REVIEW

The Rice Microbiome: A Model Platform for Crop Holobiome

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ABSTRACT

The plant microbiome, the consortium of microbes surrounding a plant, has potential for improving crop productivity and sustainability. Despite the necessity of agriculturally applicable microbiomes, plant microbiome studies have been conducted in noncrop plants because of the relative easiness of research. However, in order to make plant microbiomes useful for agriculture, a crop plant-based model is needed. In parallel, overlooked parts of microbiomes other than the bacteria-centered research need to be considered to expand our understandings on microbiomes to the ecosystem level. Beyond the microbial composition, functional properties of microbiomes over time and space will help us to select appropriate microbes that can support crop plants by providing stage-specific

functions. Less explored communities such as fungi and protists also can provide novel insights on compositional and functional dynamics of each community, including interkingdom or multitrophic interactions. Finally, identification of host factors on functional microbiomes using genetic information of both the host and the microbiomes will shift host-centered breeding to parallel breeding of host and microbiome. This review will give basic and collective information on the rice microbiome and foster the establishment of a crop plant-based model to meet agricultural needs.

Keywords: agriculture, crop microbiome, microbial ecology, plant microbiome, rice

Plants are exposed to diverse biotic and abiotic factors during their lifetime. The whole system consisting of plants, their environments, and all organisms in those environments is called the phytobiome (Leach et al. 2017). Abiotic and biotic factors of a phytobiome interact dynamically, influencing natural ecosystems and agroecosystems. Among biotic factors, the microbial communities associated with plants are referred to as the plant microbiome or microbiota (Müller and Ruppel 2014; Turner et al. 2013). The microbiota can be profiled using marker genes (e.g., 16S ribosomal RNA [rRNA] gene for bacteria and the 18S rRNA gene or internal transcribed spacer [ITS] regions for eukaryotes). However, this provides only compositional information on microbial communities. By contrast, the microbiome is defined as both the composition of a microbial community in a specific environmental

niche (microbiota) and its collective genome (Bäckhed et al. 2005; Ursell et al. 2012).

Microbial communities may have positive or negative effects on a host plant (Mendes et al. 2013). Some microbes provide nutrients needed by plants; for example, mycorrhiza in the rhizosphere solubilize phosphorus and other nutrients from the soil, which can then be taken up by the plant (Bolan 1991; van der Heijden et al. 1998). Nitrogen-fixing bacteria convert nitrogen in the air into ionic nitrogen to facilitate N uptake by plants (Francheteau et al. 2009). In addition, plant growth-promoting rhizobacteria stimulate plant growth by producing plant-growth regulators such as auxins, cytokinins, and gibberellins (Lugtenberg and Kamilova 2009). Moreover, these microorganisms enhance the environmental adaptability of plants by increasing their resistance to abiotic and biotic stresses. On the other hand, microbes compete with plants for nutrients and water, and some are pathogenic (Mendes et al. 2013).

High-throughput sequencing (NGS), also known as next-generation sequencing (NGS), and -omics technologies such as metagenomics, metatranscriptomics, metaproteomics, and metabolomics have facilitated analyses of microbial diversity and the functions of microbial communities in human and environmental samples. For instance, human intestinal microorganisms synthesize essential nutrients such as vitamin K, and decompose cellulose (Hill and Artis 2009; Zhang et al. 2015). In addition, gut microbes promote the formation of vessels (Reinhardt et al. 2012; Stappenbeck et al. 2002) and bones (Yan et al. 2016), and enhance the function of the

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nervous system of the intestine (Hyland and Cryan 2016). Dysbiosis of intestinal microbial communities is associated with conditions such as obesity, inflammatory bowel disease (Franks 2012; Tamboli et al. 2004), and chronic fatigue syndrome (Giloteaux et al. 2016).

HTS-based studies have revealed that plant-associated microbial communities are more extensively involved in promoting the health and fitness of their hosts than those of human and animal microbial communities. As an example, the root bacterial community is essential for maintaining multikingdom interactions and for maximal plant growth and health of *Arabidopsis thaliana* (Durán et al. 2018). Bacteria–bacteria interactions are also important for *Arabidopsis* root development (Finkel et al. 2019). Under stress conditions, plant microbial communities can support host activities to facilitate plant survival. For example, drought stress causes restructuring of root bacterial communities by modulating moisture availability, altering soil chemistry and plant phenotypes (Naylor and Coleman-Derr 2018). Under stress, compositional and functional shifts occurred to promote plant survival (Dai et al. 2019; Santos-Medellín et al. 2017). Similar to drought stress, microbial communities can alleviate other abiotic stresses by promoting plant growth, accumulating antioxidants and osmolytes, decreasing Na⁺ uptake, or changing the level of phytohormones and defense-related proteins (Ahmad et al. 2015; Meena et al. 2017; Qin et al. 2016; Yuan et al. 2016). Microbial communities can also protect plants from biotic stresses. Plant microbiomes can directly act as antagonists against plant pathogens by producing antibiotics or secondary metabolites (Liu and Brettell 2019; Tyc et al. 2017) or by modulating the physiology of pathogens (Chen et al. 2018). In addition, microbial communities can also prime plant defense genes, resulting in induced systemic resistance (Berendsen et al. 2012). In particular, when plants are consecutively infected by pathogens, enhanced protection by root and rhizosphere microbial communities is observed (Bakker et al. 2018; Berendsen et al. 2018; Yuan et al. 2018b). This phenomenon is called soilborne legacy. The soilborne legacy indicates that plants can actively recruit a group of disease resistance-inducing and growth-promoting microbes under pathogen pressure, ultimately giving the opportunities for their descendants to survive in the same soil. Thus, plant microbiomes as physiological partners might establish coevolutionary relationships with their host plants and directly contribute to plant health and survival in both normal and stress conditions.

We present previous studies on microbiomes of each compartment consisting of a rice plant in terms of composition. Previous findings on functions and dynamics of rice microbiomes are also included. Based on the summary on the previous studies, we further focus on less explored parts of rice microbiomes. This will give collective information for establishing a crop plant-based platform, which make the application of microbiomes feasible in agriculture.

CURRENT UNDERSTANDING ON RICE MICROBIOMES

Composition and structure of rice microbiomes. Studies of rice microbiomes aim to identify the microorganisms associated with rice and associated environments (Fig. 1 and Table 1). Before the emergence of HTS platforms, other molecular techniques such as 16S rRNA gene cloning, polymerase chain reaction-denaturing gel gradient electrophoresis (PCR-DGGE), and terminal restriction fragment length polymorphism analyses were used to evaluate the composition of microbial communities in soil and rice tissues. The emergence of HTS has accelerated research on the composition and structure of rice-associated microbial communities. In the below sections, unveiled microbial communities of each compartment are summarized in terms of composition and diversity.

Bulk soil. Bulk soil, also known as unplanted soil, is the most studied aspect of rice paddy fields. Bulk soil contributes to the accumulation of organic matter and minerals, nutrient cycling, and the capture of air and water (Chaudhari et al. 2013; Karlen et al. 1997). Soil microbial communities play crucial roles in the functions of soil by increasing organic and inorganic nutrient availability and nutrient cycling by promoting decomposition of organic matter. Typically, *Proteobacteria*, *Chloroflexi*, *Actinobacteria*, and *Acidobacteria* dominate the soil bacterial community (Hussain et al. 2011; Jiang et al. 2016) and *Ascomycota*, *Basidiomycota*, and *Glomeromycota* dominate the fungal community in rice paddy fields (Jiang et al. 2016; Yuan et al. 2018a). Interestingly, these abundance patterns at the phylum level are consistent regardless of geographical distance. These findings suggest that there might be an environmental commonality that can affect composition of paddy soil microbiotas at the phylum level. Despite the similarity in the microbial abundance at the phylum level, soil microbiotas showed high heterogeneity following chemical heterogeneity. Chemical properties are highly variable depending on location, depth, and even sampling points in a field. Accordingly, many studies have attempted to not only investigate the organisms in soils but also to link edaphic factors such as chemical properties, geographical distance, and rice cultivation regime or history (Chen et al. 2017; Conrad et al. 2009; Jiang et al. 2016; Li et al. 2018; Noll et al. 2005; Sun et al. 2018; Wang et al. 2017, 2018; Wartainen et al. 2008). For instance, the bacterial and fungal communities of paddy soils managed under four different cultivation regimes (a single rice crop, rice–wheat rotation, a double rice crop, and rice–legume–rice rotation) were investigated (Jiang et al. 2016). Variation in bacterial communities was more closely correlated with soil heterogeneity than with geographic distance, whereas fungal communities were more closely correlated with geographic distance. In another study, microbial communities in bulk soils of paddy fields were investigated according to soil depth and cultivation period (Liu et al. 2016). Microbial abundance increased as the cultivation period increased due to accumulation of organic carbon and total nitrogen. Activities of enzymes such as invertase, urease, and acid phosphatase also affect the composition of bacterial and fungal communities. Fungal abundance and enzyme activity decreased, and fungal composition varied with soil depth (Liu et al. 2016).

Soil pH has been revealed as a strong shaping factor on soil microbial communities. Soil pH is known to affect the concentration of other ions and cation exchange capacity. The changes in ion contents and redox processes also affect the diversity of bacterial and archaeal communities. In particular, the concentration of electron donors or acceptors in bulk soils can explain the composition of functional bacterial and archaeal groups of rice paddy (Yuan et al. 2019). These correlations between soil chemical properties and the distribution of functional microbial groups suggest that composition and putative functions can be predicted based on soil pH or ion concentrations. Potential productivity also can be investigated based on the composition of microbial communities. In fact, Chang et al. (2017) showed crop productivity can be predicted based on the composition of bulk soil microbiota with a machine learning technology in soybean. However, for accurate prediction and management of crop productivity based on soil microbiomes, functional aspects related to nutrient cycling have to be considered.

Methane production and emission are important processes in rice paddy fields. Of all methane emissions, 9 to 19% originate from submerged rice paddy fields due to the decomposition of root exudates or debris (Conrad 2009; Han et al. 2016). Methanogenic archaea such as rice cluster I methanogens are the major group involved in methane production in rice paddy fields (Conrad et al.

2006, 2009; Thauer et al. 2008). Several HTS studies have investigated potential associations with other microbial groups (Edwards et al. 2015; Sun et al. 2018). For instance, operational taxonomic units (OTUs) classified as methanogens, methanotrophs, syntrophs, and methane-cycling taxa (Edwards et al. 2015) or functional groups involved in methane oxidation, iron reduction, and sulfur reduction in paddy soils were tightly associated (Sun et al. 2018). These results further suggest that methane production might be controlled by modulating inorganic nutrients or methanogen-associated microbes.

Apart from the methane cycling, nitrogen metabolisms such as nitrogen fixation, nitrification, denitrification, and bacteria and archaea-mediated ammonium oxidation also actively occur in the rice paddy fields (Ishii et al. 2011). Nitrogen level affects the metabolic activity of microbial functional groups as well as plant

performance. For example, the activity of methane-oxidizing bacteria is dependent on the nitrogen level (Bodelier et al. 2000). Nitrogen cycling is also affected by methane metabolism. For instance, methane could inhibit the growth and activity of nitrifying bacterial community (*Nitrospira* and *Nitrosomonas*) (Zheng et al. 2014). In addition to these cases, methane and nitrogen metabolism can co-occur by microbial activities. Under low-nitrogen fertilizer management, diazotrophic methanotrophs (type II methanotrophic bacteria) act as nitrogen fixers as well as methane oxidizers, contributing to the accumulation of both carbon and nitrogen sources in paddy soils (Minamisawa et al. 2016). This methane-induced nitrogen fixation was also reported in a peatland soil (Larmola et al. 2014), suggesting that this form of nitrogen accumulation is ubiquitous in flooded soil environments. Based on these findings, it can be

Fig. 1. Composition of rice microbiome and its investigation approaches. Microbiomes are distributed ubiquitously in or adjacent to rice plants. Rice microbiome can be dissected into the compartments where microbial communities reside. Among the compartments, bulk soil and root system (rhizosphere and root endosphere) are more widely investigated than other compartments. Community analyses with respect to aboveground parts (phyllosphere and seed) are also employed with both culture-dependent and -independent approaches. Before the introduction of omics technologies, PCR-denaturing gel gradient electrophoresis (DGGE), terminal restriction fragment length polymorphism (T-RFLP), and clone libraries of 16S rRNA genes were used for investigating the compositions of microbiomes. However, these techniques are not enough to unveil the nature of microbiomes because of their low resolutions. With the application of omics technologies, the composition and functions of microbiomes are widely investigated. Another is a culture-dependent approach. Despite the low recovery of natural communities, this approach is inevitable in order to prove predicted functions of microbiomes. For this, isolation of microbes from samples and characterization of isolates using both in vitro and in vivo assays are conducted. This parallel application of both culture-independent and -dependent approaches can give us the chance to construct synthetic communities or combinations of metabolites as probiotics and prebiotics for improving sustainability and productivity of rice. ACC, aminocyclopropane-1-carboxylate; IAA, indole-3-acetic acid; M-, not inoculated with beneficial microbes; and M+, inoculated with beneficial microbes.

inferred that both nitrogen and methane have to be considered as regulatory factors for each other and fertilization can affect both carbon and nitrogen cycling.

Findings described above suggest that the construction and application of synthetic communities (SynComs) on soil can be achieved on the basis of understanding chemical factors, microbial functions, and microbe–microbe associations. Furthermore, it is important to define key modulating functions or association networks of microbial communities. The metabolic connections among microbes show that culturable functional microbes will increase when dependency of microbes on electron donors and acceptors such as sugars, amino acids, or inorganic matters is defined (Morris et al. 2013; Ponomarova and Patil 2015; Zelezniak et al. 2015). Enzyme, protein, or mRNA co-occurrence networks could contribute to identifying the metabolic dependency in soil microbial communities. Based on these microbial and functional association networks, functional SynComs with key functions will

be constructed and applied into rice agroecosystems to improve sustainable management of rice productivity.

Rhizosphere. The rhizosphere is defined as the soil adjacent to plant roots. Plant roots alter the chemical and nutrient composition of soil by secreting organic and inorganic substances, which also affects its physical and biochemical properties. Such secreted substances, also referred to as root exudates, are important for maintenance of root–soil contact and contribute to root growth and plant survival (Walker et al. 2003). Root exudates facilitate the physicochemical adaptation of plants to the soil environment and provide nutrients for early colonization of soil microbial communities (Bacilio-Jiménez et al. 2003). Consequently, root exudates contribute to the biological adaptation of plants in a soil environment by recruiting microbes that functionally enhance the rhizosphere. Microbes in the rhizosphere benefit plants by providing nutrients or plant hormones, suppressing pathogens, and increasing resilience to abiotic stresses such as drought (Berendsen

TABLE 1
Major findings on rice (*Oryza sativa* L.)-associated microbial communities

Subject composition	Major finding	Reference
Bulk soil	Effects of chemical factors (oxygen status and inorganic matters) and cultivation practices (crop rotation and fertilization regimes) on soil microbial communities	Noll et al. (2005)
		Liu et al. (2016)
		Wang et al. (2017)
		Jiang et al. (2016)
		Yuan et al. (2019)
		Sun et al. (2018)
Rhizosphere	Rhizosphere effects in terms of microbial communities	Breidenbach et al. (2015)
		Hussain et al. (2012)
	Effects of rice development and genotypes on soil microbial communities	Hussain et al. (2011)
		Shenton et al. (2016)
Phyllosphere	Biocontrol activities of rhizosphere bacteria against pathogens	Spence et al. (2014)
	Effects of abiotic (geographic locations, atmosphere and soil conditions, and fertilization regimes) and biotic factors (rice genotypes) on phyllosphere microbial communities	De Costa et al. (2006)
		Ren et al. (2014)
		Venkatachalam et al. (2016)
	Structure, metabolic profiles, and host factors shaping phyllosphere bacterial communities	Roman-Reyna et al. (2019)
Endosphere	Effects of abiotic (graphical location, soil conditions, and cultivation practices) and biotic factors (rice genotypes and root compartment) on microbial communities	Edwards et al. (2015)
		Ikeda et al. (2014)
		Long and Yao (2019)
		Santos-Medellín et al. (2017)
		Bertani et al. (2016)
		Fisher and Petrini (1992)
Seed	Effects of a host genetic factor on the assembly and functions of root bacterial microbiomes	Zhang et al. (2019)
	Effects of seed compartments on composition and diversity of seed microbiotas	Eyre et al. (2019)
	Inheritance of seed bacterial communities	Hardoim et al. (2012)
Community dynamics	Role of seed as a microbial pool of endophytic microbial communities of mature rice plants	Kaga et al. (2009)
		Wang et al. (2016)
Functional prediction	Community dynamics of belowground bacterial communities (rhizosphere, rhizoplane, and root endosphere) during rice development	Edwards et al. (2018)
Functional prediction	Functional characteristic (metabolic make-up) of bacterial communities associated with phyllosphere, rhizosphere, and root endosphere	Knief et al. (2012)
		Okubo et al. (2014)
		Sessitsch et al. (2012)

et al. 2012; Breidenbach et al. 2015; Mendes et al. 2011; Welbaum et al. 2004). Several studies have investigated the composition of rhizosphere microbiotas compared with bulk soil, and the factors related to rhizosphere microbiomes (Bacilio-Jiménez et al. 2003; Bhuvaneshwari and Subba-Rao 1957; el Zahar Haichar et al. 2008; Lu et al. 2004; Saleem et al. 2018).

Prior to the widespread use of HTS, PCR-DGGE was used to investigate rhizospheric microbial communities in rice (Hussain et al. 2011, 2012). The compositions of communities of rhizosphere bacteria and fungi of rice at various developmental stages were investigated using DGGE and found that both communities varied according to growth stage (Hussain et al. 2011). Improvements in meta-omics technologies have enabled investigations of the composition and diversity of rhizosphere microbiotas. For example, communities of bacteria and archaea have been found to be more abundant in the rhizosphere than in bulk soil, but the two types of soil have similar diversities of these microorganisms (Breidenbach et al. 2015). The compositions of bacterial communities in bulk soil and the rhizosphere were similar to those of the rhizoplane and rhizosphere; only 169 of 27,147 OTUs (152 enriched and 17 depleted OTUs) differed between the soil types (Edwards et al. 2015). Both marker gene-based community profiling and meta-omics approaches have also been used to assess the compositions of rhizosphere microbial communities. In particular, the distribution of anaerobic bacterial taxa belonging to *Deltaproteobacteria* indicates environmental characteristics of rice rhizosphere coexisting oxic and anoxic conditions (Ding et al. 2019). These studies also showed that bacterial communities in rhizosphere are variable depending on soil type, geographical location, growth stage, and cultivation practice.

Among the shaping factors on rhizosphere microbiome, the effects of the growth stage and rice genotypes might be correlated with variations in the composition of root exudates of rice. The quantity and profiles of organic acids contained in root exudates were significantly different during rice growth and among cultivars (Aulakh et al. 2001). The root exudation rate increased from seedling stage to flowering stage but decreased at maturity. The content of organic acids in the exudates increased as rice plants grew whereas sugar contents decreased (Aulakh et al. 2001). This temporal variation of root exudates can be correlated with compositional variations of rhizosphere microbial communities. Although indisputable evidence on temporal changes in microbial communities with rice root exudates, the communities would have a tight relationship with rice plants chemically and biologically.

Like other plants, the rhizosphere of rice is the most biodiverse environment among compartments where rice plants and microbial communities interact with each other. This high microbial diversity suggests that beneficial microbes protecting rice plants from pathogens or promoting their growth are more frequently distributed than other compartments. In fact, bacterial isolates belonging to *Pseudomonas* spp. were retrieved and characterized in vitro and in vivo analyses (Spence et al. 2014). It was also identified that rhizospheric bacteria can induce the jasmonic acid- and ethylene-dependent systemic resistance response. These findings imply that rhizosphere microbial communities are important for not only nutrient cycling but also protect the rice plant itself by triggering immunity systems.

Considering that oxic and anoxic zones coexist within the rhizosphere of rice cultivated in flooded condition, strict and facultative anaerobes as well as aerobes have to be taken into account in terms of biological and ecological functions. Although some studies identified strictly or facultative anaerobic bacteria and fungi from bulk and rhizosphere soils of rice ecosystems (Akasaka et al. 2003; Qiu et al. 2014; Tonouchi 2009), given that metabolic versatility of

anaerobic microbial communities in rice fields (Liesack et al. 2000) and the possibility that aerobic and anaerobic microbes can coexist in the aerobic state (Shabuer et al. 2015), anaerobic microbes might be key modulators or players that maintain the structure of overall rhizosphere microbial communities. Although the community analysis based on SynCom is not widely conducted in the rice microbiome research, individual microbes and SynComs of both aerobes and anaerobes will give new combined insights on microbial interactions and their impacts on rice health in the rhizosphere.

Phyllosphere. The phyllosphere is defined as the aboveground portions of plants. Although the phyllosphere is a harsh environment for microbes because of ultraviolet radiation, nutrient and water limitations, and rapid temperature shifts, it is colonized by bacteria, fungi, archaea, and protists (Müller and Ruppel 2014). Most phyllospheric microbes are commensal and very difficult to culture. Thus, the compositions of these communities have been revealed by culture-independent approaches including 16S or 18S rRNA gene clone libraries and amplicon sequencing in other plants (Copeland et al. 2015; de Souza et al. 2016; Jumpponen and Jones 2009; Rastogi et al. 2013; Vorholt 2012). Some studies of phyllosphere microbiomes have investigated the major drivers of their composition, the sources of the organisms, their genetic and functional features, and their contribution to stress adaptation (Rastogi et al. 2013).

In rice, composition of phyllosphere microbial communities is varied depending on the studies. In an amplicon-based profiling study, *Enterobacteriaceae* (*Gammaproteobacteria*) predominated the phyllosphere (Ren et al. 2014). However, a metaproteomic study showed that *Actinobacteria*, *Alpha*-, and *Betaproteobacteria* predominated the phyllosphere microbiome and revealed distinct enriched functions compared with the rhizosphere and paddy water (Knief et al. 2012). A metagenome-based approach also revealed the hidden portion of phyllosphere microbiome of rice. Using bacterial reads recovered from available reads of rice genome, bacterial communities in the phyllosphere of 3,024 rice accessions were reconstructed (Roman-Reyna et al. 2019). The authors revealed that structure and functional profile of phyllosphere microbiomes were conserved despite geographical differences and rice genotypes. This finding suggests that plants might recruit functional supporters that can fulfill common physiological needs among rice accessions. Thus, this study shows that the reassembly of phyllosphere microbiomes from the raw data of plant genome analyses is possible and this genome wide association study can shed light on identifying functional factors that regulate plant-microbiome interactions.

Culture-dependent approaches have also been used to investigate the phyllosphere microbial community of rice plants. Most studies have focused on isolating bacteria and/or fungi and analyzing their antagonistic activity against rice pathogens such as *Magnaporthe oryzae*, *Rhizoctonia solani*, and *Xanthomonas oryzae* (De Costa et al. 2006; Harsonowati et al. 2017; Ilsan et al. 2016; Krishanti et al. 2015; Thapa et al. 2018). Three bacteria (two *Erwinia* species and one *Bacillus pumilus*) as well as 18 fungi (representing *Trichoderma*, *Pestalotia*, and *Alternaria* species) inhibiting the growth of *M. oryzae* and *R. solani* were isolated (De Costa et al. 2006). Eighteen species of leaf actinomycetes of the genera *Streptomyces*, *Saccharothrix*, *Gordonia*, and *Lentzea* also showed antifungal activity against the rice blast fungus (Harsonowati et al. 2017). The potential of biofertilizers and biocontrol agents to improve rice growth and productivity has also been evaluated (Venkatachalam et al. 2016). About 34% of 86 *Achromobacter*, *Stenotrophomonas*, *Pantoea*, *Exiguobacterium*, and *Bacillus* isolates produced indoleacetic acid (IAA) as a cue to promote rice growth in vitro. The phyllosphere microbiome can also enhance plant development and

health and plays a role in nutrient cycling and remediating the residues of pesticides and atmospheric pollutants (Müller and Ruppel 2014). This suggests that phyllosphere microbial communities can be potentially applied for not only agricultural but also environmental purposes.

Considering that phyllosphere communities are exposed to the climate conditions including atmosphere, studies that connect the abiotic and biotic factors of the climate and phyllosphere communities are needed for further rice microbiome studies. In particular, as the climate conditions dramatically change, structure and functions of phyllosphere communities can further affect plant performance and ecosystem functioning (Vacher et al. 2016). In order to connect microbiomes and climate, the impacts of phyllosphere microbiomes on plant performance and ecosystem functioning need to be evaluated. Furthermore, model systems mimicking the environmental changes in the climate will help to track the compositional and functional changes in phyllosphere microbiota. Beneficial phyllosphere microbes contributing to functional resilience against the environmental changes will be identified by the models in rice and other plants.

Endosphere. The internal regions of the plant's leaves, stems, roots, fruits, and seeds are termed the endosphere, and the resident microorganisms are endophytes. Endophytes can be divided into ecological groups depending on their visible effects on plants. Commensal endophytes generally show neutral effects on plant performance, whereas beneficial endophytes confer beneficial effects on plant development or protection from pathogens and herbivores. Another group is opportunistic or latent pathogen showing detrimental effects in certain conditions (Hardoim et al. 2015; Rodriguez et al. 2009). Among these endophytes, beneficial endophytes are considered a new source of biocontrol agents and biofertilizers for increasing crop productivity.

Many studies have attempted to unveil endospheric microbial communities using NGS technologies and to collect and characterize endophytic isolates with culture-dependent approaches in several plants (Bertani et al. 2016; de Souza et al. 2016; Gottel et al. 2011; Mano and Morisaki 2008; Sengupta et al. 2017; Sessitsch et al. 2012; Sun et al. 2008; Yuan et al. 2010). Compared with other compartments, research on endosphere microbiomes have the technical limitation caused by the vast amount of genomic DNA of a host plant that can obscure the more limited contribution from the endophyte. In particular, plastid and mitochondrial DNAs are coamplified during the generation of bacterial amplicon. This high ratio of host to endophyte DNA results in low sequencing depth and quality in raw sequence data of the endophyte. In order to inhibit the amplification of the host DNAs, some studies adopted new primer sets generating amplicons spanning V5 to V7 regions of 16S rRNA genes (Beckers et al. 2016) or PCR inhibitors (peptide nucleic acid clamps) binding to plastid and mitochondrial DNAs (Lundberg et al. 2013). Despite the improvements in the sequencing quality and depth of bacterial biotas, it has not yet been introduced into rice microbiome research.

Even with this technical limitation, endophytic microbiotas or microbiomes of rice have been revealed. Most previous studies have focused on the root endosphere (Sessitsch et al. 2012; Sun et al. 2008), but a recent study on rice leaf microbiome suggests a technically possible way to explore bacterial communities in the compartments where the ratio of host to microbe DNA is high (as described in the phyllosphere section [Roman-Reyna et al. 2019]). Using a metagenome-based approach, endophytic bacterial communities in other compartments such as stem and seed can also be analyzed in the compositional and functional aspects. In another study, bacterial communities in rice leaves, stems, and roots were investigated using both 16S rRNA gene-based community profiling

and culture-dependent methods (Bertani et al. 2016). The following endophytic properties of the resulting 1,318 bacterial isolates were evaluated: nitrogen fixation, phosphorous solubilization, IAA production, 1-aminocyclopropane-1-carboxylate deaminase activity, antibacterial and antifungal activity, lipolytic activity, exopolysaccharide production, and motility. In addition, putative endophytes were inoculated into rice plants to verify their ability to promote plant growth. Unlike endophytic bacterial communities, endophytic fungal counterparts of rice are less studied at the community level. Although some studies investigated composition and diversity of endophytic fungal communities associated with rice root using ITS sequence-based community profiling (Long and Yao 2019; Santos-Medellín et al. 2017; Sun et al. 2019), understanding the functional and ecological roles of endophytic fungal communities are lacking. To expand our knowledge on microbial community, comprehensively combined approaches are required.

Seed. The seed contains nutrients for germination and survival before plants can nourish themselves photoautotrophically. The seed also carries microbes such as bacteria, fungi, and viruses. The microbial communities of seeds have been highlighted because they can improve the fitness of plants by improving seed quality and protecting early seedlings from pathogens (Nelson 2018; Shade et al. 2017). However, our knowledge of seed microbiotas and microbiomes is deficient. In rice, a culture-dependent approach recovered isolates closely related to *Bacillus firmus*, *B. fusiformis*, *B. pumilus*, *Caulobacter crescentus*, *Kocuria palustris*, *Micrococcus luteus*, *Methylobacterium fujisawaense*, *Methylobacterium radiotolerans*, and *Pantoea ananatis* from seed microbiome (Kaga et al. 2009). Regarding fungi, endophytic isolates known to be saprobes or plant pathogens such as *Alternaria alternata*, *Cladosporium tenuissimum*, *Epicoccum purpurascens*, *Fusarium equiseti*, *F. oxysporum*, and *Phoma sorghina* have been collected from surface-sterilized seeds (Fisher and Petrini 1992).

One of the interesting topics in seed is the inheritance of microbiomes. In rice, strains assigned to *Stenotrophomonas maltophilia* and *Ochrobactrum* sp. via PCR-DGGE were found to be closely related to bacteria isolated from the rice phyllosphere, rhizosphere, and paddy soil, suggesting a high level of adaptation to rice niches; in addition, about 45% of the bacterial community of the first generation was also detected in the second (Hardoim et al. 2012). Amplicon-based community profiling has been used to assess the seed microbiotas of seedlings not exposed to external microbiotas (Wang et al. 2016; Zhang et al. 2018). For instance, analyses of the endophytic bacterial and fungal biotas of field-grown flowering rice plants, rice seeds, and 4-day-old sprouts grown under sterile conditions showed that bacterial and fungal OTUs coexisted in sprouts, stems, and roots (Wang et al. 2016). For example, OTUs belonging to *Sphingomonas*, *Pseudomonas*, *Fusarium*, *Pestalotiopsis*, and *Penicillium* were detected in all rice samples; therefore, these OTUs might be transmitted to the next generation through seeds.

Apart from the temporal investigation on whole seed microbiomes, bacterial and fungal communities of seed compartments (grain, outer grain, husk, and outer husk) were also characterized in rice (Eyre et al. 2019). The authors showed that each compartment possessed distinct microbial compositions in both communities, suggesting that seed compartments shape different ecological niches. Despite the differences in niche, sampling year, location, and genotype, core microbiota members were identified. The existence of core microbiota in seed suggests that plants might carry the essential microbes that potentially promote the growth and survival of offspring. To validate this assumption, microbial cultures corresponding to core members need to be recovered from natural microbial communities, to be synchronized with NGS-based

communities, and to be characterized as performed in the works of Durán et al. (2018) and Zhang et al. (2019). In both studies, culture-independent OTUs were synchronized with culturable isolates based on the sequence similarities among OTUs and isolates from roots of *A. thaliana* (Durán et al. 2018) and rice (Zhang et al. 2019). This approach will provide more information on the in planta functions of OTUs involved in plant health and productivity. The origin and assembly of seed microbiomes are also of interest. Such communities may be formed via internal, floral, and external pathways (Nelson 2018; Shade et al. 2017). The seed microbiotas of radish, rice, and other plants are reportedly conserved for two or three consecutive years (Hardoim et al. 2012; Nelson 2018; Rezki et al. 2018). However, little is known about microbial succession during seed maturation or the genetic and functional characteristics of seed microbiomes. The functions and ecology of seed microbiomes are important as they could allow for manipulation of microbiomes for agricultural applications. A study of the microbiotas in or on apple flower stigmas, stamens, receptacles, and petals showed that their composition varied (Steven et al. 2018). Such studies could help the control of phytopathogens that can infect flowers and fruits and also elucidate the pathway that forms a seed microbiota over time and space for further rice and other plant studies.

Establishment and community dynamics of rice microbiomes.

Apart from the investigation of microbiomes at a specific time, spatiotemporal variations of the composition and diversity of microbiomes can be tracked. An understanding of microbiome dynamics, for example, the predominant taxa in each tissue and the functions required at each stage of a plant's life cycle, can be applied to enhance crop productivity. Previous studies of rice microbiotas have only focused on the composition of communities of root bacteria (Edwards et al. 2015, 2018). In one such study of the structure of the microbiotas in the rhizosphere, rhizoplane, and root endosphere in two rice-growing regions (Edwards et al. 2015), the composition of the bacterial community differed geographically and among the three root microbiotas. Moreover, a time-series greenhouse experiment showed that soil microbiotas were translocated to the rhizoplane and colonized the inner root tissue as endophytes after 24 h. The authors suggested that the rhizoplane controls the entry of bacteria into the endosphere. Another spatiotemporal study reported that the bacterial and archaeal communities were highly dynamic during vegetative development, but their composition was stable in all other developmental stages (Edwards et al. 2018). In addition, early and late colonizers of the rhizosphere and endosphere were identified, and these could be used to determine plant age. Therefore, plant growth-associated temporal changes in microbiota composition should be considered during the development of strategies to improve crop productivity. However, neither of these studies assessed the functions of microbial communities or the correlations between changes in microbiota composition and changes in plant physiology.

Functional characterization of rice microbiomes. Another important subject of microbiome research is the functional identification of microbial communities. In order to expand our knowledge on the functional aspect of microbiomes, metagenomic, metatranscriptomic, and metaproteomic approaches have been adopted. Such approaches have been applied to environmental and human microbiomes (Torres-Cortés et al. 2018; Tully et al. 2018; Turner et al. 2013; Wang et al. 2015). For example, 2,631 putative metagenomes were reconstructed from the ocean worldwide and the authors suggested that the results could be used for metatranscriptomic and metaproteomic studies (Tully et al. 2018). Similarly, meta-omics studies of rice microbiomes have provided insight into their functional characteristics (Ikeda et al. 2014; Knief et al. 2012; Okubo et al. 2014; Sessitsch et al. 2012). It was found that

endophytic root bacteria had flagella, plant polymer-degrading enzymes, protein-secretion systems, iron acquisition and storage mechanisms, quorum-sensing systems, mechanisms for detoxifying reactive oxygen species, and proteins involved in nitrogen fixation, denitrification, and nitrification (Sessitsch et al. 2012). Another study compared the microbial functions associated with the rice phyllosphere, rhizosphere, and paddy water using metagenomics and metaproteomics, and found distinct results for each biome (Knief et al. 2012). For example, proteins involved in methanogenesis, methanotrophy, chemotaxis, and nitrogen metabolism were detected more frequently in the rhizosphere than in the other regions. By contrast, proteins associated with methanol-based methylotrophy related to *Methylobacterium* and those involved in substrate uptake and stress responses were detected more frequently in the phyllosphere. In water, proteins related to photosynthesis, CO₂ fixation, and the Calvin cycle predominated. This finding showed that each microbiome in the rice agroecosystem possesses distinct functions depending on the environments where they reside. Therefore, to integrate microbiomes and related findings of each environment is inevitable in order to comprehensively understand plants and their associated microbiomes. In particular, temporal and spatial dynamics of microbial functions in parallel with dynamics of rice physiology are needed in order to identify microbial functions which affect plant performance in each stage. This approach can facilitate the formation of stage-specific Syn-Coms for maximizing physiological potential of plants.

MODEL PLATFORM FOR CROP HOLOBIOME

Mycobiome as an unexplored community. Compared with studies of bacteria, fewer studies have addressed fungal communities (mycobiomes) associated with plants. Fungal communities are as crucial as bacterial ones in terms of their effects on host physiology. For example, fungi account for only 0.1% of the total microbes in the human gut (Underhill and Iliev 2014) but have marked effects on human physiology. Indeed, fungal communities are more sensitive to changes in diet than bacterial communities are (Hallen-Adams and Suhr 2017; Huseyin et al. 2017; Underhill and Iliev 2014). In addition, dysbiosis of the mycobiome is associated with, for example, inflammatory bowel disease (Ott et al. 2008), familial Crohn disease (Hoarau et al. 2016), colorectal adenoma (Luan et al. 2015), diarrhea (Sangster et al. 2016), and intestinal allografts (Li et al. 2012).

In plants, unlike the human mycobiome, whether dysbiosis of the plant mycobiome is related to disease is unclear. However, fungi of the plant mycobiome show plant-supporting functions that can be potentially applied for agriculture. Mycobiomes such as mycorrhizal fungi and *Epichloë* spp. play a pivotal role in plant physiology. Mycorrhizal fungi are a heterogeneous group of fungi that engage in a mutualistic association with the plant root system. Root-colonizing fungi, whether intracellular or extracellular, supply water and mineral nutrients such as phosphate (Johnson et al. 1997), and prime plant immunity to respond to pathogens (Jung et al. 2012). *Epichloë* spp., obligate endophytic symbionts of grasses, infect both vegetative and reproductive organs (systemic infection) and are vertically transmitted to the next generation. Moreover, fungi not only promote plant growth but increase the productivity of forage grasses by producing herbivore-deterrent alkaloids and increasing stress resistance (Kauppinen et al. 2016). Therefore, *Epichloë* spp. have potential as a biofertilizer for sustainable agriculture. Apart from *Epichloë* spp., fungal species belonging to *Aspergillus*, *Fusarium*, *Phoma*, *Penicillium*, and *Trichoderma* showed plant growth-promoting activity by directly producing or regulating the expression of plant hormones such as gibberellins

and IAA (Bilal et al. 2018; Waqas et al. 2012; Xia et al. 2019). Fungal symbionts are also involved in enhancing plant tolerance against abiotic stresses (Hubbard et al. 2014; Rodriguez and Redman 2008; Singh et al. 2011). Thus, these plant-supporting functions of fungi could be used with functional bacteria for synergistic effects to improve plant growth and yield. In addition, recent findings revealed by network analysis show that fungi could act as hub in the interkingdom co-occurrence network (Agler et al. 2016; Brachi et al. 2017). This topological role of fungi in the network suggests that fungi mediate overall structure of not only the fungal community itself but also other communities connected with fungi. Thus, research on the influence of compositional and functional variations of the mycobiome and parallel approaches with bacteria or other microbial groups is inevitable for fully understanding the relationship between plant health or performance and microbial communities.

Wild plant and related species as sources of forgotten microbiomes. Crop plants have undergone facilitated and selected evolution by domestication and diversification. During this process, plants lose genetic diversity due to artificial selection of preferred agronomic traits such as crop quality and quantity (Meyer and Purugganan 2013). A macroorganism is considered not a stand-alone entity but rather an assemblage of species (or biomolecular networks composed of the host and its associated microbes), termed a holobiont (Bordenstein and Theis 2015; Hassani et al. 2018). Plants coevolve with their associated microbes, including those that may contribute to crop development. In addition, the domestication of crop plants accompanied by anthropogenic intervention to maintain high yields increases the use of external inputs such as fertilizers and pesticides and reduces self-supporting systems (Pérez-Jaramillo et al. 2016). Crop breeders are seeking new genetic resources to develop new varieties that require less external input but have high productivity. To do this, in the plant side, wild species and their relatives are used as breeding materials because they possess lost gene pools (Brozynska et al. 2016; Hajjar and Hodgkin 2007). In the microbe side, microbiomes are considered an alternative to agrochemical use to reduce adverse effects on the environment. In particular, the microbiomes associated with ancestors of modern cultivars have been investigated for their potential to support domesticated cultivars (Murphy et al. 2018).

To identify such microbiomes for rice, both culture-dependent and culture-independent approaches have been used (Elbeltagy et al. 2000; Shenton et al. 2016). In one such study, wild rice species were enriched in *Anaerolineae* and *Nitrospirae*, whereas domesticated cultivars were enriched in *Saprospirae*, *Burkholderiales*, *Sphingomonadales*, and *Rhizobiales* (Shenton et al. 2016). The authors suggested that symbiotic pathways may have been selected during domestication as the enrichment patterns of taxa between wild rice and domesticated cultivars were similar to the patterns of legumes which symbiotic pathways are disrupted. Despite the compositional differences, the phylogeny of the rhizosphere microbiota was weakly correlated with that of *Oryza* based on chloroplast sequences (Shenton et al. 2016). This result indicates that evolutionary relationships of microbiomes can be deciphered not by the single marker gene level but by comparison of the whole genomes of rice.

This point is connected with defining host genetic factors shaping microbial communities because of genetic and phenotypic variations between wild ancestor and modern cultivars (Fig. 2A). Host factors contributing to modulating composition of microbial community are revealed with reverse genetic approaches by considering microbiomes as another plant phenotype. For example, in *A. thaliana*, host genes responsible for the assembly of root bacterial community were discovered using mutant genotypes which were deficient in biosynthesis of, and/or signaling dependent on each defense hormone (Lebeis et al. 2015). Similar to this study, the

difference in nitrogen use efficiency between *O. sativa* subsp. *japonica* and *O. sativa* subsp. *indica* is involved in compositional and functional differences in bacterial communities using mutant genotype on *NRT1.1B* (rice nitrate transporter and sensor) (Zhang et al. 2019). Thus, based on reverse genetic approaches, investigation on genomic and physiological differences among *Oryza* spp. can help lost microbiomes of domesticated rice and related factors be unraveled. Furthermore, this research can expand opportunities for selecting and reintroducing target host factors of wild plants to domesticated plants. Finally, crop plants' ability and their associated microbes can be restored. For this, microbiome studies have to be coupled with a modern breeding system.

Multitrophic interactions in rice microbiomes. An integrated approach to studying the bacterial and fungal communities associated with rice is needed to develop strategies for sustainable agriculture. Agroecosystems are highly complex entities comprising the crop plant itself and various abiotic and biotic players, including bacteria and fungi (Fig. 2B). Among these, insects play an important role in the production of crop plants. Insect pests of rice, such as brown plant hoppers, rice weevils, rice stem borers, and rice leaf rollers, damage plants and cause economic losses (Pathak and Khan 1994). Brown plant hoppers transmit viruses such as rice stripe virus and Southern rice black-streaked dwarf virus, which can be more destructive than the pest (Jia et al. 2012; Zhang et al. 2010). Therefore, the relationships among crop plants, microbiomes, and insects must be considered when developing microbiome-based strategies to improve crop productivity. Plant microbiomes can be manipulated to influence the nutritional and physiological status of the plant, thus promoting growth. Such changes in the plant can affect insect fitness (Shikano et al. 2017). For instance, in one study, inoculation of tomato plants with beneficial microorganisms not only increased plant growth and fruit production by 35 and 61% but also increased the survival rate and weight of insect larvae by 25 and 41%, respectively (Megali et al. 2014). In another study, inoculation of tomato plants with *Pseudomonas fluorescens* WCS417r increased the survival rate of whiteflies and decreased plant defenses (Shavit et al. 2013). By contrast, microbes can promote systemic resistance to insects by increasing sensitivity to jasmonic acid and ethylene (Pineda et al. 2010). Thus, introduced microbiomes can have both positive and negative effects on insect pest. Evaluation on the effects of microbial treatment on pests is also needed in *in vitro/in vivo* assay and field trials.

Another important cue in multitrophic interactions is volatile organic compounds (VOCs) (Fig. 2B). VOCs are known to play momentous roles in plant interactions with abiotic and biotic factors and communication between plants (Farré-Armengol et al. 2016). Phyllosphere microbiomes can affect the profile of VOCs by producing their own VOCs, by modifying the production and emission of plant VOCs, and by metabolizing VOCs as a carbon source (Bringel and Couée 2015; Farré-Armengol et al. 2016). For example, methane gas produced during wax degradation by plants is degraded by methanotrophic bacteria (Iguchi et al. 2013). Plant C1 VOCs such as methanol and chloromethane are also captured by methylotrophs on the phyllosphere (Bringel and Couée 2015; Vannelli et al. 1999). Considering that methane and chloromethane are responsible for global warming and halogen-catalyzed depletion of stratospheric ozone, phyllosphere microbiomes play a role in scavenging harmful compounds in the atmosphere. In addition, phyllosphere microbiomes also can inhibit the colonization of bacterial and fungal pathogens by emitting VOCs (Bitas et al. 2013; Kai et al. 2007; Kanchiswamy et al. 2015; Schulz-Bohm et al. 2017). These findings in other plants indicate that phyllosphere microbiomes are shaped by abiotic conditions and organic compounds produced by plants and their effects on other organisms are also mediated by VOCs. This suggests that biological

characteristics of phyllosphere microbiomes can be explained by investigating large-scale interactions among atmosphere–plant–phyllosphere microbiome based on VOCs. Furthermore, VOCs produced by microbes mix with those of plants, altering insect

behavior and plant physiology (Farré-Armengol et al. 2016). Therefore, further studies of plant–microbiome–insect interactions are required to enhance our understanding of rice agroecosystems and to develop pathogen- and pest-management strategies.

Fig. 2. Proposed scheme for expanding knowledge on crop microbiomes. **A**, Wild ancestors of modern cultivars are considered as a breeding source for improving modern cultivars. Recent studies revealed that wild ancestor species possess distinct microbiomes when compared with modern cultivars. Defining host factors contributing to the differences between microbiomes of wild species and modern cultivars will shed light on microbiomes that are lost during domestication and diversification. Furthermore, as host factors can be a target for breeding strategies, the ‘lost microbiome’ that is able to support crop plants can be restored for agricultural purpose. **B**, Beyond rice microbiomes, rice phytobiomes have to be investigated to improve sustainability of the rice agroecosystem. Phytobiomes include both abiotic and biotic factors related to the ecosystems. Effects of climate, agrochemicals, and soil nutrients on functions of plant itself and plant-associated microbiomes are further subjects in terms of abiotic factors. Multitrophic interaction is another key subject for understanding an agroecosystem in case of biotic factors. To unveil multikingdom interactions within microbiome, studies on fungi and protists are needed. Other microbiome sources such as air, water, and animals (insects) have to be unveiled. Furthermore, volatile organic compounds (VOCs) as a cue on multitrophic interactions can give insights on not only plant–insect interactions but also plant–microbiome–insect interactions.

A recent review on the interactions among members of plant microbiotas emphasized their role in determining microbial community structure and maintaining plant health (Hassani et al. 2018). Protists are typically not the focus of studies of microbiomes. The Kingdom *Protista* is composed of algae (plant-like protists), protozoa (animal-like protists), and oomycota (fungus-like protists), which participate in carbon cycling, enhance plant growth, stimulate plant growth-promoting rhizobacteria, and may also be pathogenic (Xiong et al. 2017). In particular, *Pythium*, *Phytophthora*, *Peronospora*, and *Albugo* are plant pathogens found in leaves and roots. *Albugo*, an obligate biotrophic oomycete pathogen, affects bacterial colonization in *Arabidopsis*. Thus, this protist may reconfigure microbial communities (Agler et al. 2016). In addition, protist predation affects the composition and functions of the phyllosphere bacterial community (Flues et al. 2017). Therefore, microbial interactions such as competition, predation, and parasitism should be considered when formulating synthetic microbiotas to promote crop health and productivity.

PERSPECTIVE

The availability of meta-omics technologies has accelerated studies of plant microbiomes, mostly in *Arabidopsis*. Therefore, a crop plant-based microbiome model is required to improve crop productivity and establish sustainable agriculture. Most studies have focused on the composition, diversity, and functions of belowground parts, such as the root and soil microbiomes, and the mechanisms of the acquisition and succession of the root microbiota. The findings to date emphasize the complexity of these microbiomes and their effects on plant health and productivity. In addition, an increasing number of studies focus on the microbiomes of aboveground plant parts, such as leaves, stems, and seeds. In particular, seed microbiomes have received much attention due to the belief that they will facilitate the management of crop production combined with smart agriculture. However, further studies of the functional aspects of plant microbiomes are needed because of their importance for plant health and productivity. Meta-omics approaches will unravel the functions of the microbiomes associated with rice plants. The ecological traits of microbiomes must be considered for successful application of bio-control agents and biofertilizers or synthetic microbial consortia (Hawkes and Connor 2017). Above all, to fully understand agroecosystems where SynComs are applied, microbiomes and related environmental cues at the ecosystem level are comprehensively investigated and the data are integrated and deciphered. To do this, it is inevitable that a standard platform for generating microbiome data are constructed. Furthermore, investigations of plant-microbe interactions have demonstrated the effects of the microbiomes on plant physiology and health and have enabled identification of beneficial microbes. Ecological aspects are also important as they are related to microbe-microbe interactions among members of the plant microbiome. Bacterial communities have been investigated far more extensively than fungi and protists. Investigation of these neglected microbes will enhance our understanding of microbe-microbe interactions and their ecological relationships. Furthermore, establishment of a crop-based microbiome model will enable translational research with the aim of promoting sustainable agriculture.

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