

MINI REVIEW

Microbiomes in agroecosystem: Diversity, function and assembly mechanisms

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Abstract

Soils are a main repository of biodiversity harbouring immense diversity of microbial species that plays a central role in fundamental ecological processes and acts as the seed bank for emergence of the plant microbiome in cropland ecosystems. Crop-associated microbiomes play an important role in shaping plant performance, which includes but not limited to nutrient uptake, disease resistance, and abiotic stress tolerance. Although our understanding of structure and function of soil and plant microbiomes has been rapidly advancing, most of our knowledge comes from ecosystems in natural environment. In this review, we present an overview of the current knowledge of diversity and function of microbial communities along the soil–plant continuum in agroecosystems. To characterize the ecological mechanisms for community assembly of soil and crop microbiomes, we explore how crop host and environmental factors such as plant species and developmental stage, pathogen invasion, and land management shape microbiome structure, microbial co-occurrence patterns, and crop-microbiome interactions. Particularly, the relative importance of deterministic and stochastic processes in microbial community assembly is illustrated under different environmental conditions, and potential sources and keystone taxa of the crop microbiome are described. Finally, we highlight a few important questions and perspectives in future crop microbiome research.

INTRODUCTION

Soil not only serves as nutrient repository for crops, providing essential water and mineral elements, but also harbours vast diversity of microbial species that plays a fundamental role in a wide variety of ecological processes, providing the most important microbial seed bank for formation of the plant microbiome (Bakker et al., 2018; Cordovez et al., 2019; Guerra et al., 2021; Oldroyd & Leyser, 2020). The plant microbiome consists of diverse microbial taxa including bacteria, archaea, fungi, protists and viruses, which play a variety of important roles such as nutrient uptake, disease resistance, and abiotic stress tolerance for plant growth and health (Carrión et al., 2019; de Vries et al., 2020; Toju et al., 2018; Trivedi et al., 2020). Many recent

discoveries suggest that crop-associated microbiomes can be harnessed to protect the crops against pathogens (Carrión et al., 2019; Guo et al., 2022; Lee et al., 2021) and to enhance crop resilience to abiotic stresses like drought and salt (Qi et al., 2022; Schmitz et al., 2022; Xu, Dong, et al., 2021). It was reported that global demand for agricultural crops is expected to rise 70% by 2050 to feed the growing population, and the microbiome engineering was proposed as a vital biotechnological strategy to improve crop productivity and health in a sustainable way (Arif et al., 2020; Haskett et al., 2021; Singh et al., 2020). Therefore, it is imperative to obtain a systematic understanding on the fundamental ecological processes that govern the assembly and co-occurrence patterns of soil and crop microbiomes under different environmental conditions.

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The development of multi-omics approaches such as metagenomics, metatranscriptomics, metabolomics, and culturomics in recent decades has greatly promoted the investigation on diversity, composition, and functions of the microbiomes in soils and plant compartments, including the rhizosphere, phyllosphere, and endosphere (Bulgarelli et al., 2012; Duran et al., 2018; Lundberg et al., 2012; Matsumoto et al., 2021; Muller et al., 2016; Xu, Pierroz, et al., 2021). For example, a recent study based on metagenomics, metabolomics, and comparative genomics has suggested that the sorghum host can selectively recruit microbial members carrying more genes related to iron metabolism in the root microbiome by specific metabolites under drought stress (Xu, Dong, et al., 2021). Moreover, there has been an increasing research effort to unravel the ecological mechanisms underpinning microbiome assembly, plant–microbiome interactions, and microbe–microbe interactions, among which community ecology theory and eco-evolutionary feedbacks can provide a mechanistic framework to discern these complex interactions within the plant–microbiome holobiont (Cordovez et al., 2019; Fitzpatrick et al., 2020; Foster et al., 2017; Martin et al., 2017). It has been well documented that microbiome assembly and dynamics in soils and plants in natural environment are controlled by a broad range of biotic and abiotic factors, including compartment niche, plant genetic signal and age, climate, and soil type and nutrients (Almario et al., 2022; Delgado-Baquerizo et al., 2020; Harbort et al., 2020; Thiergart et al., 2020; Wagner et al., 2016). However, our knowledge of how biotic and abiotic factors together with agricultural management shape microbiome assembly, microbial co-occurrence patterns, and crop–microbiome interactions along the soil–plant continuum in agroecosystems is still largely limited. In this review, we aim to (1) provide an overview of diversity, composition, and functions of soil and crop microbiomes; (2) to explore the ecological mechanisms for microbiome assembly and network patterns under different environmental conditions; (3) to identify sources and keystone taxa and genes associated with the crop microbiome; and (4) to identify some priority areas for future research on crop-associated microbiomes.

DIVERSITY AND FUNCTIONS OF MICROORGANISMS IN AGROECOSYSTEMS

Diversity and composition of soil and crop microbiomes

Soils are a main repository of terrestrial biodiversity harbouring extremely complex and diverse microbial species that plays a central role in fundamental ecological processes (Bardgett & van der Putten, 2014; Guerra et al., 2021; Jansson & Hofmockel, 2020). It was estimated that 1 g of surface soil contains up to 1 billion

bacterial cells, approximate 200 m fungal hyphae, tens of thousands of protists, and trillions of viruses (Bardgett & van der Putten, 2014; Fierer, 2017; Sokol et al., 2022; Wagg et al., 2014). This vast diversity in belowground soils acts as the microbial seed bank for microbial colonization in crops (Cordovez et al., 2019; Trivedi et al., 2020). Plant hosts provide various microhabitats (i.e. compartment niches), such as the rhizosphere, phyllosphere, and endosphere, for the growth and proliferation of microorganisms (Figure 1) (Knights et al., 2021; Muller et al., 2016; Trivedi et al., 2020). Only selected members of soil microbiomes may move from soils to plant compartments and form complex co-associations with crop hosts (Cordovez et al., 2019; Muller et al., 2016). Sophisticated interactions between plants and their associated microbiomes have co-evolved over 400 million years in terrestrial ecosystems. Consequently, crop hosts and the associated microbiomes are thought to form a ‘holobiont’ with the stability attributed to the evolutionary selection of plant–microbiome interactions (Hassani et al., 2018; Trivedi et al., 2020). Members of the crop microbiome comprise not only the mutually beneficial microbes like mutualistic arbuscular mycorrhizal fungus and symbiotic nitrogen-fixing bacteria but also neutral and pathogenic ones (Cordovez et al., 2019; Martin et al., 2017; Trivedi et al., 2020). Understanding the diversity, composition, and functions of the microbiomes along the soil–plant continuum will be crucial for exploiting crop microbiomes for the development of sustainable agriculture.

Microbial habitats in the soil–plant continuum can be separated into bulk soil, the rhizosphere, root, stem and leaf, which host distinct diversity and composition of microbial communities (Figure 1) (Fitzpatrick et al., 2020; Muller et al., 2016). It is well documented that the rhizosphere, phyllosphere, especially for the endosphere contain much less microbial diversity in relation to bulk soil (Knights et al., 2021; Trivedi et al., 2020; Xiong, Zhu, et al., 2021). For example, a few recent studies that examined the bacterial and fungal communities along the soil–plant continuum in field-grown maize and wheat/barley demonstrated that microbial richness gradually decreased from soils to epiphytes and then to endophytes (Table 1) (Xiong, He, et al., 2021; Xiong, Zhu, et al., 2021). Similar patterns have been reported in rice and maize rhizosphere samples showing a decreasing gradient in bacterial diversity from bulk soil to the rhizosphere and to the endosphere (Edwards et al., 2015; García-Salamanca et al., 2013). Moreover, a recent work in sorghum found a significantly higher protistan alpha diversity in the rhizosphere and bulk soils than in the phyllosphere (Sun, Jiao, Chen, Trivedi, et al., 2021). It was reported that the cultivable plant endophytes can reach a density of 10^5 – 10^7 cells per gram in roots and 10^3 – 10^4 cells per gram in leaves, stems, flowers, fruits and seeds (Compant et al., 2010; Compant et al., 2021). Wang, Wang, et al. (2020) quantified root-associated bacterial

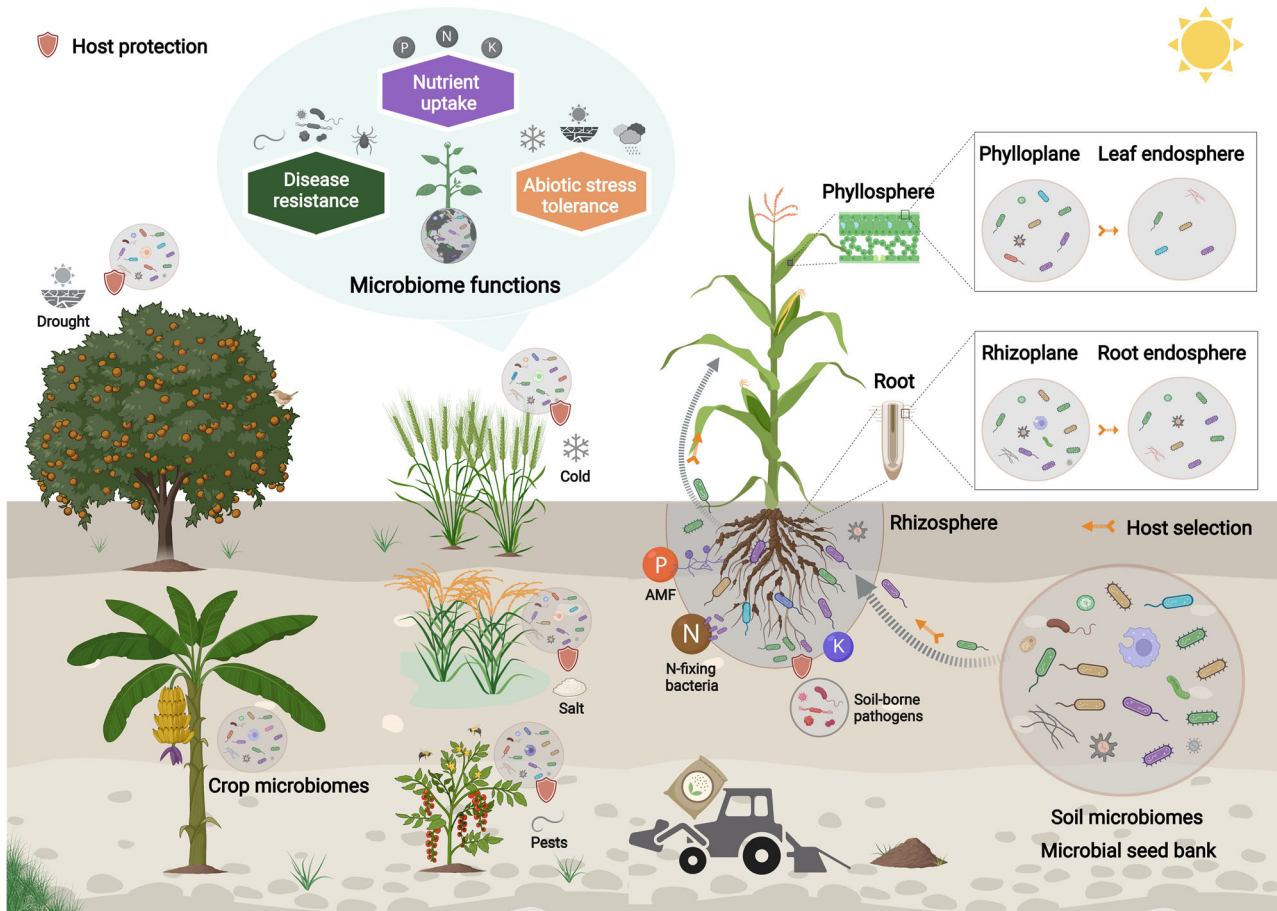


FIGURE 1 Diversity and functions of crop-associated microbiomes. Soils in agroecosystems not only are a main nutrient repository for crops, providing essential water and nutrients to the crops, but also act as the most important microbial seed bank for the crop microbiome. Plant provides multiple microhabitats such as the rhizosphere, phyllosphere, and endosphere for the development of the crop microbiome. Plant hosts have a strong selection effect on microbial diversity and composition, with microbial richness gradually decreasing from soils to epiphytes and to endophytes. Crop-associated microorganisms (i.e. the crop microbiome) provide a number of life-support functions for their hosts, including nutrient uptake, disease resistance, and abiotic stress tolerance. For example, crop microbiomes can enhance host resilience to abiotic stresses like drought, salt, and cold. Created with [BioRender.com](https://www.biorender.com)

communities in *Medicago truncatula* by spiking synthetic chimeric DNA as control and showed that the quantified abundance of bacterial communities was 6.91×10^8 , 6.44×10^9 , and 1.24×10^9 (16S rRNA gene number per gram) in bulk soil, rhizosphere, and root endosphere, respectively. Another work investigated nitrogen-cycling genes of five oilseed crops and showed that ammonia monooxygenase gene (*amoA*) expression patterns differed between archaea and bacteria (Wang, Gan, et al., 2020). The archaea *amoA* genes were expressed 10 times higher in the rhizosphere than in root, whereas the bacterial *amoA* genes showed a higher expression in root than in the rhizosphere (Wang, Gan, et al., 2020). A recent work suggested that soil aggregate sizes also significantly affected the abundance of microbial nitrogen-cycling genes (e.g. *amoA*, *narG*, *nirS/K*) (Han et al., 2021). Further, the microbiome in soil and crop system comprises a few abundant taxa having a wide niche breadth and

vast diversity of rare taxa with a greater specificity in niche requirement (Jiao & Lu, 2020; Xiong, He, et al., 2021). For instance, a previous study that explored fungal abundant and rare sub-communities based on the large-scale soil survey in agricultural fields revealed that 68.2% of fungal phylotypes were identified as rare taxa, which accounted for only 3.6% of the average relative abundance in soil (Jiao & Lu, 2020). Similar results were reported in crop microbiomes showing that the majority of mycobiome diversity (70.1%) were represented by rare taxa with a high phylogenetic diversity (Xiong, He, et al., 2021). These results indicate that crop hosts are likely to exert a strong effect on soil microbiome by enriching the abundance of a few dominant taxa but reducing the overall diversity, causing shift of abundant versus rare sub-community compositions and their ecological attributes.

It has been well documented that microbial community composition differed greatly between soil and crop

TABLE 1 Recent studies on soil and crop microbiomes under different environmental conditions

Crop/compartment	Microbes	Treatments	References
Tomato/soil, rhizosphere, and root	Bacteria	Salt stress	Schmitz et al. (2022)
Sorghum/soil, rhizosphere, and root	Bacteria	Drought	Qi et al. (2022)
Grassland/soil	Bacteria, fungi, and protists	Land-use intensification	Romdhane et al. (2022)
Citrus/phylosphere	Bacteria	Melanose disease	Li et al. (2022)
Banana/soil, rhizosphere, and root	Bacteria, fungi, and protists	Conventional and organic managements	Guo et al. (2022)
Sorghum/soil, rhizosphere, root, and leaf	Bacteria and fungi	Drought	Gao et al. (2020) and Xu, Dong, et al. (2021)
Maize, wheat, and barley/soil, rhizosphere, root, and leaf	Bacteria and fungi	Fertilization practices	Xiong, He, et al. (2021) and Xiong, Zhu, et al. (2021)
Maize and rice/soil	Bacteria, archaea, fungi, and protists	Crop systems	Jiao et al. (2020) and Jiao et al. (2021)
Chilli pepper/soil, rhizosphere, root, stem, and fruit	Bacteria and fungi	<i>Fusarium</i> wilt disease	Gao et al. (2021)
Maize/soil and rhizosphere	Bacteria and fungi	Conventional and organic managements	Schmidt et al. (2019)
Wheat–soybean rotations/soil	Bacteria, fungi, protists, and diazotrophs	Inorganic and organic fertilization	Fan et al. (2019), Fan et al. (2020)
Wheat/root	Fungi	Conventional, no-till, and organic farming	Banerjee et al. (2019)
Wheat/soil, root	Bacteria and fungi	Management type and tillage intensity	Hartman et al. (2018)

compartments in various agroecosystems such as maize-wheat/barley rotation systems (Xiong, He, et al., 2021; Xiong, Zhu, et al., 2021), monocultures of sugarcane (Hamonts et al., 2017), sorghum (Gao et al., 2020; Sun, Jiao, Chen, Trivedi, et al., 2021), barley (Bulgarelli et al., 2015), and rice (Edwards et al., 2015). Bulgarelli et al. (2015) showed that bacterial community associated with barley roots was dominated by *Comamonadaceae*, *Flavobacteriaceae*, and *Rhizobiaceae*, whereas members of Firmicutes and Chloroflexi were more abundant in bulk soil. Xiong, He, et al. (2021) and Xiong, Zhu, et al. (2021) investigated the bacterial and fungal communities associated with soil, root, and leaf in maize-wheat/barley rotation systems, and showed that the bacterial families *Enterobacteriaceae*, *Pseudomonadaceae*, and *Methylobacteriaceae* and the fungal class Dothideomycetes were significantly enriched in plant compartments. In contrast, the bacterial family *Chitinophagaceae* and the fungal class Sordariomycetes were more abundant in soil habitats. Specifically, relative abundance of bacterial class Alphaproteobacteria and fungal class Pucciniomycetes were significantly higher in the leaf endosphere than any other compartments (Xiong, He, et al., 2021; Xiong, Zhu, et al., 2021). Similarly, it was reported that Alphaproteobacteria dominated bacterial communities in sugarcane leaf and stalk samples (Hamonts et al., 2017). Fungal phylum Ascomycota preferentially colonized the sugarcane leaf and stalk, while Basidiomycota were more abundant in sugarcane roots and rhizosphere soil

(Hamonts et al., 2017). By characterizing protistan communities in multiple compartments of sorghum, Sun, Jiao, Chen, Trivedi, et al. (2021) indicated that phyllosphere protistan community was dominated by Rhizaria, Alveolata, and Amoebozoa. All these results suggest that crop hosts exert a strong selection effect on microbial diversity and composition, which very likely originate from the belowground seed bank.

Functions of soil and crop microbiomes

In agroecosystems, soil and crop-associated microbial communities provide a wide variety of functions (e.g. nutrient cycling) and benefits (e.g. pathogen resistance) to crop growth and health (Figure 1) (Arif et al., 2020; Bakker et al., 2018; Singh et al., 2020). Soil microorganisms are key game players in a cascade of intricate soil functions that underpin fundamental ecosystem services (e.g. nutrient cycling, soil fertility, and climate regulation) (Bardgett & van der Putten, 2014; Guerra et al., 2021). For example, microorganisms living in bulk soil and the rhizosphere are integral to C, N, and P cycling and play critical roles in influencing crop fitness and productivity (Guerra et al., 2021; Jansson & Hofmockel, 2020; Wu et al., 2022). It was reported that microbial communities in the agricultural soils played a key role in regulating phosphorus cycling via microbial phosphorus solubilization strategy (Wu et al., 2022). Wagg et al. (2014) suggested that soil microbial

biodiversity is a key resource for maintaining ecosystem multifunctionality and sustainability, including plant diversity, decomposition, nutrient retention, and nutrient cycling. A recent work explored the relationships between soil biodiversity of multiple organism groups and multiple ecosystem functions in 228 agricultural fields, which demonstrated that soil biodiversity was significantly positively related to multiple ecosystem functions associated with crop yield, nutrient provisioning, element cycling, and pathogen control (Jiao et al., 2021). Particularly, soil phylotypes with smaller sizes or at lower trophic levels such as archaea, bacteria, fungi, and protist phototrophs appeared to exhibit stronger biodiversity–ecosystem function (BEF) relationships in compared to those with larger sizes or at higher trophic levels like invertebrates or protist predators (Jiao et al., 2021). Within each microbial group, rare species played a more important role in driving ecosystem multifunctionality than abundant species (Zhang, Lu, et al., 2022).

In addition to soil microbiomes, microorganisms colonizing plant compartments provide a number of life-support functions for their host, including nutrient uptake, disease resistance, and abiotic stress tolerance (Figure 1) (Arif et al., 2020; Toju et al., 2018). Some plant microorganisms can simultaneously produce and degrade plant hormones, which could influence many aspects of plant growth and development (Finkel et al., 2020; Muller et al., 2016). Among the extensive and diverse microorganisms, mutualistic symbionts like arbuscular mycorrhizal fungi (AMF) and nitrogen-fixing bacteria are striking examples of plant–microbe interactions at which microorganisms promote plant growth by facilitating the acquisition of scarce nutrients (Martin et al., 2017; Parniske, 2008). For example, a field study in maize grown in nitrogen-depleted soils revealed that aerial roots provided a home to nitrogen-fixing microbes that contributed 29%–82% of the nitrogen nutrition of crops (Van Deynze et al., 2018). A recent work also demonstrated that maize stem xylem harboured conserved core bacterial taxa carrying *nifH* gene, which contributed to 11.8% of the total N accumulated in maize stems (Zhang, Zhang, et al., 2022). A meta-analysis in seven cereal crops (corn, wheat, rice, barley, sorghum, millet, and oat) suggested that AM fungal inoculation in field led to a 16% increase in crop grain yields (Zhang, Lehmann, et al., 2018). On the other hand, these beneficial fungi could interact with nitrogen-fixing bacteria to promote plant nutrient acquisition and health. For instance, facultatively biotrophic fungus *Phomopsis liquidambaris* helps rhizobial migration from soil to the peanut rhizosphere via mycelial network and further triggers nodulation (Zhang et al., 2020). Increasing studies based on metagenomic sequencing and DNA stable isotope probing also revealed that the plant microbiome plays a critical role in nutrient transformation and cycling (Crombie et al., 2018; Guerrieri et al., 2015; Xiong, Singh,

et al., 2021; Zhang, Zhang, et al., 2022). For instance, a recent study shows that the maize phylloplane microbiome possessed diverse functional genes involved in C, N and P cycling (e.g. *xylA*, *amyA*, *nosZ*, *narG*, and *pstA/B*) that vary across host growth stages (Xiong, Singh, et al., 2021).

Increasing evidences have shown that crop-associated microbiomes can enhance plant resilience to abiotic stresses such as drought, salt, and cold (de Vries et al., 2020; Schmitz et al., 2022; Xu, Dong, et al., 2021). Drought is probably the most important environmental stress limiting crop growth and agricultural productivity. Hence, much recent research effort has been made to harness the crop microbiome to increase crop resilience to drought (de Vries et al., 2020; Qi et al., 2022; Xu, Dong, et al., 2021). For example, a recent study explored the molecular mechanisms underlying crop–microbiome interactions under drought stress and revealed that microbial iron metabolism in roots is important for sorghum's response to drought (Xu, Dong, et al., 2021). Similarly, a recent study examined the effects of synthetic community (SynCom) containing 53 *Arabidopsis*-associated bacteria on sorghum growth under drought stress, which showed that plants colonized by both *Arthrobacter* and *Variovorax* performed well or better than control plants (Qi et al., 2022). Likewise, some plant properties such as total biomass, relative water content, and sugar content were enhanced by AMF symbionts at low temperatures (Acuna-Rodriguez et al., 2020). It was reported that a SynCom of five bacterial strains comprising *Ensifer* spp., *Ralstonia* spp., and *Bacillus* spp. originating from the root of the desert plant *Indigofera argentea* offers the potential to increase tomato resilience to high salt stress (Schmitz et al., 2022).

Soil-borne pathogens are a major threat to global agricultural production, and the crop microbiome is increasingly seen as a key driver contributing to plant resistance against infectious diseases (Kwak et al., 2018; Savary et al., 2019). It was proposed that plants can 'cry for help' from their microbiomes when they suffer from pathogen invasion, leading to a consideration of selectively recruiting beneficial microbes to alleviate the pathogen stress (Bakker et al., 2018; Liu et al., 2021). Recent studies in common beans (Mendes, Raaijmakers, et al., 2018), wheat (Liu et al., 2021), pepper (Gao et al., 2021), and citrus (Li et al., 2022) have shown that crop-associated microbial communities provide a first line of defence against the soil-borne pathogens. For example, a previous work suggested that the both below- and aboveground compartments of diseased plants can recruit potential beneficial bacteria such as *Streptomyces*, *Pseudomonas*, and *Bacillus* against the *Fusarium* wilt disease (FWD) (Gao et al., 2021). Metagenomic analysis further showed that the microbial communities of the diseased plants significantly enriched some functional genes

related to detoxification, biofilm formation, and plant-microbiome signalling (e.g. chemotaxis) (Gao et al., 2021). In a recent study, Li et al. (2022) also reported a marked enrichment of beneficial microbes in the phyllosphere of infected plants. Glasshouse experiments further indicated that several bacterial strains including *Pantoea* spp., *Methylobacterium* spp., and *Sphingomonas* spp. with antagonistic traits could provide important protective effects for plants against pathogen challenge (Li et al., 2022). Moreover, study in the tomato rhizosphere has demonstrated that microorganisms producing growth-inhibitory siderophores in the rhizosphere could suppress the bacterial pathogen *Ralstonia solanacearum* and thus protect crops from infection (Gu et al., 2020). The relative abundance of Firmicutes and Actinobacteria in the tomato rhizosphere was negatively related to incidence of bacterial wilt disease (Lee et al., 2021). Interestingly, the seed-endophytic bacterium *Sphingomonas melonis* can be transmitted across generations in disease-resistant rice seeds and positively affects rice resistance to pathogens by producing anthranilic acid (Matsumoto et al., 2021). Besides bacteria and fungi, accumulating evidence suggests that protists and algae are also important members of the crop microbiome, which can provide protective effect on crop health (Guo et al., 2022; Lee & Ryu, 2021; Xiong et al., 2020). For instance, a recent study showed that protistan predators can strongly enhance banana health and yield by stimulating disease-suppressive bacteria like *Bacillus* spp. (Guo et al., 2022). Algal species like prokaryotic *Anabaena* spp. and *Calothrix* spp., and eukaryotic *Chlorella fusca* have been used intensively for biological control of crop fungal pathogens such as *Fusarium oxysporum*, *Rhizoctonia solani*, and *Colletotrichum orbiculare* (Lee & Ryu, 2021). Moreover, increasing evidence indicated that through horizontal gene transfer (HGT) events the crop endophytes can acquire novel functions such as biodegradation of organic contaminants and resistance against plant pathogens and heavy metals, which play a vital role in host adaptation (Compant et al., 2021). Together these findings reveal the prominent roles of crop-associated microbiomes in host fitness and health under various environmental stresses, which can help to develop microbiome-based tools aiming to sustainably improve agricultural productivity.

MICROBIOME ASSEMBLY AND DYNAMICS ALONG THE SOIL-PLANT CONTINUUM

Transmission route and origin of the crop microbiome

Ecological theories suggest that microbial community is shaped by a complex interaction of four fundamental

eco-evolutionary processes, including dispersal (e.g. the microbial movement between local communities), selection (e.g. the community is influenced by abiotic and biotic factors), diversification (e.g. genetic variation), and ecological drift (e.g. stochastic variation in growth and death) (Figure 2) (Cordovez et al., 2019; Fitzpatrick et al., 2020). Among them, dispersal and diversification are key factors influencing the assembly and diversity of microbial communities, and selection and ecological drift can affect the abundance of microorganisms within the microbiome (Cordovez et al., 2019). Increasing evidences showed that microorganisms can be transferred to the crop hosts via the vertical transmission from the parent plants and seeds, as well as via the horizontal transmission from the surrounding environment, including the soil microbial seedbank, the atmosphere, neighbouring plants and insects, and even interacting animals (Figure 2) (Abdelfattah et al., 2021; Fitzpatrick et al., 2020; Meyer et al., 2022; Xiong, Singh, et al., 2021). For example, a recent study on oak seedlings in a microbe-free environment has confirmed the microbial transmission route from seed to the phyllosphere and root (Abdelfattah et al., 2021). Similarly, a previous study on the clonal plant *Glechoma hederacea* showed that a significant proportion of the bacterial and fungal communities can be transferred from the mother plants to the daughters (Vannier et al., 2018). Moreover, findings from previous studies in multiple below- and aboveground compartments of crops showed that crop-associated microbiomes are mainly derived from soils and gradually enriched and filtered at different plant compartments at which the rhizosphere and rhizoplane are important interfaces for microbial transmission (Xiong, Singh, et al., 2021; Xiong, Zhu, et al., 2021). During the processes of microbial enrichment, some members within *Enterobacteriaceae*, *Pseudomonadaceae*, and *Methylobacteriaceae* were significantly enriched in plant compartments (Xiong, Zhu, et al., 2021). Many members within these bacterial families were also reported as core taxa of the crop microbiome in previous studies (Bourceret et al., 2022; Cernava et al., 2019; Schmitz et al., 2022; Walters et al., 2018), suggesting that they are able to adapt to host-specific selection stresses such as plant metabolites and immune system. In addition, the neighbouring plants and local air also play a role in the dispersal processes of the crop microbiome. By using the plastic leaf of artificial plants as 'local background controls' in the field across plant developmental stages, Xiong, Singh, et al. (2021) showed that air-borne microorganisms were important sources (52%–92%) of both bacterial and fungal communities in the maize phyllosphere. In a recent work, Meyer et al. (2022) examined how the phyllosphere microbial community is shaped by dispersal from the nearby plants including tomato, pepper, and bean plants and demonstrated that local dispersal is a key factor influencing the assembly of phyllosphere

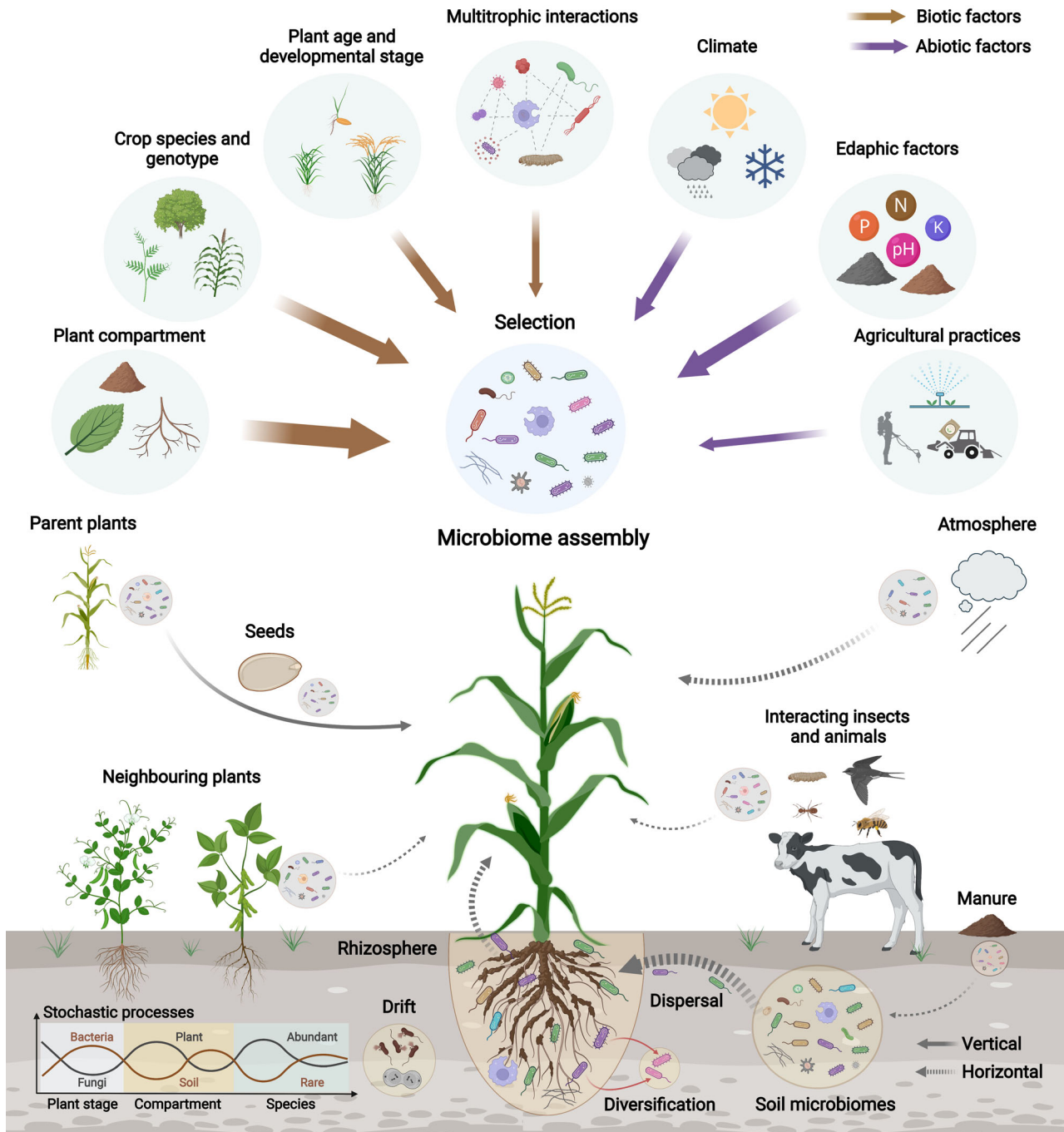


FIGURE 2 Ecological processes shaping the assembly of soil and crop microbiomes. Ecological theories suggest that microbiome assembly is shaped by a complex interaction of four eco-evolutionary processes, including dispersal, selection, diversification (e.g. genetic variation), and drift (e.g. random birth and death). Microorganisms can be transferred to the crops via the vertical transmission from the seeds, as well as via the horizontal transmission from soils, the atmosphere, neighbouring plants, and interacting insects and animals. The assembly of crop microbiomes is influenced by multiple biotic and abiotic factors, such as plant compartment, crop species and genotype, developmental stage, climate, soil type and nutrients, and agricultural practices. In addition to these deterministic factors, stochastic processes (e.g. drift) also have a role in community assembly, and the relative importance of the stochastic processes versus deterministic processes varies according to developmental stage, plant compartment, and microbial species. Created with [BioRender.com](https://www.bio-render.com/)

microbiomes. Biological and ecological traits such as plant identity, biomass, and age of the nearby plants are important determinants of phyllosphere microbiome diversity (Meyer et al., 2022). Some plant endophytes like *Pseudomonas* spp. and *Enterobacter* spp. can

enter the internal plant tissues through root tip and root hair, stomata and hydathodes, damaged trichomes or wounds, and plant cracks and even cross the endodermis and colonize the entire plant body via plant vessels (Compant et al., 2021; Muller et al., 2016; Synek

et al., 2021). All these results provide empirical evidences supporting the diverse sources of the crop microbiome, and an important challenge for further research is whether different environmental stresses will affect microbial dispersal processes and transmission routes of the crop microbiome.

Host and environmental factors shaping microbial communities

Changes in crop microbiome diversity and composition are associated with a broad range of host and environmental factors, including plant compartment, crop species and genotypes, developmental stage, climate, soil type, and agricultural managements (Figure 2) (Muller et al., 2016; Philippot et al., 2013; Singer et al., 2019; Trivedi et al., 2020). Increasing studies on crop plants grown under different environmental conditions have demonstrated that plant compartment (i.e. host microhabitats) is the most influential factor determining the assembly of crop-associated microbiomes (Bourceret et al., 2022; Edwards et al., 2015; Gao et al., 2020, 2021; Hamonts et al., 2017; Singer et al., 2019; Tkacz et al., 2020; Xiong, Zhu, et al., 2021). For example, recent studies examining both bacterial and fungal communities in the soil–plant continuum of maize plant revealed that microbiome assembly is shaped predominantly by host selection rather than by soil managements (Bourceret et al., 2022; Xiong, He, et al., 2021; Xiong, Zhu, et al., 2021). Similarly, Gao et al. (2020) characterized fungal communities associated with soil, rhizosphere, roots and leaves of sorghum plants and suggested that variation in fungal communities was mainly explained by plant compartment followed by developmental stage and host genotype. These results can be explained by the fact that plant metabolisms as well as physical and chemical properties significantly vary in different plant microhabitats, which selectively recruit microbial species with specific ecological niches (Philippot et al., 2013; Trivedi et al., 2020; Vorholt, 2012).

In sub-habitats or compartments of plant, growing evidences indicated that effects of host and environmental factors on microbial community largely depend on ecological attributes of the compartment (e.g. below- or aboveground compartments), difference in host identity (e.g. species or genotype), and scale and degree of environmental stress (e.g. geographic distance) (Chen et al., 2019; Grady et al., 2019; Xiong, Zhu, et al., 2021; Xu et al., 2018). For instance, site (i.e. soil type) had the strongest impact on microbial communities in the bulk soil but weaker in plant compartments like root, and the leaf endosphere (Tkacz et al., 2020; Xiong, Zhu, et al., 2021). In contrast, the effects of crop species on microbial community assembly increased from soils to crop surfaces and to the crop endosphere (Xiong, Zhu, et al., 2021). Similar

results were also reported in the pepper (Gao et al., 2021), Wheat (Hartman et al., 2018), and Sorghum (Gao et al., 2020). Furthermore, an increasing research effort is to explore the impact of host signals on crop microbiome assembly. A large-scale replicated field study on 27 maize inbred lines has shown that plant age is the strongest factor shaping maize rhizosphere communities, followed by field location and plant genetics (Walters et al., 2018). Further analyses identified 143 OTUs belonging to Alphaproteobacteria, Betaproteobacteria, and Actinobacteria as heritable taxa whose relative abundances were significantly related to plant genotype (Walters et al., 2018). Moreover, by investigating root microbiomes of four maize inbred lines from the vegetative stage to the reproductive stage, a recent work identified 26 stable OTUs belonging to Proteobacteria and Actinobacteria that persisted throughout the host life cycle (Bourceret et al., 2022). By characterizing the root metabolome and ionome of wildtype plants at the vegetative and reproductive stages, Bourceret et al. (2022) found that plant developmental stage is an important driver influencing root metabolisms and microbiomes. Similar results were also reported in the rice root (Zhang, Zhang, et al., 2018) and the soil–plant continuum of the maize (Xiong, Singh, et al., 2021), revealing that plant developmental stage had significant influence on microbiome assembly and functions. In a recent study, Wagner et al. (2020) compared the microbiomes of diverse maize inbred lines and their F1 hybrid offspring and showed that both bacterial and fungal communities in the rhizosphere and leave differed between inbred lines and hybrids. Additionally, a recent study revealed that circadian rhythms also plays a role in shaping rice rhizosphere microbial communities, in which light exposure exerts an effect on rhythmic variation of community structure (Zhao et al., 2021). Further, it was recently demonstrated that soil microbial communities harbour circadian indicator taxa that can influence microbial circadian rhythms by regulating community diversity, network patterns, and assembly processes (Zhao et al., 2022).

Given that most of agroecosystems are under intensive management, microbial community assembly in the soil–plant continuum was also influenced by agricultural managements and fertilization practices (French et al., 2021; Schmidt et al., 2019). For example, Fan et al. (2019) suggested that long-term fertilization drastically reduced N fixation and significantly influenced associated diazotrophic communities. Moreover, previous study in soil and wheat root microbial communities under different agricultural managements suggested that management regime (i.e. conventional and organic managements) had significant impact on root bacterial community but not on the fungal community (Hartman et al., 2018). For microbiome in soil, management type had greater influence on fungal

communities while bacterial communities were primarily influenced by tillage intensities (Hartman et al., 2018). Further, several recent studies indicated that soil microbiomes were more sensitive to different fertilization practices than crop microbiomes (Sun, Jiao, Chen, Wu, et al., 2021; Xiong, He, et al., 2021; Xiong, Zhu, et al., 2021). Although fertilization regimes had less effects on the crop microbiome, some microbial taxa such as potential plant pathogen and protistan consumers in the phyllosphere can be significantly influenced by fertilization (Sun, Jiao, Chen, Trivedi, et al., 2021; Xiong, He, et al., 2021). Additionally, recent studies have suggested that organic farming has multiple positive effects on crop-associated microbiomes and crop health, such as increasing microbial alpha diversity and network complex complexity, recruiting some beneficial bacteria like *Bradyrhizobium* and *Bacillus*, and protecting crops against plant pathogens (Guo et al., 2021; Guo et al., 2022; Karlsson et al., 2017; Khoiri et al., 2021; Wittwer et al., 2021).

Together these results demonstrate that host selection exerts a strong effect on a number of traits of crop microbiomes, and in addition agricultural management regime plays an important role in shaping microbial

communities. A better understanding of crop–microbiome interactions under different agricultural regimes will be a key step for harnessing the crop microbiome to improve agricultural production.

Quantification of deterministic and stochastic processes in microbiome assembly

Elucidating the relative importance of deterministic and stochastic processes driving the assembly of crop-associated microbiomes is a great challenge in microbiome research (Table 2). Community ecology theory suggests that microbiome assembly is determined by multiple interactions of deterministic (e.g. selection) and stochastic (e.g. stochastic dispersal or drift) processes (Cordovez et al., 2019; Fitzpatrick et al., 2020). For microbiomes in agroecosystems, the relative importance of deterministic and stochastic processes remains unclear, but growing evidences showed that both processes are likely to contribute to microbiome assembly (Table 2) (Gao et al., 2020; Jiao et al., 2020; Xiong, Singh, et al., 2021). For example, a previous

TABLE 2 Relative importance of deterministic and stochastic processes in the assembly of soil and crop microbiomes

Crop/compartment	Factors	Stochasticity/determinism	References
Wheat/soil	Spatial scale	Dominant stochastic processes on the North China Plain (150–900 km), while dominant deterministic processes on the Tibetan Plateau (130–1200 km)	Shi et al. (2018)
Maize and rice/soil	Microbial groups	Dominant stochastic processes (dispersal limitation) in fungal abundant sub-community, while dominant deterministic processes (homogeneous selection) in rare sub-community	Jiao and Lu (2020)
Maize, wheat, and barley/soil, rhizosphere, root, and leaf	Microbial groups	Dominant stochastic processes in fungal abundant sub-community in plant compartments, while dominant deterministic processes in rare sub-community	Xiong, He, et al. (2021)
Maize/soil, rhizosphere, root, and leaf	Developmental stage, microbial groups, and compartment	Dominant deterministic processes (heterogeneous selection) in soil, rhizosphere, and plastic leaf; dominant deterministic processes in bacterial communities in plant compartments at the early stage, while dominant deterministic processes in fungal communities at the late stage	Xiong, Singh, et al. (2021)
Sorghum/soil, rhizosphere, root, and leaf	Developmental stage and community size	Stochastic processes (e.g. drift or stochastic dispersal) had a role in fungal community assembly in leaves and roots at the early stage; community size was negatively correlated with the stochastic processes	Gao et al. (2020)

study that investigated the influence of spatial scale on the relative role of stochasticity and determinism in 243 sampled sites across 1092 km distance demonstrated that stochastic processes played a dominant role in microbiome assembly from 150 to 900 km and deterministic processes dominated at the scale of larger than 900 km (Shi et al., 2018). Another large-scale soil survey on fungal microbiome in agricultural fields across eastern China revealed that the assembly of abundant sub-community was governed primarily by dispersal limitation, while rare sub-community was mainly determined by homogeneous selection (Jiao & Lu, 2020). Similarly, a recent study on fungal microbiome in the maize–wheat/barley rotation system has suggested that abundant sub-community in the plant compartments is largely shaped by stochastic processes, while the rare sub-community is mainly determined by deterministic processes and is more sensitive to host selection caused by crop species and compartment niche (Xiong, He, et al., 2021).

Furthermore, host selection pressure that regulates the relative importance of deterministic versus stochastic processes varies depending on plant developmental stage (Figure 2) (Gao et al., 2020; Xiong, Singh, et al., 2021). For instances, a previous study in the sorghum system indicated that stochastic processes (e.g. drift or stochastic dispersal) had a role in fungal community assembly in leaves and roots at the early stage of host development with fungal community size negatively correlated to the relative importance of stochastic processes (Gao et al., 2020). Xiong, Singh, et al. (2021) examined both bacterial and fungal communities at three developmental stages of maize and found that plant developmental stage had an important impact on the relative contribution of deterministic and stochastic processes in crop microbiome assembly, with deterministic processes exerting a stronger influence on bacterial communities at the early stage and on fungal communities at the late stage, respectively. In contrast, both bacterial and fungal communities in soil and the rhizosphere were mainly driven by the heterogeneous selection over time (Xiong, Singh, et al., 2021). The relative importance of ecological processes is also related to geographical distance and crop type. Jiao et al. (2020) examined archaeal, bacterial, and fungal communities in adjacent pairs of maize and rice fields and found that crop species and latitudes played important roles in influencing the deterministic and stochastic processes in soil microbiome assembly. Dispersal limitation played a more important role in soil microbiome assembly in rice fields than in maize fields, with soil microbiome assembly in high latitude rice fields being more driven by dispersal limitation (Jiao et al., 2020). Moreover, soil physicochemical attributes like available sulfur also played a key role in mediating the balance between stochastic and deterministic processes in microbiome assembly (Jiao & Lu, 2020).

All above findings suggest that the relative importance of deterministic versus stochastic processes in microbiome assembly of agroecosystems varies according to spatial scale, crop type, plant developmental stage, and microbial sub-community (e.g. abundant or rare species) (Figure 2). Yet in the context of global change, if and how environmental perturbations like precipitation and fertilization regime affect deterministic and stochastic processes in microbiome assembly along the soil–plant continuum are not well known, and multiple experimental and statistical approaches are needed to further uncover these enormously complex and mysterious processes.

MICROBIAL INTERACTIONS AND KEYSTONE TAXA OF CROP-ASSOCIATED MICROBIOMES

Multiple factors influence microbial co-occurrence patterns

A better understanding of complex interactions within the microbial communities in soils and plant compartments is essential for sustainable management of agroecosystem. Microbial co-occurrence network analysis provides a useful approach to decipher potential interactions within microbial communities (Barberan et al., 2012; Coyte et al., 2015; van der Heijden & Hartmann, 2016). Increasing studies have revealed that microbial interactions play important roles in shaping the overall microbiome assembly and microbiome stability (Coyte et al., 2015; Duran et al., 2018; Niu et al., 2017; van der Heijden & Hartmann, 2016). Niu et al. (2017) explored the role of microbial interactions in community assembly dynamic using a simplified maize root community consisting of seven species (including *Enterobacter* spp., *Stenotrophomonas* spp., *Ochrobactrum* spp., *Herbaspirillum* spp., *Pseudomonas* spp., *Curtobacterium* spp., and *Chryseobacterium* spp.). It was revealed that removal of just one species *Enterobacter* spp. can lead to a significant decrease of the abundance of five bacterial strains but promote the predominance of one species *Curtobacterium* spp. This finding suggests that *Enterobacter* spp. acting as keystone taxa plays a vital role in controlling the microbiome assembly of maize root (Niu et al., 2017). Some members within *Enterobacter* were also identified as dominant taxa in maize, wheat, and barley plants, supporting the essential role of *Enterobacter* spp. in crop microbiomes (Xiong, Zhu, et al., 2021). It was recently reported that microbial SynCom not only offers a consistent protection against salt stress for tomato plants but also influences the microbial network by increasing the average connectivity (Schmitz et al., 2022). Further, growing evidences suggested that pathogen invasion had important impact on microbial co-occurrence patterns in below- and aboveground compartments of

crops (Gao et al., 2021; Ge et al., 2021; Li et al., 2022). For example, Li et al. (2022) showed that pathogen invasion increased bacterial network connectivity and complexity in the phyllosphere of citrus plant. The increased connectivity after pathogen invasion was mainly related to interactions among epiphytic microbes. In contrast, Gao et al. (2021) reported that the *Fusarium* wilt disease (FWD) in pepper decreased bacterial network complexity but increased fungal network complexity. Bacterial–fungal interkingdom network analyses showed that FWD decreased the proportion of negative edges and modularity of the network, indicating a more unstable co-occurrence patterns in the diseased plants (Gao et al., 2021). In addition, a more complex microbial co-occurrence network was recorded in *Fusarium oxysporum*-resistant cultivar of common bean compared with susceptible cultivar (Mendes, Mendes, et al., 2018).

Moreover, agricultural systems and fertilization practices had a significant impact on microbial co-occurrence patterns in soils and plant compartments (Banerjee et al., 2019; Sun, Jiao, Chen, Trivedi, et al., 2021; Xiong, He, et al., 2021). For instance, findings from field work in the maize and rice soils showed that microbial co-occurrence network was more intensive in maize soils than in rice soils, and the species co-occurred patterns differed between the high-latitude region and the low-latitude region (Jiao et al., 2020). It was reported that grapevine rootstocks can significantly influence bacterial network properties in roots, with grafted grapes supporting a higher network complexity than ungrafted grapes (Marasco et al., 2018). Plant secondary metabolites like maize synthesized benzoxazinoids can affect specific microbial clusters within the root microbial co-occurrence networks (Kudjordjie et al., 2019). Another work found that cropping practices markedly alter bacterial–fungal co-occurrence network patterns (Hartman et al., 2018). Furthermore, Banerjee et al. (2019) found a greater fungal network complexity in organic farming than in conventional and no-till farming systems. Organic fertilizer amendment increased the relative abundance of bacterivorous and omnivorous protists but reduced plant pathogenic protists (Xiong et al., 2018). Additionally, recent study in a long-term field experiment under different levels of land-use intensity has shown that land management not only had a major impact on the structure and composition of bacterial, protistan and fungal communities but also affected microbiome network complexity (Romdhane et al., 2022). In a recent study, Bazany et al. (2022) found that water deficit stress can significantly influence inter-kingdom microbial connections in the rhizospheres of corn and sugar beet. Recent studies on the bulk soil and the rhizosphere indicated that microbial circadian clock is also a strong determinant in regulating microbial co-occurrence patterns (Zhao et al., 2021; Zhao et al., 2022). All these findings

significantly broaden our knowledge of microbial interactions along the soil–plant continuum. It is now a major challenge to investigate the real ecological and biological roles of microbial species within the complex microbial interactions under different environmental stresses and agricultural managements.

Identification of keystone taxa and functional genes of the microbiome

It has been well documented that microbial communities in soils and plant compartments contain keystone taxa that potentially play a central role in the structure and function of terrestrial microbiome (Table 3) (Banerjee et al., 2018; Banerjee et al., 2019; van der Heijden & Hartmann, 2016). Technically keystone taxa reflect the network hubs, core taxa, and/or biomarker taxa in a community. Current approaches used to identify keystone taxa include network analysis, Random Forest Model analysis, and SynCom experiment (Banerjee et al., 2019; Bertani et al., 2016; Hamonts et al., 2017; Knapp et al., 2021). For instance, Wei et al. (2019) explored correlation between initial soil microbiome and disease outcomes caused by soil-borne plant pathogen *Ralstonia solanacearum* and identified *Massilia*, *Dyadobacter*, *Terrabacter*, *Arachidicoccus*, and *Dyella* genera as keystone taxa in the initial microbiomes of healthy plants, which were closely related to tomato disease outcomes (Table 3). Further, the initial microbiomes of healthy plants harboured more abundant functional genes related to non-ribosomal peptide and polyketide synthases (e.g. COG3321 and COG1020), which involve in the production of antimicrobial compounds that could either directly inhibit plant pathogen or contribute to the assembly of a pathogen-suppressing microbiome (Wei et al., 2019). A previous study in sugar beet plants demonstrated that the infection plants could enrich some disease-suppressive bacteria belonging to *Chitinophagaceae* and *Flavobacteriaceae* in the root endosphere (Carrión et al., 2019). Further metagenomics and network analysis revealed a significant enrichment of functional genes related to chitinase (e.g. GH18) and biosynthetic gene clusters encoding the production of non-ribosomal peptide synthetases (NRPSs, e.g. BGC396, BGC471, and BGC592) and polyketide synthases (PKSs, e.g. BGC298) in the root endosphere of the diseased plants (Carrión et al., 2019). Similarity, Lee et al. (2021) analysed the rhizosphere microbial community of a healthy and diseased tomato and identified *Brevibacterium frigoritolerans*, *Bacillus niacini*, *Solibacillus silvestris*, and *Bacillus luciferensis* as plant-protective microbes, which significantly facilitates host disease suppression by activation of plant immunity. Findings in the wheat rhizosphere also indicated that *Stenotrophomonas rhizophila* can contribute to

TABLE 3 Identification of keystone taxa for soil and crop microbiomes

Crop/compartment	Keystone taxa	References
Tomato/soil	<i>Massilia</i> , <i>Dyadobacter</i> , <i>Terrabacter</i> , <i>Arachidicoccus</i> , and <i>Dyella</i>	Wei et al. (2019)
Maize/soil and rhizosphere	<i>Sphingobacteriales</i> , <i>Cytophagales</i> , <i>Rhizobiales</i> , <i>Tremellales</i> , and <i>Agaricales</i>	Schmidt et al. (2019)
Maize/soil, root, and leaf	<i>Burkholderiaceae</i> , <i>Streptomycetaceae</i> , <i>Rhizobiaceae</i> , <i>Coniothyriaceae</i> , <i>Mycosphaerellaceae</i> , and <i>Symmetrosporaceae</i>	Xiong, Singh, et al. (2021)
Grassland/soil	<i>Nitrospira</i> and <i>Gemmatimonas</i>	Xun et al. (2021)
Tomato/rhizosphere	<i>Brevibacterium frigidolerans</i> , <i>Bacillus niacini</i> , <i>Solibacillus silvestris</i> , and <i>Bacillus luciferensis</i>	Lee et al. (2021)
Wheat/rhizosphere and root	<i>Stenotrophomonas rhizophila</i>	Liu et al. (2021)
Banana/rhizosphere and root	<i>Cercozoa</i> and <i>Bacillus</i>	Guo et al. (2022)
Sugar beet/root	<i>Chitinophagaceae</i> and <i>Flavobacteriaceae</i>	Carrion et al. (2019)
Wheat/soil	<i>Chloroflexi</i> , <i>Nitrospirae</i> , and <i>Mesorhizobium</i>	Fan et al. (2020)
Wheat/residues	<i>Pedobacter</i> , <i>Rhizobium</i> , <i>Sphingomonas</i> , <i>Streptomyces</i> , <i>Neorhizobium</i> , and <i>Epicoccum</i>	Kerdraon et al. (2019)
Oilseed rape/soil, rhizosphere, and root	<i>Cytophagaceae</i> , <i>Acidobacteria</i> , <i>Skermanella</i> , <i>Methylotenera</i> , <i>Flavobacterium</i> , and <i>Bradyrhizobium</i>	Hilton et al. (2021)
Wheat/soil and root	<i>Peptostreptococcaceae</i> , <i>Erysipelotrichaceae</i> , <i>Chloroflexaceae</i> , and <i>Microbacteriaceae</i>	Hartman et al. (2018)
Maize/rhizosphere	<i>Agrobacterium</i> , <i>Devosia</i> , <i>Comamonadaceae</i> , and <i>Sinobacteraceae</i>	Walters et al. (2018)

protection of plants against plant pathogens via modulation of the plant immune system (Liu et al., 2021).

During crop developmental stage, some members of bacterial families *Burkholderiaceae*, *Streptomycetaceae*, and *Rhizobiaceae* were significantly enriched at the seedling stage and were identified as potential beneficial microbes of the crop microbiome (Xiong, Singh, et al., 2021). In contrast, some members of fungal families *Coniothyriaceae*, *Mycosphaerellaceae*, and *Symmetrosporaceae* were more abundant at the mature stage and were identified as network hubs for the crop microbiome (Xiong, Singh, et al., 2021). As for agricultural practices, a recent study revealed that organic fertilizer could significantly reduce *Fusarium* wilt disease (FWD) incidence via enhancing predatory interactions between predatory protists Cercozoa and pathogen-suppressive bacteria *Bacillus* spp., among which microbial secondary metabolite biosynthesis genes (e.g. nonribosomal peptide synthetase gene, COG1020) involved in the production of antimicrobial compounds play an important role in inhibiting plant pathogens (Guo et al., 2022). Moreover, some network hubs belonging to Sphingobacteriales, Cytophagales, Tremellales, and Agaricales were also identified as indicators for conventional system, and a network hub *Rhizobiales* was indicators for organic system (Schmidt et al., 2019). Further, a field long-term fertilization experiment provided empirical evidences supporting the central role of keystone taxa such as *Chloroflexi*, *Nitrospirae*, and *Mesorhizobium* in maintaining soil nutrient cycling and crop production after four decades of fertilization (Fan et al., 2020). On the other hand, evidences from microbial dilution experiment have suggested that the metabolic functions such as nitrogen metabolism and phosphonate and phosphinate metabolisms of keystone taxa belonging to *Nitrospira* and *Gemmatimonas* played an important role in sustaining soil microbiome stability (Xun et al., 2021). A large-scale field study showed that five heritable taxa related to *Agrobacterium*, *Devosia*, *Comamonadaceae*, and *Sinobacteraceae* were also the core taxa of maize rhizosphere microbiome that were present in 100% of samples (4911 samples) (Walters et al., 2018). All these results indicate that the crop host has a strong selection effect on the keystone taxa of the crop microbiome across plant developmental stages and under different environmental stresses. Additionally, whilst our understanding of keystone taxa of soil and crop microbiomes is advancing, increasing studies have indicated that some potential soil-borne human pathogens such as *Clostridium botulinum*, *Salmonella enterica*, and *Burkholderia pseudomallei* may transfer to human system via soil–plant–food chains (Brevik et al., 2020; Nieder et al., 2018; Samaddar et al., 2021; Yan et al., 2022). However, our knowledge of ecological mechanisms that influence this harmful microbial loop along the soil–plant–food continuum is still limited.

Revealing the ecological mechanisms that govern the beneficial and harmful microbial loops along the soil–crop–food continuum and identifying a key atlas of protective functional genes of the crop microbiome are critical questions for further microbiome research.

On the other hand, the above examples provide evidences showing the advantage and significance of multi-omics techniques in exploring diversity, assembly, and function of the crop microbiome. In future study, more integrative and advanced approaches such as metaproteomics, epigenomics, phenomics, single-cell genomics, CRISPR-based genomic editing are expected to provide powerful tools for deciphering biological mechanisms that govern crop–microbiome interactions and engineering plant microbiome function to improve crop production and health (Hatzenpichler et al., 2020; Lawson et al., 2019; Xu, Pierroz, et al., 2021).

CONCLUDING REMARKS

Increasing evidences suggest that soil and crop microbiomes provide a number of life-support functions for their host plants, including growth promotion, nutrient uptake, disease resistance, and abiotic stress tolerance. Cultivating crop-associated microbes favourable to crop productivity and health has been considered as one of the most promising biotechnological strategies to achieve food security and sustainable production. A systematic understanding of ecological mechanisms that govern microbiome assembly, microbial co-occurrence patterns, and crop–microbiome interactions along the soil–plant continuum could provide important knowledge for future microbiome engineering. In the present review, we have highlighted how multiple host and environmental factors shape the microbiome assembly and network patterns under different environmental conditions. We suggested that host selection mediated by plant compartment is the most dominant factor determining diversity, composition, and network patterns of crop-associated microbiomes. The effects of host and environmental factors on microbial community in each compartment depend on ecological attributes of the compartment and the degree of host signals and environmental stresses. Both deterministic and stochastic processes have a role in community assembly of soil and crop microbiomes, and the relative importance of these processes varies according to spatial scale, plant compartment and developmental stage, and microbial groups. Advanced approaches like network analysis and synthetic community experiment have identified some keystone taxa such as *Bacillus*, *Streptomyces*, *Rhizobium*, and *Flavobacterium* for crop microbiomes.

Although recent findings significantly broaden our understanding on the structure and functions of soil and crop microbiomes, our knowledge of molecular

mechanisms that govern crop–microbiome interactions along the soil–crop–food continuum under different environmental stresses remains scarce. For example, some critical questions remain largely unexplored: (1) How do crops recruit beneficial microbes with desired functions under various environmental conditions? (2) Which kinds of keystone functional genes in the crop microbiome enhance crop resistance to pathogens and abiotic stresses? (3) If and how soil-borne human pathogens and antimicrobial resistance can be transfer to human system via soil–crop–food chains? (4) How do crops and their microbiomes interact and co-evolve in response to agricultural management and global change at a long-time scale? Answering these questions should contribute to our knowledge of the underlying mechanisms that govern crop–microbiome interactions and provide an essential information for precisely harnessing crop microbiomes for development of agricultural sustainability.

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CONFLICT OF INTEREST

The author declares that there is no conflict of interest that could be perceived as prejudicing the impartiality of the research reported.

DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new datasets were created or analyzed in this study.

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