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EDITED BY
Riyaz Zafar Sayyed,
PSGVP Mandal's Arts, Science and Commerce College, India

REVIEWED BY
Sugitha Thankappan,
Karunya Institute of Technology and Sciences, India
Frédérique Reverchon,
Instituto de Ecología (INECOL), Mexico

*CORRESPONDENCE
Marouane Baslam
✉ mmm.baslam@gmail.com

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# Holo-omic applications to unveil microbiome shaping sustainable horticultural production

Mohamed Ait-El-Mokhtar[1] and Marouane Baslam[2,3,4]*

[1]Laboratory of Biochemistry, Environment and Agri-Food URAC 36, Department of Biology, Faculty of Science and Techniques – Mohammedia, Hassan II University of Casablanca, Mohammedia, Morocco, [2]Laboratory of Biochemistry, Department of Applied Biological Chemistry, Faculty of Agriculture, University of Niigata, Niigata, Japan, [3]Centre d'Agrobiotechnologie et Bioingénierie, Unité de Recherche Labellisée CNRST (Centre AgroBio-Tech-URL-CNRST-05), Université Cadi Ayyad, Marrakech, Morocco, [4]Laboratory of Agro-Food, Biotechnologies and Valorization of Plant Bioresources (AGROBIOVAL), Department of Biology, Faculty of Science Semlalia, Cadi Ayyad University (UCA), Marrakesh, Morocco

Plant-associated microorganisms play a key role in the future sustainability of terrestrial ecosystems. In nature, plants and their associated microbiome can form an assemblage of species, considered interacting metaorganisms or holobionts. Horticultural plants, including vegetables, fruit and berries, and ornamentals live in intimate association with complex and diverse microbial communities that have evolved a myriad of cooperative and competitive interaction mechanisms that shape the holobiont fitness. Nonetheless, our understanding of these interactions in shaping more complex microbial horticulture communities, along with their relevance for host growth, fitness, stress resilience, and health in a more natural context remains sparse. In this perspective, the holo-omic landscape that requires careful consideration of study design and integrates multi-omic data from both host and microbiota domains is a promising approach to unveil the interplay between the two to advance horticultural production. The analysis of horticulture (meta)-omics and phenotyping, along with mechanistic experiments in model systems, is revolutionizing research by enhancing our ability to understand the structure and core function of the plant-associated microbiome. These advancements are complemented by improvements in the throughput and accuracy of DNA sequencing, enabling us to delve deeper into the genomes of microbial communities. Yet, many challenges remain. We focus this review on the potential for holo-omics to generate a more holistic perspective of molecular networks, and we further discuss the implementation and current limitations of the holo-omic approach within microbial horticulture. We argue that holo-omics will pave the way to improve, from a horticultural perspective, food security and safety, sustainability, breeding practices, development of microbiota- and host-tailored horticultural crops' health treatments and increasing production efficiency.

KEYWORDS

**horticulture, sustainable production, holobiont, holo-omic analysis, microbiome, host-microbiome fidelity**

## 1. Introduction

Horticultural crops are an essential part of agriculture for both food and nutritional security. In recent years, impressive progress has been made in improving the growth, productivity, and quality of horticultural crops. Given the distinct features of plant growth and development, research in the horticultural associated-microbes have increasingly been addressed. Many studies revealed an important diversity of the microbiome associated with horticultural crops affecting the quantity and quality of their products and their tolerance to biotic and abiotic stresses through close interactions with plant roots (Bulgari et al., 2019; Emmanuel and Babalola, 2020; Ma et al., 2020; Zulfiqar, 2021). Research has fundamentally altered our perception of plant-microorganism interactions to more understanding of their complex network biological processes. In their environment, plants coexist with a variety of microbes including bacteria, fungi, archaea, and protists constituting the plant microbiota (Lindow and Brandl, 2003; Buée et al., 2009; Berendsen et al., 2012; Vorholt, 2012; Turner et al., 2013). Several studies conducted on microbes originating from the phyllosphere, rhizosphere, and in endophytic plant compartments have reported a series of promoting effects on plant health and performance, including enhancement of nutrient acquisition (Anli et al., 2020; Lahbouki et al., 2022), boosting plant immune defense (Rolfe et al., 2019; Zheng et al., 2020), protection against pathogens (Ait Rahou et al., 2020; Liu H. et al., 2020), resistance to environmental stresses (Ait-El-Mokhtar et al., 2020; Ben-Laouane et al., 2020; Boutasknit et al., 2021), and promoting hormone production (Wang et al., 2017). Plants and their associated microorganisms interact in a bidirectional fashion. The microbes provide the necessary metabolites to boost plant health and fitness and the host plant supplies its microbial associates with metabolic capacities, resulting in the establishment of niche-specialized inhabitants providing positive (mutualistic), detrimental (pathogenic), or neutral (commensalistic) actions on plant performances (Thrall et al., 2007).

These interactions are based on complicated molecular connections including a mutual perception between the two partners and the management of resources and nutrients critical for their survival (Cotton et al., 2019; Finkel et al., 2019b; Huang et al., 2019; Campos-Soriano et al., 2020; Stassen et al., 2021). Furthermore, current discoveries suggest that the outcome for host performances may rely not only on host/microbe exchange of supplies but also on signaling and metabolic exchanges between microbiome members (Durán et al., 2018; Finkel et al., 2019a; Harbort et al., 2020). These investigations show that comprehending the plant microbiome will most likely need an analysis of these connections at different layers, such as activity and functional capacity and molecular interaction involving host and microorganisms. Although many advances were accomplished in the functional understanding of plant microbiome interactions especially through combining metabolomic and metatranscriptomic studies, this aspect is still lacking, in part because of the system's complexity. One aspect of this complexity is that the phytomicrobiome is built from and lives in one of the most varied habitats on the planet: the soil (Compant et al., 2019; Fitzpatrick et al., 2020). Soils support a diverse microbial ecology interacting in complicated framed networks and shifting in abundance, composition, and activity which enhance the diversity of the whole system (Griffiths et al., 2011; Chemidlin et al., 2014; Terrat et al., 2017; Wei et al., 2019). Another level of complication is related to the quantity and composition of the metabolites exuded by plant roots that are in continuous changes (Jacoby et al., 2020), resulting in the differential recruitment of rhizospheric microbes. These aspects combine to form a dynamic and linked biological scheme that has tested our capacity to grasp the fundamental molecular mechanisms that build and sustain it. Still, our choice of assets may be a bigger reason for our delayed progress toward a functional understanding of plant microbiome interactions. Until recently, the majority of plant microbiome investigations have focused on descriptive studies of community structure with help of amplicon-based sequencing, including Internal Transcribed Spacer (ITS) sequencing for fungi and 16S rRNA sequencing for bacteria (Griffiths et al., 2011; Terrat et al., 2017).

While these data have provided a significant understanding of the broad dynamics that orchestrate the general structure of the plant microbiome and the relative intensity of their influence (Lundberg et al., 2012; Coleman-Derr et al., 2015), they frequently fail to provide mechanistic perception to interactions with the host plant. More recently, a growing number of research has started to investigate additional microbiome characteristics, such as functional capacity and activity, using shotgun metagenomics and metatranscriptomics (Galloway-Peña and Hanson, 2020; Jo et al., 2020; Gao et al., 2021; Singh et al., 2022). Even with this rise, there is still a scarcity of research relating plant microbiome information to plant physiology, metabolism, genetics, and other host aspects (Brunel et al., 2020), which might supply additional data from this unexplored aspect of plant-microbiome interactions. Emerging trends and research hotspots in this field—as co-cited references in Figure 1A—revealed a total of 16 clusters, where each one corresponds to a line of research. Except "#7 shoot tips" cluster, all the other clusters were closely related to the topic of the microbiome of horticultural crops. Among these clusters, "#0 disease resistance," contains most of the nodes, has been widely reported followed by "#1 plant growth promoting rhizobacteria" and "#2 mycorrhizae" as the most active research areas. Studies from 2010 and 2017 were focused on cluster "#0 disease resistance," but in the last 5 years, the hotspots and frontier trends highlight plant associated-beneficial microorganisms ("#1 plant growth-promoting rhizobacteria" and "#2 mycorrhizae"), apple replant disease, and internal transcribed spacer (ITS) (Figure 1B). To gain a more comprehensive understanding of plant microbiome function, we advocate for experimental datasets that combine host-centered omic approaches like transcriptomics, epigenomics, metabolomics, and proteomics with microbial-focused approaches like shotgun metagenomic, amplicon sequencing, metatranscriptomics, and exometabolomics. The term "holo-omics" characterize research that includes data from many-omic layers from both the host and microbial domains (Nyholm et al., 2020). We believe that holo-omic investigations have the potential to clarify the functionality of plant microbiome interactions by producing a picture of what is expressed, translated, and generated through plant-microbiome interactions (Griffiths et al., 2011). This multimodal view can assist narrow down results from various datasets to significant biological signals, as well as generate support for certain hypotheses using data gained *via* orthogonal methodologies. After the introduction of the holo-omic approach (Nyholm et al., 2020) and its adoption in plant microbiome interactions (Xu L. et al., 2021; Xu Q. et al., 2021), this review focuses on the potential of holo-omics to generate a more holistic understanding of molecular networks and discusses the implementation and current limitations of the holo-omic approach within the horticultural microbiome. More understanding of

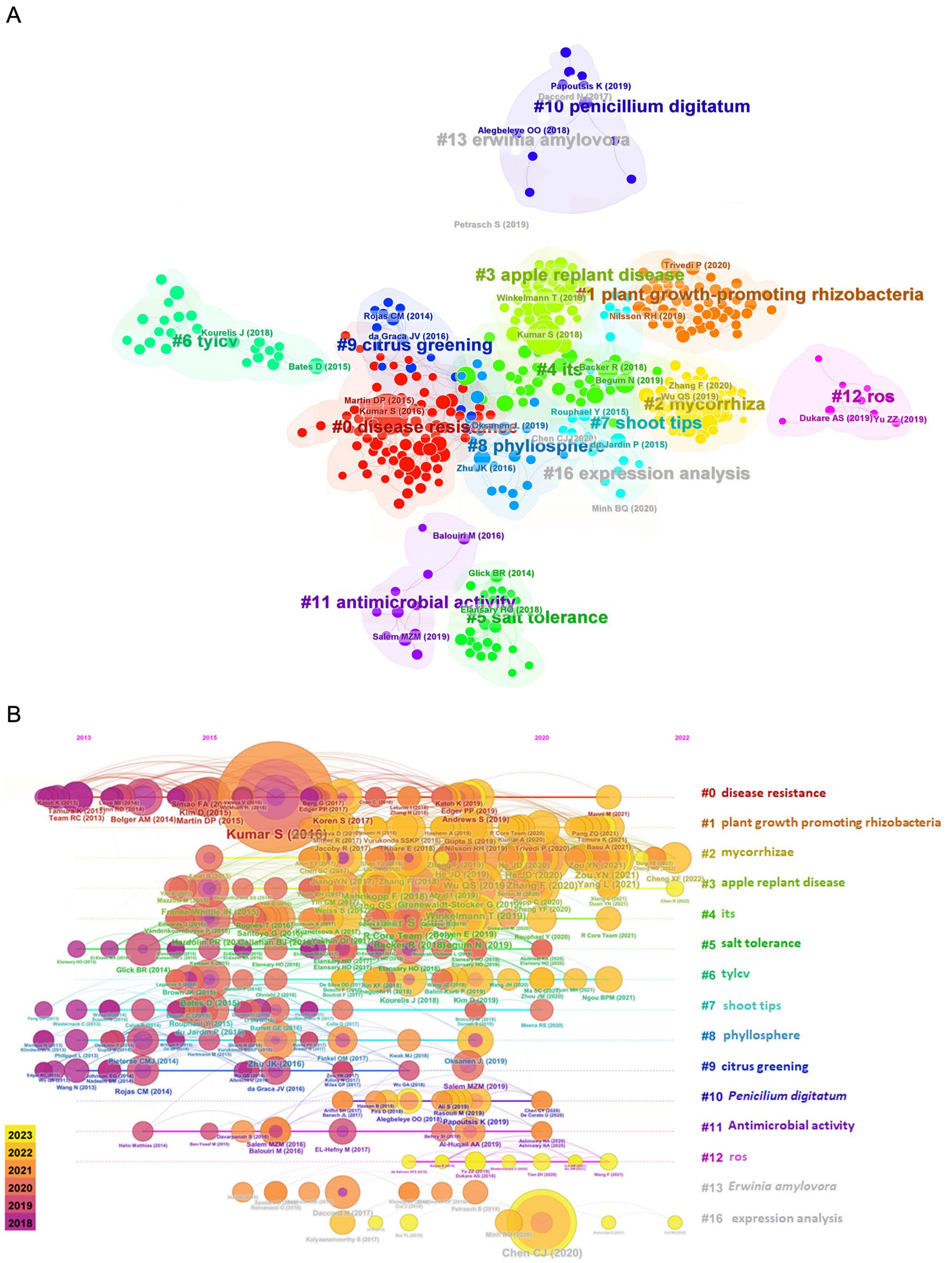

FIGURE 1
Co-cited references **(A)** and timeline visualization **(B)** of keyword co-occurrence clustering analysis in the study of microbiome associated with horticultural crops from 2018 to 2023. ITS, internal transcribed spacer; TYLCV, tomato yellow leaf curl virus; ROS, reactive oxygen species.

microbiome-horticultural crop interactions will harness the development of microbial tools for climate-proof horticulture production. We first highlight the horticultural-associated microbiome and discuss the different beneficial/pathogenic interactions between the host plant and the microbes, with a focus on experimental design considerations for plant holo-omic. Finally, we discuss the current challenges in appraising holo-omics datasets.

## 2. Composition of horticultural microbiome and structuring factors

### 2.1. Bacterial and archaeal microbiota of horticulture

Multiple studies reported the diversity of bacterial and archaeal microbiota of horticultural plants and their functional traits influencing the host plant and the associated microbial community. Previous studies confirmed that there is no hazard in the establishment of the bacterial community on plants since this process is managed by an assemblage of specific rules (Dong et al., 2019; Yang H. et al., 2023). Many structuring factors of plant-associated bacterial communities such as soil type (Liu et al., 2020; Xu et al., 2020), plant compartment (López-Angulo et al., 2020; Bettenfeld et al., 2022), host genotype/species (Cheng Z. et al., 2020; Sousa et al., 2020; Shakir et al., 2021), plant immune system (Kohl, 2020; Knights et al., 2021), plant trait variation/developmental stage (Liu et al., 2020; Compant et al., 2021), and residence time/season (Chernov and Zhelezova, 2020; Wang et al., 2021; Yi et al., 2021). Various bacteria such as *Alphaproteobacteria*, *Actinobacteria*, *Gammaproteobacteria*, *Firmicutes*, *Pseudomonas*, and *Paraburkholderia* spp. were discovered in the rhizosphere of different horticultural crops (carrot, potato, neep, beetroot, onion, and topinambur) (Kõiv et al., 2019). Cheng F. et al. (2020) and Cheng Z. et al. (2020) reported that the rhizomicrobiome of 11 tomato cultivars is composed of a diversified community dominated by bacteria from the phyla Proteobacteria, Bacteroidetes, and Acidobacteria, mainly comprising Rhizobiales, Xanthomonadales, Burkholderiales, Nitrosomonadales, Myxococcales, Sphingobacteriales, Cytophagales, and Acidobacteria subgroups. Meanwhile, the pathogenic bacterial community has been found in a variety of horticultural crops; *Pseudomonas syringae* in olive, tomato, and green bean, *Xylella fastidiosa* and *Ralstonia solanacearum* in potato and banana, *Escherichia coli* strains in leafy greens and sprouts, *Listeria monocytogenes* in fresh-cut salad and melons, *Salmonella* spp. in tomato, spices seeds, and sprouts, *Norovirus* in berries, and *Shigella* in green onion (Mansfield et al., 2012; Leff and Fierer, 2013; Li et al., 2015; Deng et al., 2019; Shi et al., 2019). Although the important diversity of bacterial microbiota reported here and the myriad factors controlling the establishment of this microbiota, the bacterial community in both above- and belowground compartments of horticultural plants are dominated by *Proteobacteria*, *Actinobacteria*, and *Bacteroidetes* phyla, as is the case for most plants (Rai et al., 2021). Comparing root- and leaf-associated communities using an operational taxonomic unit (OTU) showed significant overlap in many crops, such as grapevine and tomato (Zarraonaindia et al., 2015; Dong et al., 2019). However, Bai et al. (2015) demonstrated through large-scale genome sequencing and re-colonization of germ-free plants that host-associated microorganisms are specific and adapted to their respective cognate plant organs. Despite representing *ca.* 36% of plant-associated microbiota (Müller et al., 2015), archaeal microbiota have not received the same level of attention as their bacterial counterparts, possibly because no archaeal pathogens have been reported. Therefore, more research should be conducted on archaeal members, particularly to clarify their interactions and significance for their host plants.

### 2.2. Fungal microbiota of horticulture

Community profiling studies showed a huge diversity of plant-associated fungi with *Ascomycota* and *Basidiomycota* as the main phyla (Sweeney et al., 2021; Zhou et al., 2021). A great number of phytobiome research identified many fungal microorganisms from the horticultural microbiome, including *Trichoderma* and mycorrhizal fungi, *Penicillium* sp., *Cladosporium* sp., *Colletotrichum* sp., *Cryptococcus*, *Rhodotorula*, *Hanseniaspora,* and *Sphingomonas* with beneficial effects on plant growth performances (Shi et al., 2019; Jo et al., 2020; Knapp et al., 2021; Liu and Howell, 2021; Darriaut et al., 2022; Fournier P. et al., 2022; Sangiorgio et al., 2022). Recent studies have identified several fruit trees-associated fungi (e.g., *Fusarium*, *Cladosporium*, *Taphrina*, *Phoma*, *Septoria*) as phytopathogenic fungi (Padraic et al., 2019; Nicoletti et al., 2020; Gusella et al., 2021; de Jager and Roets, 2023; Yang Y. et al., 2023). In the rhizosphere of sweet potato, Gao et al. (2019) revealed the presence of plant growth-promoting fungi, including *Chaetomium* and pathogenic fungi such as *Fusarium*, *Verticillium*, *Guehomyces*, and *Colletotrichum*. A phytobiome study on tomato identified several beneficial fungi, including *Aspergillus*, *Hyphodiscus*, *Chrysosporium*, *Trichoderma*, and *Oidiodendron* (Lee et al., 2019). Similar to bacteria, there are several structuring factors that govern the fungal phytobiome, including soil type, plant compartment, plant species, and seasons (Onufrak et al., 2020; Knapp et al., 2021; Liu and Howell, 2021; Runge et al., 2023). Fungal populations have high endemism and limited biogeographic dispersal due to their sensitivity to stochastic variations and distinct responses to environmental factors when compared to bacterial communities (Powell et al., 2015; Thomson et al., 2015; Vacher et al., 2016; Zhang et al., 2021; Wei et al., 2022). Studies examining plant-associated fungi and bacteria have shown that fungal microbiota is more influenced by biogeography than bacterial microbiota (Onufrak et al., 2020; Liu and Howell, 2021; Zhang et al., 2021; Wei et al., 2022; Runge et al., 2023). However, it remains unclear whether the taxonomic resolutions brought forth by the 16S rRNA and ITS marker loci impact this trend (Peay et al., 2016).

### 2.3. Horticulture-associated protist

Little importance was given to protists as a component of the rhizosphere microbiome, although they are ubiquitous and play a key role in soil and plant functioning. The most known protists to interact with plants are belonging to the lineages of Oomycota (Stramenopiles) and Cercozoa (Rhizaria) which belong to the supergroup of Stramenopiles-Alveolata-Rhizaria (SAR) (Ruggiero et al., 2015). *Phytophthora*, *Pythium*, *Albugo*, and *Peronospora* genera, within Oomycota, contain some species closely associated with horticultural roots or leaves (Arcate et al., 2006; Coince et al., 2013; Sapkota and Nicolaisen, 2015; Agler et al., 2016). The main oomycete species are well known to induce deleterious effects on plants and thereby a significant decline in global crops production (Kamoun et al., 2015). In contrast, some oomycetes species that colonize roots can boost plant fitness and health performances (Benhamou et al., 1997, 2012; Van Buyten and Höfte, 2013), confirming the existence of beneficial protists with non-harmful interactions with plants. Protists profiling community studies have revealed unexpected diversity of soil protists (Dupont et al., 2016; Mahé et al., 2017). Oomycetal communities associated with horticultural crops showed very low diversity (Coince et al., 2013; Sapp et al., 2015), where they are mostly represented in plant tissue by species belonging to the Pythiaceae family (Sapp et al., 2015), while Cercozoan communities presented high diversity in plant leaves and roots (Sapp et al., 2015; Ploch et al., 2016). Protistan communities are controlled by many environmental factors (Geisen et al., 2015; Dupont et al., 2016) and they have been recently considered as determinant bioindicators of soil quality (Fournier B. et al., 2022). These studies highlight the importance of protists—especially Oomycota and Cercozoa—for holobiont functioning and sustainability.

The horticultural microbes provide many services through their effective bidirectional interactions with plants. These services (see Figure 2) are reviewed in the next section.

# 3. Cascading consequences of holobionts on plant growth and health

## 3.1. Interplay between the host beneficial microbiome and horticultural metabolic pathways

Previous studies have provided evidence of the promising role of plant interactions with beneficial soil microbes in agriculture sustainability (see reviews by Arif et al., 2020; Liu H. et al., 2020; Liu L. et al., 2020; Ali et al., 2022; Bai et al., 2022; Trivedi et al., 2022). This section does not intend to give a detailed account of horticulture–beneficial microbe interaction and the reader is directed to other publications to read about the beneficial interaction for plant growth promotion (Patel et al., 2018; Kumawat et al., 2019; Ullah et al., 2020), disease suppression (De Vrieze et al., 2018; Sharma et al., 2018; Ait Rahou et al., 2020), bioremediation (Ma et al., 2015; Bücker-Neto et al., 2017; Belimov et al., 2020), and abiotic stress tolerance, including heat stress (Mukhtar et al., 2020; Sangiorgio et al., 2020), salinity stress (Ait-El-Mokhtar et al., 2019; Toubali et al., 2020), drought stress (Silambarasan et al., 2019; Anli et al., 2020; Huang et al., 2020).

Signaling from horticultural plants to microbes through plant-secreted compounds has been demonstrated to promote various beneficial aspects for plants (Goddard et al., 2021; Lazazzara et al., 2021; Montesinos et al., 2021). This signaling process has been mainly investigated in close symbiotic associations, especially those involving mycorrhizal fungi and rhizobial bacteria (Emmanuel and Babalola, 2020; Sharma et al., 2020; Hanaka et al., 2021; Dabré et al., 2022). For instance, under nutrient-deficient conditions, the host plant enhances strigolactone secretion to stimulate the establishment of AMF and root colonization as a mechanism for nutrient acquisition (Li et al., 2023). Another group of signaling molecules involved in the communication between horticultural plants and microorganisms is flavonoids. These compounds have been shown to boost root infection by rhizobacteria that induce the formation of nodules allowing N fixation in legumes (Wang et al., 2022; Zhang et al., 2022). Plants emit flavonoids that serve as chemo-attractants and nodulation gene (Nod) inducers for symbiotic Rhizobia when N levels are low. Apigenin and luteolin, two of the Nod-inducing flavonoids, were both potent chemoattractants, whereas naringenin elicited a very weak response in *Rhizobium leguminosarum* biovar phaseoli (Dent and Cocking, 2017; Abedini et al., 2021), showing that various flavonoids play distinct roles. Besides these characterized signaling molecules, the plant-derived aromatic metabolite benzoxazinoids (BXs) can act as chemo-attractants for several beneficial microbes in addition to their role as toxins toward pathogens (Bhattarai et al., 2021). It has been shown that the presence of coumarins in root exudates alters the microbial makeup of the roots by promoting/restraining the growth of specific microorganisms. According to Stringlis et al. (2018), scopoletin, an antimicrobial coumarin, preferentially inhibits the

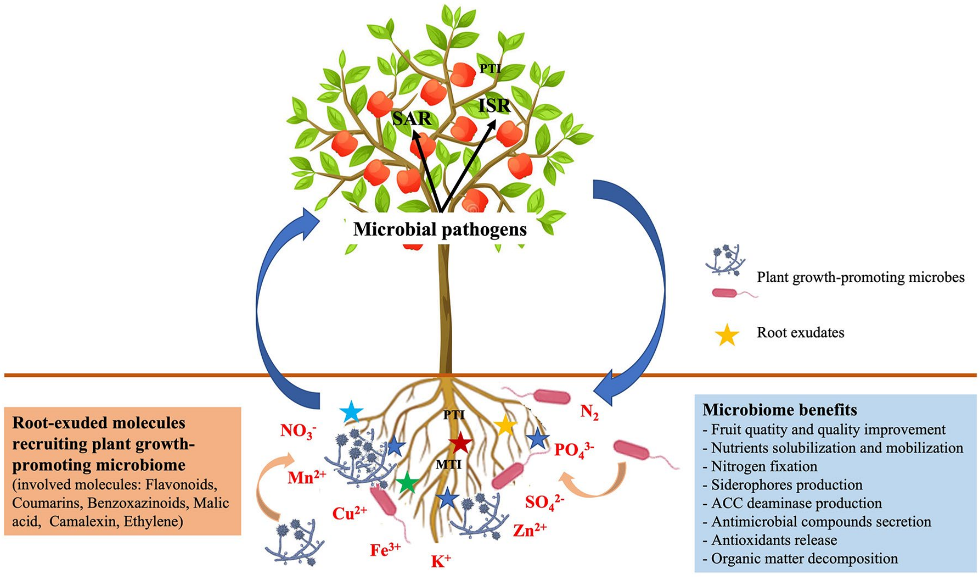

FIGURE 2
Microbiome services provided by beneficial/pathogenic horticulture–microbe interactions. SAR, Systemic acquired resistance; ISR, induced systemic resistance; MAMPs, microbe-associated molecular patterns; PGPM, plant growth-promoting microbes.

growth of the pathogenic *Fusarium oxysporum* and *Verticillium dahlia* (both known to be associated with horticultural crops), while having no effect on the beneficial rhizobacteria *Pseudomonas capeferrum* and *Pseudomonas simiae*. Moreover, a wide range of amino acids is recognized by microbial chemoreceptors, which drive the bacteria to nutrient-rich niches around the plant roots (Dent and Cocking, 2017). For the development of symbiotic relationships, the capacity to utilize amino acids provided by the host plant for nourishment may be essential. For instance, Hida et al. (2020) demonstrated that *Pseudomonas protegens* CHA0, a rhizobacterium that promotes plant growth of various species including tomato, possesses four putative chemoreceptors for amino acids that may enhance chemotaxis toward amino acids. In the same vein, glycerol-3-phosphate (G3P) roots secretion is essential for strain-specific exclusion of non-desirable root-nodulating bacteria and the associated foliar pathogen immunity in soybean (Shine et al., 2019). Under stressful conditions, horticultural plants produce chemicals that specifically attract microbes that can increase plant resilience (Cheng F. et al., 2020; Xu Q. et al., 2021). Furthermore, plants interact with the microbiome through volatile compounds (VCs), such as aldehydes, terpenoids, phenylpropanoids, and common monoterpenes (i.e., limonene, − pinene, benzenoids, −caryophyllene) (Wolfgang et al., 2019; López et al., 2021; Jiuyun et al., 2022). Along with the low-molecular-weight organic acids, many other important bioactive agents (i.e., phenolics, flavonoids, cutin, monomers) and many other unidentified molecules are involved in plant-microbial chemical interactions (Gulati et al., 2020; López et al., 2021; Jiuyun et al., 2022).

Horticultural plants can detect signaling molecules produced by microorganisms that have an impact on the host gene expression, immune system, development, and stress responses (Shine et al., 2019; Fu et al., 2021; Oyserman et al., 2022). Microbe-associated molecular patterns (MAMPs), such as lipopolysaccharide, peptidoglycans, flagellin, and chitin are used by rhizosphere microbes to elicit plant responses (Fu et al., 2021; Oyserman et al., 2022). MAMPs cause induced systemic resistance (ISR) and they prime the rhizosphere-beneficial microorganisms. Systemic acquired resistance (SAR), primarily induced by pathogens, can also be triggered by MAMPs (Kim et al., 2020; Dye and Bostock, 2021). To initiate symbiosis with plants, several well-known chemicals are employed by microorganisms, including legumes rhizobium and mycorrhizal factors (Shine et al., 2019; Ge et al., 2022). In addition to plant signaling chemicals, metabolic interactions between microbes *via* quorum sensing (QS) are crucial in defining microbial communities. According to extensive research, the QS molecule N-acyl homoserine lactone (AHL), produced by Gram-negative bacteria, not only acts as a signaling molecule within and between bacterial species but also between bacteria and plants, influencing thereby gene expression and functions related to plant development, stress response, and immunity (Schuhegger et al., 2006; Ferluga et al., 2008; Babenko et al., 2022). QS compounds, such as cis-2-unsaturated fatty acids, pyrones, alkyl quinolones, and dialkyl resorcinols have recently been discovered. Beyond QS mechanisms, numerous microbial compounds such as VCs have been reported to act as signaling molecules, inducing directed movement of fungal-bacterial and plant-microbe associations. VCs from bacterial metabolic activity could be used by plants in stressful environments (Sangiorgio et al., 2020; Jiuyun et al., 2022; Nakayasu et al., 2023). *Pseudomonas* and *Bacillus* species have been found to produce VCs that either directly inhibit plant pathogens by changing the transcriptional expression levels of numerous genes involved in motility and pathogenicity or indirectly by increasing ISR in plants (Raza et al., 2016a,b). However, little is known about the processes through which microbial VCs promote growth and nutrient absorption. Besides, microorganisms regulate the nutritional and hormonal balance of plants and promote systemic tolerance to (a) biotic stimuli and plant growth. Several root-associated microbes produce auxins, cytokinins, gibberellins, salicylic acid, abscisic acid, and cytokinins (French et al., 2019). In a changing climate, the plant microbiome is also involved in host phenotypic plasticity, which can have an impact on plant phenology (Dastogeer et al., 2020). For instance, by altering the N cycle and converting the amino acid tryptophan in root exudates to the indoleacetic acid phytohormone, rhizosphere bacteria can control the flowering time (Lu et al., 2018).

## 3.2. Pathogenic microbiome interactions with key metabolic pathways of host plants

Plants are equipped with multilayer defense strategies to cope with microbe attacks. A myriad of studies has highlighted the induced response during the horticultural plant-pathogen interaction at different levels. Advanced research in genomic profiling allows the sequencing of the whole genomes of horticultural pathogens. Table 1 shows a list of sequenced genomes of horticultural plant pathogens.

Transcriptomic studies have implicated the upregulation of several phenylpropanoid and terpenoid biosynthesis-related genes and the downregulation of photosynthesis-related genes at 48 h post-inoculation of lettuce with *B. cinerea* (De Cremer et al., 2013). Proteomics studies added a new layer to the understanding of plant-pathogen interaction. Margaria et al. (2013) investigated the proteome profile of grapevine infected by *Flavescence doree* (phytoplasma pathogen disease). In infected grapevine, 48 different proteins were de-regulated, including isocitrate dehydrogenase and glutathione S-transferase known by their antioxidant role. Another study (Parker et al., 2013) identified the tomato proteome during the infection by *Pseudomonas syringae* pv. tomato DC3000 (Pst). A total of 2,369 proteins were de-regulated in tomato leaves of which 477 Pst redox proteins such as glutathione S-transferase, thioredoxin, and superoxide dismutase as the most up-regulated proteins. Li et al. (2013) identified 38 proteins (i.e., antifungal proteins, PR proteins, and cell wall strengthening-related proteins) differentially expressed in *Fusarium oxysporum* f. sp. cubense infected-banana. Using LC–MS analysis, the metabolite profile changes were observed during the infection of grape with *B. cinerea* (Hong et al., 2012). The results provided evidence of carbohydrate and lipid metabolisms reprogramming toward the increased synthesis of secondary metabolites involved in plant defense, such as trans-resveratrol and gallic acid. The study provided metabolic biomarkers of infection (i.e., azelaic acid, a substance known to prime plant defense responses, arabitol, ribitol, 4-amino butanoic acid, 1-O-methyl- glucopyranoside, and several fatty acids) that alone or in combination can be used to monitor *Botrytis* early infection in the vineyard. In potato, The infection with *Phytophthora infestans* showed a resistance characterized by the presence of flavonoids, alkaloids, and phenylpropanoids (Yogendra et al., 2015). Soybean plants infected with *Rhizoctonia solani* yielded an altered metabolites profile with major antioxidant molecules (i.e., phytoalexins, flavonoids, coumarins,

**TABLE 1** List of horticulture pathogens whose genomes are sequenced using -omics technologies.

| Host plant | Pathogen | Genome size (Mb) | References |
|---|---|---|---|
| Potato | *Pectobacterium carotovorum* | 4.97 | Niemi et al. (2017) |
| | *Phytophthora infestans* | 240 | Haas et al. (2009) |
| | *Dickeya solani* | 4.92 | Khayi et al. (2014) |
| | *Ceratocystis fimbriata* | 29.41 | Markus Wilken et al. (2013) |
| Tomato | *Clavibacter michiganensis* | 3.298 | Gartemann et al. (2008) |
| | *Ralstonia solanacearum* | 5.8 | Salanoubat et al. (2002) |
| Banana | *Ralstonia solanacearum* | 5.43 | Xu et al. (2011) |
| | *F. oxysporum (Foc1)* | 47.838 | Guo et al. (2014) |
| | *F. oxysporum (Foc4)* | 53.111 | Guo et al. (2014) |
| Bean | *Pseudomonas syringae* | 5.93 | Joardar et al. (2005) |
| Plum | *Monilinia fructigena* | 43.125 | Landi et al. (2018) |
| Apple | *Erwinia amylovora* | 3.8 | Sebaihia et al. (2010) |
| Chestnut | *Cryphonectria parasitica* | 43.8 | Crouch et al. (2020) |
| Strawberries | *Phytophthora fragariae* | 73.68 | Gao et al. (2015) |
| Citrus | *Xylella fastidiosa* | 2.68 | Simpson (2000) |
| Peach | *Taphrina deformans* | 13.3 | Cissé et al. (2013) |

and hormones) likely to limit the invasion of the pathogen (Aliferis et al., 2014).

Characterizing the entire range of bioactive substances generated by plant pathogens is another crucial task for metabolomic studies in plant-microbes interactions. These compounds could be employed as plant-attacking non-protein effectors (Pusztahelyi et al., 2015). Pathogenic organisms of *Aspergillus*, *Alternaria*, *Burkholderia*, *Fusarium*, and *Pseudomonas* create a wide range of chemically varied toxins that include aflatoxin, alternariol, toxoflavin, fumonisin, or coronatine (Lee and Ryu, 2017; Adeniji et al., 2020). In addition, root pathogens must identify chemical cues in the rhizosphere to infect root tissues. For instance, the oomycete pathogen *Phytophthora sojae* recognizes trace amounts of the compounds daidzein and genistein released by soybean and uses them as chemotrophic cues to guide its growth (Hua et al., 2015). Similarly, cochliophilin A, belongs to the class of flavones, from spinach root exudates attracts *Aphanomyces cochlioides* causing root rot disease (Chen et al., 2021). Plant root exudates typically play a significant role in both pathogen attraction to the roots and their deterrence or activation of microbiome processes, as part of the action to defend against invading pathogens (Sasse et al., 2018; Jacoby et al., 2020). Most of the current studies on the interactions of microbial members with potential pathogenic behavior (pathobiota) with horticultural crops have employed basic simulation models containing a single host entity and a single pathogen entity. Yet, in their natural habitat, plants are in continuous interaction with a myriad of susceptible pathogens (Bartoli et al., 2018) and the establishment of these harmful microbes relies on whether the pathobiota cooperate with or compete with the plant microbiome. The next step is therefore to understand the way pathobiota and plant microbiomes interact in a long-term process in a realistic ecological context.

## 3.3. Microbe-assisted production-related traits improvement

One of the aspects of the positive impact of the horticultural-associated microbiome on crop performance is the promotion of fruit quantity, quality, and/or functionality (Agnolucci et al., 2020; Emmanuel and Babalola, 2020). Bona et al. (2016) revealed that the inoculation of tomato with AMF (*Glomus aggregatum*, *G. viscosum*, *Rhizophagus intraradices*, *Claroideoglomus claroideum*, and *C. etunicatum*) and PGPB (*Pseudomonas* sp.) induced early flowering and fruiting and a significant increase in fruit length, diameter, and weight, providing thereby fruit with high commercial value. Mycorrhizae significantly improved sugar concentration in bigarade orange, eggplant, and grape berries (Antolín et al., 2020; Hadian-Deljou et al., 2020; Sabatino et al., 2020). Apple roots inoculated with *Rhizophagus irregularis* accumulated higher sugar concentration, especially under drought conditions. Similarly, inoculation of strawberry with PGPB strains increases yield, sugars, nutrients, and vitamins content in fruit (Esitken et al., 2010; Todeschini et al., 2018). It has long been noted that horticultural crops–beneficial microorganisms interactions are significantly influenced by the amounts of soluble sugar in the host plants (Agnolucci et al., 2020; Emmanuel and Babalola, 2020). Todeschini et al. (2018) showed an increase in fruit glucose and fructose levels in *Septoglomus viscosum*-inoculated strawberry, whereas Bona et al. (2015) revealed that the application of commercial inoculum Mybasol improved glucose and sucrose concentrations in strawberry fruits. Tomato plants inoculated with the same commercial inoculum yielded higher levels of glucose (Bona et al., 2016). The synthesis of fruits amino acids is favorably impacted by the beneficial microorganisms. Mycorrhizal cherry tomatoes showed an increase in valine, isoleucine, leucine, and lysine content in the fruits (Carillo et al., 2020). Todeschini et al. (2018) revealed that mycorrhizal inoculation can also differentially affect acid production in a strain-dependent manner. In fact, *F. mosseae* significantly affected total organic acid and citric acid content, while *R. irregularis* and *S. viscosum* altered the concentrations of ascorbic, malic, and fumaric acids. The dual inoculation of AMF and PGPB altered tomato fruit VCs production, indicating that the synergistic effect of both microorganisms is important in determining the sweet-fruity taste and flavor (Todeschini et al., 2018). Compared to the single inoculation, the dual inoculation significantly enhanced the total phenolic compounds and flavonoid levels in spinach (Khalid et al., 2017). In this vein, the production and quantity of anthocyanins in strawberry fruits were enhanced after the application of a mixture of *Glomus* sp. and *Pseudomonas* sp. strains (Lingua et al., 2013). Metabolic profiling revealed increased sugars, acids, and multiple secondary metabolites levels following

AMF + PGPB inoculation. These combinations, however, did not induce the same effects, and fruit concentration of some elements and/or volatilome profile can be affected by the presence of specific beneficial soil microorganisms. For instance, Todeschini et al. (2018) revealed that fruits from each microbial strain were different and this can result in unique organoleptic and qualitative characteristics. In fact, the combined application of *F. mosseae* and *P. fluorescens* Pf4 produced sweeter fruit, while the dual application of *R. irregularis* and *Pseudomonas* sp. 5Vm1K induced low-acid fruits. The comparison studies above provide a demonstration of the differences between strains within the same species, indicating that the use of the right strain (or right combination) matters and could help boost plant growth and ultimately, is more likely to increase crop yield and/or quality in sustainable agriculture (Turrini et al., 2018; Plouznikoff et al., 2019).

## 4. Horticultural microbiome in light of holo-omics

### 4.1. Implementing the holo-omics approach in horticulture

A growing number of studies adopted "omics" and holo-omic approaches to study horticultural plant–microbes interaction (Table 2). The implementation of the holo-omics approach in horticulture required the use of a variety of methodological assets within different experimental setups with a need for diverse statistical and analytical approaches. Research depends on targeted approaches such as targeted RNA sequencing, amplicon sequencing, and western blot to link the host and the microbiota domains. Yet, untargeted approaches including shotgun DNA sequencing, shotgun proteomics, and shotgun metabolomics are increasingly completing and still used instead of targeted approaches since they provide a non-selective snapshot of the nucleotides, proteins, and metabolites present in the samples. Indeed, host/microbe-generated data from untargeted approaches seem to be more advantageous than those obtained from targeted approaches since the shotgun sequencing approach can generate metagenome-assembled genomes (MAGs) from metagenomic data and the construction of individual genomic profiles (Nyholm et al., 2020). In addition, Vieira-silva et al. (2021) confirm that steadily decreasing sequencing costs associated with improvements in computational methods are likely to promote the use of the shotgun sequencing approach.

TABLE 2 Examples of holo-omic studies in the microbial horticulture.

| Plant host | Sample type(s) | Approaches | References |
|---|---|---|---|
| Tomato, lettuce | Root | Shotgun metagenome, metatranscriptome, and host RNA-seq | Zolti et al. (2020) |
| Tomato | Root | Metatranscriptome and host RNA-seq | Chialva et al. (2020) |
| Cucumber | Root | Metagenomics, host RNA-seq, and metatranscriptomic | Ofek-Lalzar et al. (2014) |
| Peanut | Root, rhizosphere | Shotgun metagenome, metatranscriptome, and host RNA-seq | Li et al. (2019) |
| Mustard | Soil, rhizosphere, root | Ionomics, metabolomics, phenome, and 16S | Ichihashi et al. (2020) |
| Pea | Shoot | Host RNA-seq and metatranscriptome | Zhuang et al. (2012) |
| Canola | Shoot | Host RNA-seq and Metagenomics | Lowe et al. (2014) |
| Lettuce | Leaf | Host RNA-seq | De Cremer et al. (2013) |
| Potato | Leaf | Host genomic | Jupe et al. (2013) |
| | | Host RNA-seq | Gyetvai et al. (2012) and Gao et al. (2013) |
| | | Proteomics and transcriptomics | Ali et al. (2014) |
| Banana | Leaf | Host RNA-seq | Passos et al. (2013) |
| Grapevine | Root | Proteomic | Li et al. (2013) |
| | Leaf | Proteomic | Margaria et al. (2013) |
| Black gram | Fruit | Metabolomic | Hong et al. (2012) |
| | Leaf | Proteomic | Kundu et al. (2013) |
| Tomato | Leaf | Metabolomic and proteomic | Parker et al. (2013) |
| Kiwi | Shoot | Proteomic | Petriccione et al. (2013) |
| Potato | Leat and shoot | Metabolomic | Yogendra et al. (2015) |
| Soybean | Root and shoot | Proteomic | Delmotte et al. (2014) |
| | Root | Metabolomic | Aliferis et al. (2014) and Scandiani et al. (2015) |

The construction of high-dimensional data is the first step in implementing a complete holo-omics approach with horticultural host/microbe multiple-omics layers. According to the objectives of the research, the obtained data from each study sample could include genomic, transcriptomic, proteomic, and/or metabolomic measurements. For instance, millions of genes, thousands of gene orthologs, or hundreds of MAGs may be employed to characterize the microbiota. As a result, the huge amount of information and the multidimensionality of the generated data is challenging classic statistical methods including linear models and correlation-based methods. To reduce the complexity of the generated data, several authors suggest the reduction of dimensionality. For this purpose, Alberdi et al. (2022) proposed gathering MAGs following taxonomy or ecological guilds, and Ayesha et al. (2020) suggested clustering genes according to their functional properties. While this dimensionality reduction abridges analyses and diminishes computational complexity, it may induce pertinent data loss Ayesha et al. (2020).

The first studies in holo-genomics identified correlations among hosts and associated microbes using association analysis methods such as genome-wide association studies (GWASs). This approach associated precise loci in the host genome with the occurrence of beneficial/pathogenic microorganisms (Batstone et al., 2022; Demirjian et al., 2022). Similar methods were applied to study epigenomes (Zhang et al., 2023), proteomes (Zancarini et al., 2021), and metabolomes (Deng et al., 2021). Metagenome-wide association studies (MGWASs) were developed from GWASs to link specific loci in the metagenome to specific characters of the host phenotype (Ayesha et al., 2020). To date, the main applied methods to gather multi-omics data from host and microbiome domains were based on traditional statistical models including general linear and linear mixed methods in GWASs and MGWASs (Ayesha et al., 2020; Nyholm et al., 2020). The used models are frequently hindered by the complex dimensionality of the metagenomic data, which suggests the development of specific models to manage the complexity of holo-omics data (Xu L. et al., 2021).

To make progress in the holo-omics approach and overcome the association analyses issue, Limborg et al. (2018) developed a two steps methodological framework to expose the implemented mechanisms during host-microbiome interactions that modulate host phenotype variation. During the first step, an initial association is performed based on GWAS and MGWAS analysis to identify variants (SNPs) inside the genome and metagenome (e.g., amplicon sequence variants, MAGs, operational taxonomic units, or genes) related to specific host phenotypes. In the second step, the interactions between the associated GWAS variants and other-omic levels are investigated, resulting in the identification of the main molecular features orchestrating the pathway from host genotype to phenotype. Although the two-step method allows us to drill down into the interactions among the diverse-omic levels that impact host phenotype, the efficiency of the GWAS, carried out in the first step, in identifying causal variants still limits the number of interactions that should be cross-examined. The integrated inference by leveraging different-omics big data is challenging, and the development of computational methods in this field has been hindered by the inherent complexity of holo-omics and the biological process underlying them. So far, integrating various-omics datasets is based on different approaches including regularized regression-based methods (Pan, 2021), network-based approaches (Xiao et al., 2022), or other specialty tools (Abbott et al., 2021). None of these approaches, however, were developed to analyze metagenomic, metatranscriptomic, or metametabolomic data.

## 4.2. Experimental setups of holo-omics studies in microbial horticulture

Many decisive considerations should be taken into account to obtain meaningful and precise data from holo-omics-related microbiome studies (Nyholm et al., 2020; Xu L. et al., 2021). The first consideration is the reflected choice of the type of study. Longitudinal studies (studies with sampling occurring throughout horticultural plant development, but not permanently from the same plant host) present substantial benefits for holo-omic research in comparison to the end-point studies. During microbiome end-point experiments, data are collected at a single defined time point in the experiment to explore the alterations of microbial communities under diverse treatments. Yet, choosing a suitable time point is challenging since there is frequently slight or no *a priori* information about when host and microbiome interactions will happen. In contrast, longitudinal studies aim to assess the evolution of the microbiome over time. These studies allow for a type of pseudo-replication as patterns recorded at several time points are most probably the consequence of actual biological processes. Further, longitudinal experiments improve the possibility of identifying modifications that occur exclusively during a certain period after treatment. As already stated in this review, samples gathered at a single randomly determined time point could miss the key treatment-dependent variations occurring outside the chosen temporal frame.

In addition, a longitudinal approach may help detect correlations across data types that are influenced by a delay of time (Chen et al., 2022). Signal transduction and decoding among host and microorganisms may be time-consuming (Pan, 2021; Xiao et al., 2022) as can the delay between transcriptional shifts and downstream changes affecting the biosynthesis of proteins and metabolites in the host (Jamil et al., 2020). Temporal delay is anticipated to have an even greater influence on microbiome composition and abundance, as well as the development of macroscopic host phenotypes. Finally, in orthogonal datasets, a longitudinal design may aid in the development of a clear hypothesis for the interconnection between associated characteristics. However, the longitudinal approach for holo-omics studies is constrained by the requirement of multiple rounds of sampling, effective scheduling of the sample collection timing to avoid the introduction of confusing variables (i.e., circadian variations) (Hubbard et al., 2018), abiotic factors, diurnal variations, and downstream statistical analyses. Indeed, several host-related data types, e.g., transcriptomics, are influenced by circadian variations and will need samples to be gathered in a restricted window at a set time of day during the experimental design when collecting huge numbers of samples, particularly in the field (Xu L. et al., 2021). While developing integrated holo-omics research, it is necessary to take into account the sample and sampling procedure restrictions. For instance, the compatibility of each gathered sample type for certain required data types should be considered, which may need changes to the sampling method in some circumstances. Phyllosphere microbiome samples would include more DNA, RNA, and proteins derived from the horticultural plant than from the microorganisms. Therefore, some microbial methods may be impossible to perform without removing horticultural plant-derived contamination. When an environment presents low microbial biomass, such as droughted sandy soils, a higher number of samples must be collected for the extraction of nucleic acids. Furthermore, collection methods or sampling time may differ following the horticultural plant compartments, which may have unintended consequences for sample viability and data results, particularly for -omics approaches owing to their high-sensitivity to time and temperature.

A thorough examination of what data type combinations are most achievable and appropriate for the system under study, the objectives of the study, and available resources for the project are required (Lucaciu et al., 2019). For instance, holo-omics could be more difficult in non-model plants (e.g., horticultural crops) than in other host species due to the presence of various organelles, integration, and interpretation of incomplete genomes, high metabolic diversity, and complicated interaction links with pathogens and symbionts at the same time (Jamil et al., 2020). It is worth mentioning that holo-omics designs for deciphering plant-microbiome interactions are quite expensive to implement owing to the integration of multi-omics approaches, specifically shotgun metagenomics and metatranscriptomics remain highly expensive, whereas others (i.e., amplicon analysis) can cost one to two orders of magnitude less per sample. Before conducting holo-omic research, focused pilot surveys, with less expensive techniques or limited sampling possibility, are highly recommended to determine whether the experimental factors in question have a significant impact on microbial community dynamics, warranting further holo-omic investigation. This will also allow preliminary system evaluations to be performed without requiring broad technological and biological knowledge.

Developing staging within holo-omic investigations in horticultural-microbes interaction, in which procedures require a larger investment, are deployed later and may reduce resource expenditure in longitudinal designs by selecting crucial periods to focus on less expensive early datasets. However, not all data types are equally suitable to this method; certain sample types require instant or quick analyses (RNA, metabolites), while others (DNA) may be retained for considerably longer periods for subsequent use.

## 4.3. Integrated multi-omics for deciphering horticultural-microbiome interactions

The emergence of -omics technologies, such as genomics, transcriptomics, proteomics, metabolomics, lipidomics, hormonomics, and ionomics has permitted to identify components associated with plant-microbe interactions including molecular regulatory circuitries, how influential and important horticultural microbiomes play in plant fitness, plant disease, (a)-biotic stress susceptibility/tolerance, soil health, multi-organismal communication, and nutrient transfer and cycling, thus underpinning factors paving the way to harnessing the power of the microbiome to boost productivity and quality of horticultural crops.

With continual improvements, the integrated study of the genetic features of a horticultural host and its associated microbes is becoming more feasible, though still underdeveloped, approach to understanding horticultural holobionts. The combination of host and microbial genomic and transcriptomic information is critically important to improving our understanding of the plant holobiont (Figure 2). Yet, the microbial genetics contribution in holobionts is still difficult to assess owing to the vast majority of microbes lacking reference genomes. Across the complex landscape of studying horticultural–microbe interactions, transcriptomics only provides information on expressed gene levels and does not provide specifics on post-translational shifts, which are supplied by the proteomic method. Meanwhile, metabolites are the end products of biological activities supplied by the metabolomics platform. As a result, investigations are being conducted using a mix of -omics methodologies, which aids in the construction of bridges connecting all elements of cellular changes. This aids in the precise understanding of the complicated dynamics of cellular systems in both partners during plant-microbe interactions.

This section gives an overview of the application/integration of -omics techniques of what has been successfully achieved in microbial horticulture studies (Table 2). For instance, *Bradyrhizobium japonicum* bacteroid metabolism in soya bean root nodules was investigated using proteomics and transcriptomics datasets (Delmotte et al., 2014). A considerable number of proteins related to various forms of bacterial metabolism that were not previously thought to be present during symbiosis were revealed. Transcriptome and proteome data of potato during compatible and incompatible interactions with *Phytophthora infestans* (Ali et al., 2014) revealed the de-regulation of over 17,000 transcripts and 1,000 expressed proteins. Kunitz-like protease inhibitors, RCR3-like proteins, and several TFs were strictly activated during incompatible interactions. The change in transcript abundance corresponded to a change in half of the differentially abundant proteins. The protein and metabolite profiles of genetically near-resistant and susceptible tomato lines against tomato yellow leaf curl virus (TYLCV) infection were compared (Adi et al., 2012). In the susceptible line, antioxidant, pathogenesis-related, and wound-induced proteins were prominent, whereas protein and chemical chaperones preserved homeostasis. Carbon and nitrogen metabolisms were less influenced by resistant vs. susceptible ones. Recently, Chialva et al. (2020) sought to investigate whether host-targeted transcriptomics can identify the taxonomic and functional diversity of root microbiota by using an RNA-seq dataset generated for tomato plants growing on different native soils. The authors were able to reconstruct the microbial communities and grasp an overview of their functional diversity. By comparing the host transcriptome and the meta-transcriptome, the composition and metabolic activities of the microbiota seem to influence plant responses at the molecular level. Zolti et al. (2020) reported that microbial profiling can reveal stress signals that cannot be detected even when the host transcriptome is analyzed, providing a different method of assessing the *in-situ* conditions that host organisms encounter. The presence/absence and quantity of certain biological components may be precisely measured by applying and comparing transdisciplinary -omics techniques on horticultural plant-microbe interactions (Figure 3).

## 4.4. Big data integration and computational tools used in holo-omics

Different statistical methods can be used to analyze the metabarcoding data to determine which microbiome characteristics are most explanatory of the variation in the functional feature of interest. These explanatory features can be aggregated properties at the community, network layers (i.e., microbial network connectance or community alpha-diversity), presence or abundance of specific microbial taxa, or microbial functional groups (Barroso-Bergadà et al., 2021). According to Borokini et al. (2021), the PCNM eigenvectors method created for geographic distance matrices can be used to transform the compositional dissimilarity matrix between samples (community beta-diversity) into explanatory vectors. In the statistical model, the functional trait of interest will be considered as the dependent variable while the microbiome characteristics and environmental factors will be considered as explanatory variables (i.e., drought tolerance, Cambon et al., 2022; yield, Asad et al., 2021; an example of paired samples, Pérez-Valera et al., 2020). The differential abundance analysis methods (Nearing et al., 2022) or pTITAN2 approach (Figary et al., 2022) can be used to determine which microbial taxa are the determinant components when the microbiome significantly influences the functional trait of interest. Moreover, deep learning or machine learning approaches may also be used (Xu et al., 2022). For instance, the Random Forest algorithm has been applied to find combinations of horticultural yield indicative microbial taxa (Yergeau et al., 2020). Structural equation models (SEM) can test

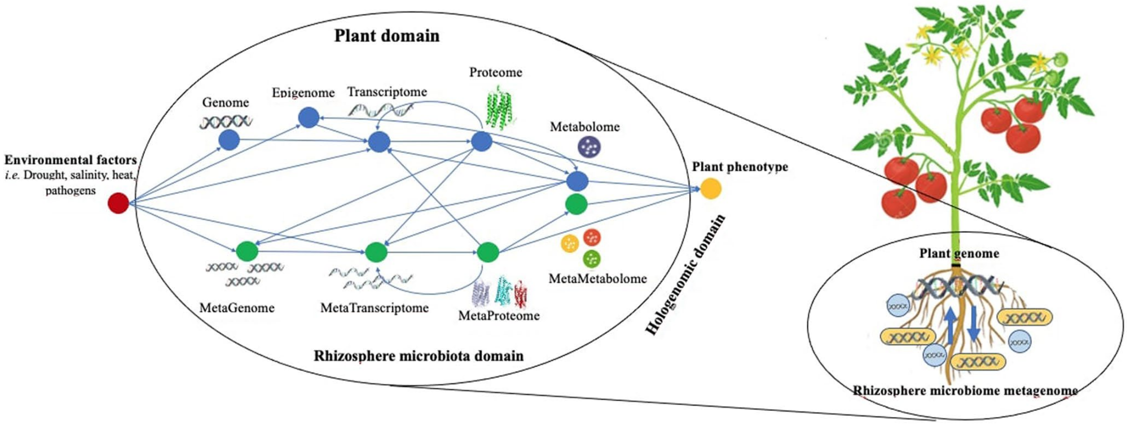

FIGURE 3
Exploring the diverse approaches and relationships in holo-omics for microbial horticulture.

particular hypotheses regarding the direct and indirect impacts of the explanatory factors (e.g., microbiome) on the functional trait of interest in horticultural crops (Xiao et al., 2021).

The wealth of -omics data generated by high-throughput methods is used by computational methods to infer networks of ecological interactions within microbial taxa, reveal the trophic and metabolic relationships underlying them, and examine how these relationships affect microbiome dynamics at various time scales. Metabarcoding has been utilized for a long time by microbial ecologists to discover ecological connections between microbial taxa. Data showed that patterns in relative shifts in frequency may reveal information about the structure of the ecological interaction network since interactions between microbial taxa in the past or present may have an impact on their frequencies (Kerdraon et al., 2019; Cobo-Díaz et al., 2022). This procedure is not simple since metabarcoding data are always compositional and can be skewed by amplification and sequencing abnormalities (Arribas et al., 2022). SparCC (Chen et al., 2022) was one of the methods used for estimating interaction networks from relative sequence counts. SparCC avoided the compositional effect by obtaining correlation using log-transformed components. Correlation-based measurements were refined by other tools like CCLasso (Matchado et al., 2021) or SPIEC-EASI (Liu et al., 2023). While MPLasso (Chen et al., 2022) incorporates the application of prior microbiological knowledge by data-mining of external sources of information, PLN (Chiquet et al., 2019) improves inference accuracy by utilizing sample covariance. Recently, HMSC was used to estimate microbial networks and incorporates variables on samples and taxa (Abrego et al., 2020; Fort et al., 2021). These methods could be rapidly employed on even rather big datasets and are resistant to noise in experimental data. The statistical computing powerhouse R integrates the majority of these methods, which makes handling data from various sources easy (Dohlman and Shen, 2019; Tikhonov et al., 2020). These tools allow us to connect the identified positive and negative interactions and the ecological mechanisms. Explainable machine learning can link inferred interaction networks to ecological mechanisms (Tamaddoni-Nezhad et al., 2021). Several horticultural crops-microbiome interactions (i.e., mutualism, competition) affect the frequency of different species in different ways (Song et al., 2020; Venkataram et al., 2023). With minimal to no human involvement in the interpretation stage, explainable machine learning translates these requirements into logical rules that explicitly infer ecological interactions (Barroso-Bergadà et al., 2021). Through a process that simultaneously detects interactions and categorizes them as mutualism, competition, commensalism, or amensalism, hypotheses of ecological interactions among taxa pairs could be generated. This straightforward method is especially useful for reconstructing microbial networks in previously unexplored ecosystems, where human interpretation expertise may be deficient.

## 5. Essential challenges facing the holo-omics approach in microbial horticulture and future perspective

The combined collection of horticultural host and microbial data is a potential strategy for uncovering plant-microbiome interactions by creating mechanism-based questions and testable hypotheses. However, analyzing holo-omics has its own set of challenges; the high cost of the used techniques in holo-omic approaches such as shotgun sequencing. In some circumstances, targeted sequencing or DNA microarray techniques can be more cost-effective than shallow shotgun sequencing, which can recover better taxonomic resolution at the same cost, while also offering direct insight regarding functioning (Hillmann et al., 2018). Researchers may be able to show a link between the presence of certain microbes and genetic or phenotypic features of the host plant using targeted techniques, but shotgun sequencing will frequently be required to achieve whole-genome resolution. The implementation of holo-omics methods needs a wide range of experts. Indeed, plant and microbial biologists will need statisticians and computational biologists for the identification and implementation of the approaches with suitable statistical precision (Joyce and Palsson, 2006). Additionally, the lack of completely established analytical methods constitutes another key problem, and there is a considerable need for the development of adapted bioinformatic assets. For the existing assets, choosing which one to use can be challenging since some will be dependent on the specific problems under inquiry, while others will be generalizable to all experiments and data types (Franzosa et al., 2015). There is generally significantly more software suited for multi-omic analysis of either the host or microbiome in isolation (Xia et al., 2010; Rohart et al., 2017; Chong et al., 2018; Rahnavard et al., 2018; Jamil et al., 2020; Subramanian et al., 2020) than tools for integrating information from both at the same time (Gui et al., 2020; Su et al., 2020). For instance, gNOMO is a bioinformatic channel particularly intended to process and analyze non-model organism materials at up to three meta-omics layers including metagenomics, metatranscriptomics, and metaproteomics in an integrated way (Muñoz-Benavent et al., 2020), although analysis does not support the host information. The development and implementation of statistical approaches that directly combine orthogonal datasets into a single analytical framework remain challenging. Currently, the majority of plant microbiome studies employing the holo-omic approach focus on discrete -omic analyses first, then combine results from various levels afterward based on existing data and prior knowledge (Limborg et al., 2018; Liu et al., 2021). While this method is very simple to execute, it may overlook key correlations between various-omics levels (Chen et al., 2012; Sun and Hu, 2016). Another area of importance is the development of methods to integrate holo-omic with non-omic analyses. López de Maturana et al. (2019) suggested a joint modeling approach to increase our understanding of the extent of the impact of host-microbes interaction that will exceed host performances to theoretically broader environmental and evolutionary shifts.

## 6. Conclusion

Holo-omics figures as a useful asset that may be utilized to increase our understanding of the basis of horticultural plant-microbiome interactions. Implementation of this approach will need the boost of developing alternative sequencing-data integration techniques with potential applications outside of plant biology. Following this approach would inspire plant and microbial biologists, ecologists, statisticians, and computational scientists to collaborate in creating combined experimental frameworks that involve multiple scientific views. This process of technical and conceptual harmonization of approaches throughout the scientific community is, possibly, the most difficult obstacle to a comprehensive understanding of the natural environment. A better understanding of the plant-microbiome interactions through the holo-omics approach will provide more potentialities to predict, mitigate, and promote horticulture productivity under a changing climate. It is necessary to investigate how much we can alter the plant microbiome to boost sustainable agricultural productivity while preserving the environment. The influence of host genetics on the research of microbiome diversity and structure has the potential to aid in the selection of microbiomes with particular features. There is a need for the integration of a holo-omics method that might link the relationship between the microbial communities, horticultural plant, and environmental function to obtain advanced fundamental knowledge about the specific host–microbe interaction under changing global climate, taking into account the community context.

## Author contributions

MB contributed to conceptualization, visualization, research design, and funding acquisition and revised and edited the review. MA-E-M drafted the first version of the manuscript with editorial input from MB. MB and MA-E-M designed the figures. All authors have read and agreed to the published version of the manuscript.

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## Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

## Publisher's note

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