and restoring damaged microbiome networks relating to the food system (256, 257).

While understanding microbiome composition is increasingly achievable, deciphering the functional roles of microbiome constituents remains a challenge. Culture-based approaches are crucial for translating this research into innovations and for understanding the causality behind correlations. Similarly, the generation and integration of omics data needs to be complemented with synthetic biology, high-throughput screening, and targeted experimental approaches in order to validate the functions of these microbiomes. These strategies can enable the translation of microbiome research into innovations within food systems, with the potential to improve human and animal health as well as the health of the planet at large.

Statements

Author contributions

PF-G: Conceptualization, Visualization, Writing – original draft, Writing – review & editing.

DL: Conceptualization, Visualization, Writing – original draft, Writing – review & editing.

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Data availability statement

The original contributions presented in the study are included in the article/supplementary material. Further inquiries can be directed to the corresponding author.

Funding

The authors declared financial support was received for this work. Research in the group of PC was funded through Science Foundation Ireland (SFI) under grant number (SFI/12/RC/2273) (APC Microbiome Ireland), and SFI together with the Irish Department of Agriculture, Food and the Marine (SFI/16/RC/3835) (VistaMilk). Research in the Cotter laboratory was funded Tby Friesland Campina, PrecisionBiotics Group, PepsiCo and Danone.

PC received support from Abbott, PepsiCo, Yakult, Lallemand and H&H to attend/present at scientific meetings/conferences.

PF-G received funding from the European Union's Horizon 2020 Research and Innovation Programme under the INSPIRE COFUND Marie Skłodowska Curie grant agreement (No. 101034270).

Conflict of interest

FB and OOS were employed by VistaMilk Science Foundation Ireland (SFI) Research Centre, a research center which collaborates with industry partners as disclosed in their web page (https://www.vistamilk.ie/industry-partners-2/).

LL was employed by LL-BioEconomy, Research & Advisory.

AS was employed by AIT Austrian Institute of Technology GmbH, research centre funded by both the government of Austria (majority shareholder) and the Federation of Austrian as listed on their web page (https://www.ait.ac.at/en/about-the-ait).

MW was employed by FFoQSI GmbH - Austrian Competence Centre for Feed and Food Quality, Safety and Innovation, a research center which collaborates with industry partners as disclosed in their web page (https://ffoqsi.at/index.php/en-us/about-ffoqsi/partner-en).

Research in the Cotter laboratory was funded by Friesland Campina, PrecisionBiotics Group, PepsiCo and Danone.

PC received support from Abbott, PepsiCo, Yakult, Lallemand and H&H to attend/present at scientific meetings/conferences and is the Head of Microbiology and a co-founder of SeqBiome Ltd.

Neither the funders nor the non-funding companies were involved in the study design, collection, analysis, interpretation of data, the writing of this article, or the decision to submit it for publication.

The remaining authors declared that this work was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

The reviewer MG declared a past co-authorship with the author PC to the handling editor.

The authors DL, GB, TC, TCC, LC, LL, EM, OO'S, HS, and TK declared that they were an editorial board member of Frontiers at the time of submission. This had no impact on the peer review process and the final decision.

Generative AI statement

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