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# Soil microbiota manipulation and its role in suppressing soil-borne plant pathogens in organic farming systems under the light of microbiome-assisted strategies

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**Abstract**

Soil microbiota plays a key role in suppressing soil-borne plant pathogens improving the natural soil suppressiveness. Microbiome disturbance triggers specific perturbation to change and shape the soil microbial communities' network for increasing suppression against phytopathogens and related diseases. Very important goals have been reached in manipulation of soil microbiota through agronomical practices based on soil pre-fumigation, organic amendment, crop rotation and intercropping. Nevertheless, to limit inconsistencies, drawbacks and failures related to soil microbiota disturbance, a detailed understanding of the microbiome shifts during its manipulation is needed under the light of the microbiome-assisted strategies. Next-generation sequencing often offers a better overview of the soil microbial communities during microbiomes manipulation, but sometime it does not provide information related to the highest taxonomic resolution of the soil microbial communities. This review work reports and discusses the most reliable findings in relation to a comprehensive understanding of soil microbiota and how its manipulation can improve suppression against soil-borne diseases in organic farming systems. Role and functionality of the soil microbiota in suppressing soil-borne pathogens affecting crops have been basically described in the first section of the paper. Characterization of the soil microbiomes network by high-throughput sequencing has been introduced in the second section. Some relevant findings by which soil microbiota manipulation can address the design of novel sustainable cropping systems to sustain crops' health without use (or reduced use) of synthetic fungicides and fumigants have been extensively presented and discussed in the third and fourth sections, respectively, under the light of the new microbiome-assisted strategies. Critical comparisons on the next-generation sequencing have been provided in the fifth section. Concluding remarks have been drawn in the last section.

**Keywords:** Agronomical practice, Amplicon sequencing, Biocontrol agent, Horticulture, Illumina, Soil microbiome disturbance

## Background

Plant diseases caused by soil-borne plant pathogens (filamentous fungi, oomycetes and bacteria) can be effectively suppressed by biotic and abiotic factors of the soil despite the presence of virulent pathogens and susceptible hosts [13]. Suppressiveness is a natural characteristic of soil that is accepted worldwide as a management strategy to create sustainable food production ensuring high agricultural productivity levels and low environmental footprints in intensive cropping systems under high pressure of pathogens [113]. Microbiota plays a key role in soil health-regulating dynamics of soil organic matter (SOM) and plant nutrient availability in agroecosystems [115,

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171]. Microbiota represents one of the most important factors that address the success or failure of a defense strategy based, for example, on addition of different levels of municipal waste compost under greenhouse condition for controlling soil-borne pathogens [162].

Combining agronomical practices based on compost and wood to vegetable grown under plastic tunnel, the soil resilience to soil-borne diseases can be consistently reduced over time [25]. However, for turning from a conducive soil into a suppressive ones, robust strategies that by-pass the natural resistance of the soil microbial communities manipulating core microbiomes are needed [82, 203, 208]. Soil microbiota manipulation by organic amendment has been applied since 1980s to reduce either pathogen inoculum or its virulence in conducive soil, although effectiveness of these approaches depends on the pathogen/host system [196]. Very important goals have been reached stimulating the specific disturbance of soil microbiota through agronomical practices focused to change and shape the microbial communities' network for increasing the natural suppressiveness of soil [208, 232]. Supplementation of beneficial exogenous microbiota provided by selected biological control agents (BCAs), organic amendments (OAs) and composts seemed to be promising strategies since 2000s for increasing suppression of conducive soils [40, 56, 94, 181, 210]. OAs from agro-industrial wastes restore soil fertility and enhance the suppressiveness of depleted soils. Efficiency of OAs in suppressing soil-borne plant diseases is generally lower in highly infested soils or in co-infested soils by different pathogens. For instance, robust strategies in fusaria and Verticillium wilts' management were needed if pathogen inoculum is excessive in the soil [114]. Organic amendment was employed as a part of a more complex strategical picture in controlling more soil-borne pathogens basing on their capability to induce disease suppression [15, 93, 127, 128, 156]. Authors documented that combining OAs with BCAs, more beneficial effects in suppressing soil-borne pathogens were obtained [184]. Organic amendment offers promising results in controlling soil-borne diseases also in combination with soil pre-fumigation, where a severe initial destroying of the soil wild microbiota followed by replacement with new microbiomes were both stimulated [194]. Combining soil pre-fumigation with application of bio-organic fertilizer induced pathogen inoculum reduction and disease suppression [193]. Nevertheless, if from one hand OAs can stimulate soil suppressiveness, on the other hand it can increase disease incidence and/or disease severity inducing soil to become conducive [24]. Despite some contradictory data, the integrated agricultural strategies based on the combined use of OAs and BCAs tailored composts and microbial consortia from disease-suppressive composts, and novel bio-organic fertilizers with organic additives (as silicon and chitin) were accepted worldwide for controlling multiple soil-borne pathogens [50, 56, 57, 97, 138, 238]. These practices induce rhizosphere health by beneficial alterations of its microbiota. To limit inconsistencies, drawbacks and failures related to soil microbiota disturbance, a detailed understanding of the microbiomes is needed under the light of microbiome-assisted strategies [152]. From one hand, authors have excellently reviewed how soil microbiota and tree crops health can be assessed in forest agroecosystems by next-generation sequencing (NGS), where high-throughput sequencing (HTS) offers a wide overview of the soil microbial communities under disturbance of their microbiomes more than traditional microbiological and biochemical-based methods [159]. On the other hand, very fewer papers regarding the critical revision of the impacts of agronomical practices on agroecosystem health for increasing disease suppression in horticultural farming systems have been found in the literature.

This review work reports and discusses the most reliable findings in relation to a comprehensive understanding of soil microbiota and how its manipulation can improve suppression against soil-borne diseases in organic farming systems. Role and functionality of the soil microbiota in suppressing soil-borne pathogens affecting crops were basically described in the first section of the paper. Characterization of the soil microbiomes network by high-throughput sequencing was introduced in the second section. Some relevant findings by which soil microbiota manipulation can address the design of novel sustainable cropping systems to sustain crops' health without use (or reduced use) of synthetic fungicides and fumigants were extensively presented and discussed under the light of the new microbiome-assisted strategies in the third and fourth sections, respectively. A critical comparison and some advancements on next-generation sequencing technology for agricultural purposes were provided and discussed in the fifth section. Concluding remarks were drawn in the last section.

## Role and functionality of the soil microbiota in suppressing soil-borne plant pathogens

Soil microbiota in suppressing soil-borne pathogens was studied since 1970s. Researches showed that suppressive soils can control pathogens, thus stimulating further studies in search of different types of disease-suppressive soils. The most recent works documented that microbiota of certain soils can create adverse environmental conditions for development of plant pathogens, so generating an additional suppressiveness level to those naturally present in the soils. Suppression is mainly

driven by the soil microbial community and SOM, and also its capacity to improve plant nutrition and vigor. Natural capacity to suppress pathogens has been studied in many disease-suppressive soils against the oomycetes and fungi *Pythium ultimum*, *Pythium irregulare*, *Pythium aphanidermatum*, *Phytophthora nicotianae*, *Phytophthora capsici*, *Phytophthora cinnamomi*, *Rhizoctonia solani* and *Fusarium oxysporum* [105]. The understanding of disease suppressive mechanisms is a crucial step to enhance the suppressive effect by manipulation of the soil microbiota. More specifically, the suppressive properties can be explained through combined antimicrobial actions exerted by molecules and microbes or mechanisms of antagonism among microbes and pathogens. The biological factors based on disease suppression generally include a combination of different actions. The mechanisms underlying the suppressive effect are primarily associated with the biological activity of soil microbiota which interacts with the SOM as well as the host plant. The most important factors are represented by the increased microbial activity [155] and fungistasis [27], enhanced soil structure [32], release of mineral nutrients during SOM decomposition [18], activation of competition for space and nutrients [170], elicitation of microbiostasis and hyperparasitism [92], release of diffusible antibiotic-like compounds [224] and activation of systemic disease-resistance in the host plant [33]. A "general suppression effect" is attributed to microbial biomass affecting more than one pathogen simultaneously where diversified mechanisms are activated offering a basal protection against a broad range of pathogens. Competition and production of antibiotics are involved in the general suppression mechanisms that do not easily transferable from one soil to another. Unlikely, a "specific suppression effect" is most easily transferable among soils because it is attributed to few microbial taxonomic groups active against one or few pathogens. Predation, parasitism and activation of disease resistance are involved in the specific suppression mechanisms. These two broad soil classes are not mutually exclusive in relation to their suppression models but often co-exist [105].

Biocontrol-based microbiota includes bacteria (*Bacillus*, *Paenibacillus* and *Pseudomonas*), actinomycetes (*Streptomyces*) and filamentous fungi (*Trichoderma*, *Fusarium*, *Gliocladium, Aspergillus* and *Penicillium*) that can trigger all mechanisms associated to disease suppression. In particular, microbiota of disease-suppressive compost contains Plant Growth-Promoting Rhizobacteria (PGPR) and non-pathogenic species of *Fusarium* and *Pythium* (i.e., *F. oxysporum* and *Pythium oligandrum*) which can improve plant growth and vegetative vigor, so rending host more resistant or tolerant to disease [39, 101]. Certain soils can even stimulate plant growth and vigor and/or induce nutrient availability and uptake for promoting crop productivity by a varied microbiota of fluorescent pseudomonads, species of *Bacillus*, *Paenibacillus*, actinomycetes and arbuscular mycorrhizal fungi (AMF) related to disease suppression. Fluorescent pseudomonads directly not only suppress pathogen in rhizosphere [29], but can also improve nutrient uptake [64] and produce plant growth-promoting substances [185]. *Paenibacillus brasilensis* can fix atmospheric nitrogen [216] and produce auxin [53] and cytokinin [206]. Species of *Bacillus*, actinomycetes and AMF can increase the soluble phosphorus uptake [58]. Species of AMF and *P. oligandrum* can induce anatomical and morphological change in root system [177], alter rhizosphere profile [161] and balance the root loss with new biomass [48]. Evidence suggests that soil capability to suppress plant pathogens primarily depends on capacity of soil to support microbial growth and bioactivity. The complex interactions among beneficial microbes, pathogens, SOM and physicochemical properties (as pH, electrical conductivity, macro–micronutrients content) are the focal points of the success (or failure) of disease-suppressive compost-amended soils [84].

Suppression of Fusarium wilts is triggered by restrict groups of microorganisms acting synergistically [2, 23, 124, 145]. Authors have highlighted that competition for nutrients is one of the primary mechanisms by which disease-suppressive soils are capable for controlling Fusarium diseases [3]. Soil suppressiveness to Fusarium wilt of tomato has been ascribed to carbon and iron competition between the pathogenic *F. oxysporum* isolates in rhizosphere with the non-pathogenic endophytic strain Fo47 of *F. oxysporum* and the wild populations of fluorescent pseudomonads, respectively [83, 130]. Production of siderophores is identified as the primary mechanism by which fluorescent pseudomonads suppress Fusarium wilt of tomato. Siderophores can chelate ferric ion ($Fe^{3+}$) from the soil into living cells of fluorescent pseudomonads such rendering iron unavailable for the pathogen. Siderophores play a crucial role in nutrient competition for the infection sites among pathogens and beneficial microorganisms [119]. In addition, other overall mechanisms include the production of secondary metabolites resulted to be toxic for pathogen. Particularly, the genera *Bacillus* and *Paenibacillus* are both highlighted as two among the most representatives "top-BCAs" in suppressing Fusarium wilt of tomato, regulating the microbial community of rhizosphere through production of toxic metabolites for increasing plant protection and growth stimulation (Aydi Ben [11]. *Paenibacillus polymyxa* NSY50 is reported as an effective top-BCA for controlling Fusarium wilt of cucumber [195]. A

direct inhibition on conidial germination and mycelium growth of plant pathogens induced by *Bacillus*, *Pseudomonas*, *Streptomyces*, *Trichoderma* and *Penicillium* has been documented against phytopathogenic fungi using compost water extract [72, 153, 196]. Actinobacteria resulted to be consistent in suppressive compost-amended soils where the increased population of beneficial microorganisms should be more competitive for the ecological niches, so leading to reduction in pathogen infection. The genus *Streptomyces* has been reported as the strongest producer of antibiotics and/or others toxic metabolites (over two-thirds of the natural antibiotics are produced by *Streptomyces* sp.) for inducing disease suppression and promoting plant growth in enhancing the beneficial bioactivity of plant-associated bacteria by direct and indirect mechanisms [117, 173]. The genus *Streptomyces* has been identified as an effective top-BCA against Fusarium wilt of cucumber and tomato being associated with the suppressive properties against bacterial and fungal wilts [157]. For instance, *Streptomyces violaceus-niger* XL-2 produces tubercidin, phosphalactomycin, candicidin and other antifungal compounds [100, 192]. *Streptomyces albospinus* CT205 can act alone [219] or synergistically with *Bacillus amyloliquefaciens* SN16-1 [217] to control Fusarium wilt of cucumber and tomato, respectively. Authors have studied the suppressive effect against tobacco bacterial wilts treating the soil with *B. amyloliquefaciens* ZM9 to enrich tobacco rhizosphere with new phyla associated to potential BCAs [226]. Suppression of *Fusarium oxysporum* f. sp. *melonis* in wilt-suppressive soils and composted green wastes-amended soils has been associated to populations of *Aspergillus*, *Streptomyces* and fluorescent *Pseudomonas* [43, 200]. Sewage sludge compost suppresses *F. oxysporum* f. sp. *melonis* wilt on tomato if combined with selected *Trichoderma asperellum* isolates [49]. Others authors instead concluded that species of *Penicillium* can act as top-BCAs against *Fusarium oxysporum* f. sp. *lycopersici* of tomato [99].

Likely to suppression of fusaria-related wilts, suppression of *V. dahliae* of cotton after soil supplementation with olive mill compost has been related to populations of *Actinomycetes* (mainly *Streptomyces*) [10]. Influence of different application rates and delivery methods on crop protection triggering various host defense mechanisms and rhizosphere populations of BCAs against *V. dahliae* wilts was studied by [5]. Suppression of *Verticillium dahliae* wilt of olive planting stocks by root-associated fluorescent pseudomonads was investigated by Mercado-Blanco et al. [160]. Suppression of *V. dahliae* of eggplant by supplementation with composted tomato waste in conducive soil has been attributed to biological action of *Bacillus* and fluorescent pseudomonads [112] or to systemic resistance induced by species of *Trichoderma* [95].

Suppression of Rhizoctonia diseases also resulted to be induced by restrict groups of microorganisms acting synergistically [212]. Suppression of Rhizoctonia damping-off, collar rot and root rot by soil amendment with green composts resulted to be most variable and unpredictable in many horticultural soil-less systems [45, 120, 122, 175]. The primary mechanism of action ascribed to *Trichoderma harzianum* in suppressing Rhizoctonia diseases is primarily related to cell wall degrading of the pathogen due to action of lytic enzymes such as β-1,3-glucanase, chitobiase, hydrolases and chitinase [59]. As *Trichoderma* recognizes the host, it attaches itself the host and afterward grows along the host hyphae or coils around them by secreting lytic enzymes [212]. It has been documented that chitinolytic enzymes from *T. harzianum* inhibit spore germination and germ tube elongation in plant pathogens [46, 88]. Capability of degrading cell walls or inactivating overwinter resistant propagules of *R. solani* has been attributed to action of *Trichoderma aureoviride* DY-59 and *Rhizopus microsporus* VS-9 [169]. As well, harzianic acid showed antibiotic activity against *R. solani* and *P. irregulare* [214], while strains of *Trichoderma* can produce non-volatile antibiotics that inhibit and predispose the host hyphae to infection before contact being occurred [212]. Authors have studied a significant suppressive potential of the purified active compounds from cultural filtrate of *Bacillus subtilis* subsp. *subtilis* C9 for using as BCA against *R. solani* on Zoysia grass, as well as plant growth promoter with the ability to trigger induced systemic resistance on grass [102].

Suppression of the oomycetes *Pythium* spp. and *Phytophthora* spp. causing damping-off and root rot is instead driven by nonspecific mechanisms determining a biological buffering power in soil rather than elicit specific suppressive responses [116]. Basal protection can be stimulated by soil supplementation with compost for enhancing the microbial activity [16]. Authors have documented that microbial biomass is able to suppress *P. ultimum*, *P. aphanidermatum*, and *P. irregulare* in cucumber, tomato, and melon, respectively; *P. nicotianae* in tomato; and *P. cinnamomi* in azalea [55] eliciting overall mechanisms related to SOM accumulation and optimization of its humification degree [44, 87, 147, 188]. Microbial consortia engage in a competition with the pathogens for space and nutrients, or resulting in antagonism among biocontrol-based microorganisms and pathogens. Moreover, authors highlighted an increased soil biological activity in disease suppression by an enhanced biological activities of the soil respiration rate, fluorescein diacetate hydrolysis, as well as several enzymatic activities (overall β-glucosidase, dehydrogenase, arylsulphatase and

alkaline phosphatise). In the case of soil supplemented with on-farm composted tomato residues, all biological activities resulted to be significantly increased and directly correlated to active microbial biomass for controlling Fusarium wilt in a tomato cropping system [174].

It is important to underline that plants grown in compost-amended soils are colonized by large variety of microorganisms from which several strains capable of inducing resistance *in planta* have been described [60, 136, 151, 222]. Once resistance is induced, abundance of the strains declines without affecting resistance [183], but such strains must be present above a certain threshold abundance for inducing valuable disease-resistance effects.

## Characterizing the soil microbiomes by NGS technology

Microbial genome sequencing has become main tool in the applied soil microbiology and ecology due to the increasing affordability and improvements in the speed of sequencing and quality of the data. This is a consequence of the advancement in NGS technologies that encompass both massively parallel and single-molecule sequencing by providing short and long sequencing reads, respectively. Short-read sequencing is highly accurate and produces read lengths of 100–300 bp which are afterward assembled into draft genomes since complete genomes cannot be generated from the short-reads obtained in a single sequence run, due to difficulties in assembling repetitive regions and large genomic rearrangements such as insertions, deletions and inversions. For many applications, including comparative genomics and phylogeny studies for soil microbial communities, complete genomes are required for determining complex genomic regions where longer reads are needed. Long-read sequencing produces read lengths from 10 to 50 Kb, but this is at the cost of higher error rates [139]. Currently, microbial DNA sequencing performed on Illumina, Ion Torrent, PacBio and Nanopore sequencing are well described [63, 191, 198]. Where technology is used depending on what the sequencing data are to be used for the amplicon throughput sequencing. Maximizing high throughput capabilities will result in low sequencing cost per sample. However, the number of samples sequenced in a single run is a function of the desired output and coverage, and this depends on the application. For example, single nucleotide polymorphism analysis of bacterial genomes can be performed with relatively low coverage meaning more DNA samples processed in a single sequencing run. In contrast, metagenomics analysis aimed at identifying all microbial genes present in a sample needs far greater coverage such as limiting the number of samples that can be processed in a single run and increasing the sequencing cost per sample.

NGS probes the species and functional diversity of the soil microbial communities without culture media through two main approaches: (i) amplicon sequencing (or metabarcoding), which involves the amplification and sequencing of specific marker gene families; and (ii) metagenomics, that includes the random shotgun sequencing of the whole genomic content of the microbial communities. It is important to differentiate among these two approaches that are sometime erroneously combined under the term metagenomics or often confuse among them [77]. Authors recommend of using the term "metabarcoding" when applying amplicon-based techniques and the term "metagenomics" only when untargeted shotgun sequencing is applied. However, both techniques eliminate the requirement for single colony isolation in a growing medium and have been highly successful for identifying and investigating uncultivable microorganisms [34]. In particular, amplicon-based microbial community profiling requires the isolation of DNA directly from the sample that can include a soil, compost, biochar, OAs and microbial consortia. Extracted DNA undergoes targeted PCR amplification of phylogenetic marker genes; commonly the 16S rRNA gene for Prokaryotes (Archaea and Bacteria), the 18S rRNA gene for Eukaryotes (Protists), and the internal transcribed spacer (ITS) of the ribosomal gene cluster sequences for other Eukaryotes (Yeast, Oomycetes and Fungi). Massive parallel sequencing of amplicons afterward generates an array of profiling information of the complex microbiota associated with the microbiome profiles. The sequencing data are then processed by dedicated bioinformatics pipelines to structure and annotate this raw information into knowledge. One of the most benefits of amplicon sequencing is the ability to follow the succession of microbial populations at various taxonomic levels over time, so allowing the differentiation of closely related microbial taxa using 16S rRNA gene sequence data for bacterial characterization [73]. If compared to random shotgun sequencing (metagenomics), metabarcoding provides a more cost-effective overview of the taxonomic composition of a sample. In fact shotgun metagenomics, generating sequencing information from the genetic material in a sample, permits the identification of individual strains and allows the prediction of functions encoded by microbial communities. This approach has allowed the measurement of population diversity levels in situ [14, 213] and the determination of specific genes in a habitat [211]. However, shotgun metagenomics provides an opportunity to survey the diversity and the dynamic abundance of microorganisms within a sample in a less-biased manner

than metabarcoding being used to improve culture-based enrichment methods [77]. Shotgun metagenomics can provide a valuable and speed view of the presence of genetic markers specifying species, serotype, virulence genes, etc., although these markers usually cannot be assigned to specific bacterial genomes due to the complexity of the metagenomic data [132, 235].

NGS resulted to be a better option for understanding the BCAs population shifts in composts [52, 118, 207]. The 16S rRNA gene has been a mainstay of the sequence-based analysis for decades [52]. Sequence analysis of smaller rRNA-subunit genes in bacteria (16S rRNA) from soil-extracted nucleic acids samples was PCR-amplified for microbiome analyses. Sequence analysis of larger fragments of the internal transcribed spacer 1 (ITS1) region of the ribosomal RNA (ITS rRNA) gene in fungi was amplified for microbiome analyses [178, 189]. Amplicon HTS have developed multiple integrated platforms of 1st and 2nd generation (Roche 454-pyrosequencing and Illumina/Solexa (or Illumina), respectively) with higher processing speed due to their high production capacity in a single sequencing run. Advancements based on the HTS platforms of 3rd and 4th generation (Ion Torrent/Ion Proton, PacBio and Oxford Nanopore, respectively) can be applied for deeper understanding the soil microbiota. Microbial rRNA gene sequences can be targeted using appropriate databases by comparing with known microorganisms [106]. For instance, taxonomic and phylogenetic affiliation of fungi can be based either on databases provided by the National Centre for Biotechnology Information (NCBI) or on most stable and reliable bioinformatics pipelines for soil fungal sequence-based identification (UNITE). Metagenomics libraries and databases for assessing the microbial community structure and functionality related to disease suppression have been developed [1, 47, 62] thanks to the implementation of new platforms [36, 37, 69–71, 144, 231]. Sequence Read Archive (SRA) database stores microbiome sequence data from the researchers' network as a new bio-project providing an international identification code number for each one. SRA helps to provide detailed information about the microbiota structure in terms of abundance, richness, diversity, evenness and composition, such allowing to identify potential unknown BCAs and functional genes involved in plant disease suppression during microbiome manipulation [66, 168, 180]. However, there are other ways of analyzing amplicon sequencing data. Important initiatives have been implemented by the Earth Microbiome Project (EMP) (http://www.earthmicrobiome.org) and the Genomic Standards Consortium (GSC). Both the projects provide a number of standards and guidelines for soil microbiome analyses which are helpful if the data from a single bio-project are compared with those of relevant studies in meta-analysis contexts. EMP and GSC both intend to standardize the pipelines and bioinformatics platforms giving recommendations and guidelines for performing the soil microbiome analyses [131].

## Soil microbiota disturbance for increasing soil disease suppression addresses the design of novel organic farming systems under the light of microbiome-assisted strategies

The four major questions to better understand the abundance, composition and diversity of the soil microbiome communities including biocontrol-based microbiomes are the following: (i) Who are there? (ii) How many are there? (iii) How are they different? and (iv) What are they doing? As a result of the most recent advancements in NGS, our understanding of the soil microbiomes may help to respond, at least partly, the first three questions. Due to their high reliability and sensitivity more than culture-based enrichment methods, amplicon sequencing represents a powerful toolbox to study the microbiome shifts in manipulated soils where a relevant number of new insights have been published over the last decades [165].

Soil microbiota manipulation has implemented a great number of studies related to suppression of plant pathogens adopting suitable agronomical practices for sustainable agroecosystems. Novel organic farming systems based on the reduced use (or without use) of synthetic chemicals (fungicides and fumigants) have been designed under the light of microbiome-assisted strategies [232]. At this regard, a recent work was aimed at determining the soil microbiota change using Illumina MiSeq sequencing. The BCA populations involved in soil disease suppression against *Fusarium oxysporum* f. sp. *cubense* of banana were tracked in both suppressive and conducive soils during the pathogen colonization [172]. The hypervariable V4 region of the bacterial 16S rRNA gene was amplified using the primer pair 520F/802R. The fungal ITS 1 region of the ITS gene was amplified using the primer pair ITS1F/ITS2R. The authors have found distinct microbiome patterns among the soils. Alpha- and Beta-diversity parameters for comparing the microbial diversity [141] resulted to be increased (or did not significantly changed) and decreased in the suppressive soil and conducive soil, respectively, so indicating that the microbiomes were notably different between the two soils. The microbiome network resulted more complex in a phylogenetic context showing a higher number of negative correlations between abundance of bacterial taxa and incidence (and severity) of Fusarium wilt in the suppressive soil than in those conducive. The authors identified the bacterial genera *Chryseolinea*, *Terrimonas*

and *Ohtaekwangia* as "new key taxa" that likely conferred an additional suppressiveness level to soil against Fusarium wilt of banana. The results of this study may help to guide efforts for targeting suitable cultivation systems which may lead to develop new and effective biocontrol-based tools against soil-borne diseases basing on the new potential BCAs.

To reveal new insights from soil microbiota manipulation that can be taken as future case study for increasing soil disease suppression, it is fundamentally important to address this paper toward the most reliable agronomical practices supported by microbiome-assisted strategies that use amplicon sequencing platforms. Particularly, the long-term supplementation of plant residues, alone or in combination with OAs and BCAs (Table 1); the combined treatment of soil pre-fumigation with application of composts, un-decomposed plant residues and biochar; and the microbiota recruitment techniques from compost into top soil (Tables 2 and 3) have been reported in literature as suitable tools.

Since application of OAs, BCAs and composts seems to be the most reliable strategies, it is due to recall that different typologies of OAs made of plant residues and green manure [90, 202], organic wastes [51, 209] and biochar [110, 129] have been studied as the effective means for recovering the fertility loss in depleted soils and in increasing disease-suppressiveness for conducive soils. The beneficial effects of soil suppressiveness in many host/pathogen systems by supplementation of OAs have been described [80, 96, 186] and the mechanisms to explain the beneficial effects of OAs on soil suppressiveness and plant health have been in-depth studied [91, 126, 179]. Nonetheless, OAs could have significant drawback effects that limit their applicability in agroecosystems because the suppressive capability can be inconsistent or difficult to predict [204]. On the other hand, compost is defined as "*a matured and stabilized organic matter naturally enriched during composting process with hydrophobic carbonaceous molecules and humic substances, such as humic and fulvic acids and umina, which make it a biomass more recalcitrant to further degradation*" (ISO/IEC 17025:2005). Compost derives from a biological oxidative process termed as "bio-composting" by which biodegradable organic substances are aerobically transformed into stable and humified substances after curing period. Composts are used in organic farming systems for their positive effects that induce on plant growth and crop protection (ISO/IEC 17025:2005). Bio-composting has been recognized as one of the most cost-effective biological treatments of the agricultural biomass being defined as "*a natural and sustainable biological process which transforms highly degradable organic biomasses into stabile and mature biomasses due to the action of endogenous microbiota*" (ISO/IEC 17025:2005). Bio-oxidative transformation is due to complex interactions between substrate and microbiota in the solid phase where the production of high temperature (ranging from 55 to 78 °C) for at least 5–7 consecutive days during the thermophilic phase represents a crucial step that allows biomass sanitization up to pathogen-free compost. Compost is technically defined as an organic amendment (or bio-fertilizer) that maintains and enhances the fertility and productivity of soils inducing a manipulation of the soil microbial communities [176, 187] under intensive farming systems [190]. Studies have demonstrated that compost addition not only provides important macro- and micronutrients in soil [68, 75, 81], but also increases soil organic carbon stock [89], improves soil structure [41] and water-holding capacity [38], enhances crop yield [237] and suppresses soil-borne pathogens [28, 54]. Authors have observed that soil microorganisms were more sensitive to compost addition in a significant manner using different application rates [8, 78], while other studies have showed that compost addition may have positive [17, 242], neutral [164] or even negative effects on soil microbial diversity and biological activity [150].

Table 4 shows that Roche 454-pyrosequencing has been used to study the crop yield improvement and soil fertility in an Italian rocket cropping system [26, 42]. Manipulating soil microbiomes by fumigation treatment in combination with application of straw, compost and biochar at different rates, frequencies and application times, these authors have obtained significant microbiota shifts in suppressing soil-borne rocket diseases. Other study has investigated the beneficial effects of the on-farm co-composted cow manure and maize straw at different application rates in a soybean cropping system [234]. Since the soil fungi community determines the agroecosystems' functionality being strongly influenced by the amendment with compost, these authors have studied the soil fungal community profiles of the new microbiome patterns using Illumina MiSeq sequencing in different soybean growing stages (seedling, flowering and harvesting) in relation to yield and quality improvement. Other study has investigated the soil microbial activity related to the bacterial and fungal microbiomes by Illumina in a pre-conditioned biochar-amended plant growth medium for enhancing the indigenous microbial community [104]. These authors have evaluated the maximum benefit for plant productivity and disease suppression against *P. aphanidermatum* damping-off in a cucumber cropping system. Other authors have focused their interest on the impact of manipulated rhizospheres in an organic farming system by long-term supplementation of plant residues in combination with BCAs [65]. They provided new insights on the beneficial effects regarding the SOM

**Table 1 Combining organic amendments with biocontrol agents for controlling soil-borne plant pathogens**

| Organic amendment | Biocontrol agent | Target pathogen (fungi and oomycetes) | Disease/host plant | References |
|---|---|---|---|---|
| Fungi | | | | |
| Wheat bran, peat moss | *Trichoderma harzianum* | *Sclerotium cepivorum* | White rot/Allium | Avila Miranda et al. [9] |
| Vermicompost, neem cake | *T. harzianum* | *Fusarium solani* f. sp. *melongeneae* | Fusarium wilt/Eggplant | Bhadauria et al. [20] |
| Vineyard pruning waste | *T. harzianum* | *Fusarium oxysporum* f. sp. *melonis* | Fusarium wilt/Melon | Blaya et al. [23] |
| Cow dung | *T. harzianum* | *F. oxysporum*<br>*Sclerotium rolfsii* | Foot rot/Lentil | Hannan et al. [86] |
| Green compost from pig manure, rice straw, alcohol, vinegar | *Trichoderma harzianum* SQR T037 | *Fusarium oxysporum* f. sp. *cucumerinum* | Fusarium wilt/Cucumber | Yang et al. [233] |
| Fresh chicken manure | *Trichoderma asperellum*<br>*Trichoderma atroviridae* | *Macrophomina phaseolina* | Charcoal rot/Strawberry | Domínguez et al. [67] |
| Farm yard manure and poultry manure | *Trichoderma viridae* | *Pythium* sp., *Rhizoctonia solani*, *Phytophthora* sp., *Fusarium* sp. | Damping off/Tomato | Joshi et al. [111] |
| Green compost from cork, grape, olive marc, and spent mushroom | *T. asperellum* | *R. solani* | Damping-off/Cucumber | Trillas et al. [210] |
| Composted sawdust, potato waste, and rice straw | *T. harzianum*<br>*Penicillium oxalicum Chaetomium globosum* | *F. oxysporum* | Fusarium wilt/Legumes | Haggag and Saber [85] |
| Bacteria | | | | |
| Compost from pig manure, canola cake | *Bacillus subtilis* SQR 9 | *F. oxysporum* f. sp. *cucumerinum* | Fusarium wilt/Cucumber | Cao et al. [35] |
| Amino acid fertilizer from rapeseed meal fermentation, and compost from pig manure | *B. subtilis* | *Verticillium dahliae* | Verticillium wilt/Cotton | Lang et al. [123] |
| Amino acid fertilizer from rapeseed meal | *Bacillus pumilus* SQR-N43 | *R. solani* | Damping-off/Cucumber | Huang et al. [98] |
| Compost from pig manure, canola cake | *Bacillus amyloliquefaciens* W19 | *Fusarium oxysporum* f. sp. *cubense* | Fusarium wilt/Banana | Wang et al. [221] |
| Pig manure, rice straw | *B. amyloliquefaciens* | *Ralstonia solanacearum* | Bacterial wilt/Tomato | Wei et al. [223] |
| Farm yard manure, compost, poultry manure, press mud, vermicompost, and neem cake | *Pseudomonas fluorescens* | *Pythium aphanidermatum* | Damping off/Tomato | Jayaraj et al. [107] |
| Fungi + Bacteria | | | | |
| Neem cake, farm yard manure, and micronutrient | *T. viridae*<br>*P. fluorescens*<br>*B. subtilis* | *Lasiodiplodia theobromae* | Physic nut collar and root rot | Latha et al. [125] |
| Mustard oil cake | *P. fluorescens*<br>*Glomus sinuosum*<br>*Gigaspora albida* | *R. solani* | Root rot/Bean | Neeraj [167] |
| Olive mill waste | *B. amyloliquefaciens*<br>*Burkholderia cepacia* | *V. dahliae* | Verticillium wilt/Olive | Vitullo et al. [215] |
| Compost from pig manure, canola cake | *T. harzianum Paenibacillus polymyxa* | *Fusarium oxysporum* f. sp. *niveum* | Fusarium wilt/Watermelon | Wu et al. [227] |
| Commercial organic fertilizer made of compost from pig manure, canola cake | *P. polymyxa*<br>*B. subtilis*<br>*Penicillium* spp.<br>*Aspergillus* spp. | *F. oxysporum* f. sp. *melonis* | Fusarium wilt/Melon | Zhao et al. [239] |

**Table 2 Next-generation disease-suppressive composts collection**

| Compost item | Compost code | Feedstock: Agricultural waste and agro-industrial residues and co-product | Feedstock: Plant green-waste, Plant sludge | Feedstock: Organic fraction of municipal solid waste, cattle manure and other bio-wastes | Target pathogen (fungi and oomycetes) | Susceptible host |
|---|---|---|---|---|---|---|
| Green composts#1 | Com-A[a] | Defatted olive marc | Fennel waste | – | *Verticillium dahliae Rhizoctonia solani Phytophthora nicotianae Phythophthora cinnamomi Pythium ultimum Pythium irregulare* | Eggplant Bean, Pea Tomato Azalea Cucumber Melon |
| | Com-B[a] | Un-defatted olive marc | Artichoke waste | – | | |
| | Com-C[a] | Coffee ground | Celery waste + carrot waste | – | | |
| | Com-D[a] | Tea bag | Tomato waste + lettuce waste | – | | |
| Green composts#2 | Com-E[a] | Wood chip | Tomato waste + escarole waste | – | *V. dahliae R. solani P. nicotianae P. ultimum* | Eggplant Bean Tomato Cucumber |
| | Com-F[a] | Aspen chip | Artichoke waste + fennel waste | – | | |
| | Com-G[a] | Vineyard pruning wastes + vinery residues + wheat straw | Potato waste + pepper waste | – | | |
| Green composts#3 | Com-C1[b] | Vineyard pruning wastes | Pepper sludge + pepper waste | – | *P. nicotianae* | Pepper |
| | Com-C2[b] | Vineyard pruning wastes | Pepper waste + artichoke waste | – | *P. nicotianae* | Pepper |
| | Com-C3[b] | Vineyard pruning wastes | Pepper sludge + pepper waste + garlic waste + carrot waste + almond shells | – | *P. nicotianae* | Pepper |
| | Com-C4[b] | Vineyard pruning wastes + compost | Artichoke sludge + artichoke waste | – | *P. nicotianae* | Pepper |
| Traditional composts from municipal bio-waste | Com-H[a] | – | – | Urban bio-waste | *Fusarium oxysporum* f. sp. *melonis F. oxysporum* f. sp. *lycopersici F. oxysporum* f. sp. *basilici* | Melon Tomato Basil |
| | Com-I[a] | – | – | Wet bio-waste | | |
| | Com-L[a] | – | – | Cow manure + household waste | | |

[a] [55]

[b] [22]

quality and accumulation, *Pseudomonas* community structure and disease suppression under greenhouse condition using Illumina. Other authors have documented the disease-suppressive impact of new microbiome profiles after long-term supplementation of OAs [133]. Particularly, they observed significant microbiome changes using Illumina HiSeq sequencing that resulted to be very consistent in suppressing pepper blight disease by *P. capsici*. They demonstrated that suppression of pepper blight was primarily due to antagonistic action of populations of *Bacillus* spp. in rhizosphere during the recruitment process of beneficial microorganisms from pepper plant into top soil. Other authors have instead compared the different chemical properties and the microbiome shifts using Illumina in different rhizosphere samples coming from the *F. oxysporum*-non-infested soil, *F.*

**Table 3 Amplicon sequencing platforms for identifying the biocontrol-based microbiota of the composts showed in Table 2**

| Compost item | Suppressive model | Amplicon sequencing platform | Primer | References |
|---|---|---|---|---|
| Green composts#1 | Multi-suppressive (both general and specific) | Amplicon sequencing of the bacterial 16S rDNA gene and the fungal ITS1 and ITS2 regions of the ITS rDNA gene. *Trichoderma* is identified by sequencing the ITS1-5.8S-ITS2 gene regions of the rDNA | Multiple primer pairs sets for bacteria 8F/120R, 388F/534R, 968F/1073R and 8F/361R<br>Universal primer pairs sets for fungi ITS5F/ITS2R and ITS3F/ITS4R<br>Universal primer pairs sets for *Trichoderma*: ITS1F/ITS4R<br>Primer pairs for *Trichoderma harzianum*, *Trichoderma Asperellum* and *Trichoderma atroviride* Chit42-1a and Chit42-2a | De Corato et al. [55] |
| Green composts#2 | General | Amplicon sequencing of the bacterial 16S rDNA gene and the fungal ITS1 and ITS2 regions of the ITS rDNA gene. *Trichoderma* is identified by sequencing the ITS1-5.8S-ITS2 gene regions of the rDNA | Multiple primer pairs sets for bacteria 8F/120R, 388F/534R, 968F/1073R and 8F/361R<br>Universal primer pairs sets for fungi ITS5F/ITS2R and ITS3F/ITS4R<br>Universal primer pairs sets for *Trichoderma* ITS1F/ITS4R<br>Primer pairs for *Trichoderma harzianum*, *Trichoderma Asperellum* and *Trichoderma atroviride* Chit42-1a and Chit42-2a | De Corato et al. [55] |
| Green composts#3 | General | Amplicon sequencing of the bacterial 16S rRNA gene and the fungal ITS1 and ITS2 regions of the ITS rRNA gene using Ion Torrent PGM sequencing | Multiple primer pairs sets for bacteria 8F/120R, 388F/534R, 968F/1073R and 8F/361R<br>Universal primer pairs for fungi ITS5F/ITS2R and ITS3F/ITS4R | Blaya et al. [22] |
| Traditional composts from municipal biowaste | Specific | Amplicon sequencing of the bacterial 16S rDNA gene and the fungal ITS1 and ITS2 regions of the ITS rDNA gene. *Trichoderma* is identified by sequencing the ITS1-5.8S-ITS2 gene region of the rDNA | Multiple primer pairs sets for bacteria 8F/120R, 388F/534R, 968F/1073R and 8F/361R<br>Universal primer pairs sets for fungi ITS5F/ITS2R and ITS3F/ITS4R<br>Universal primer pairs sets for *Trichoderma* ITS1F/ITS4R<br>Primer pairs for *Trichoderma harzianum*, *Trichoderma asperellum* and *Trichoderma atroviride* Chit42-1a and Chit42-2a | De Corato et al. [55] |

*oxysporum*-infested soil and watermelon-waste-amended soil to assess the potential role of the new microbiome in plant health and Fusarium wilt suppression in a watermelon cropping system [158]. Other study has showed by Illumina the soil microbial communities' shifts either inducing a Rhizoctonia-disease-inoculum reduction or perturbing the agronomic traits of wheat crop by beneficial and detrimental interactions in the soil, respectively, where the microbial communities resulted to be significantly changed after inoculation of the *Streptomyces* biocontrol strains to wheat seeds [7]. Finally, as last relevant case study, it is due to underline the beneficial effects of the microbiota recruited from the rhizosphere of a soil amended with disease-suppressive green composts either on the plant fitness (vegetative growth and productivity) or on the root protection against Fusarium and Verticillium wilts in a tomato cropping system, although using the Terminal-Restriction Fragment Length Polymorphism (T-RFLP) rather than Illumina sequencing [6].

On the other hand, several agronomical practices as the land-use management, different tillage systems and different fertilization practices have also enhanced suppression against soil-borne pathogens (Table 4). At this regard, stability of the soil bacterial community along the seasonal changes, overall in spring and autumn under different land-use management in Mediterranean agroecosystems, have been assessed by T-RFLP [19]. Finally, to evaluate the fungal community shifts for suppressing fusaria root rot of wheat, more investigation on the impacts of different tillage systems (strip tillage vs. conservation tillage) and fertilization practices (intensive vs. extensive) in two crop rotation systems (winter wheat–maize vs. winter wheat–rapeseed) were established by Illumina in a long-term field trial [199].

**Table 4 Research works listed in chronological order where microbiome-assisted strategies are implemented by the high-throughput sequencing platforms for characterizing the soil microbiomes in sustainable agroecosystems**

| Research work | Amplicon sequencing platform | Primer | References |
|---|---|---|---|
| Soil bacterial community response to differences in agricultural management along with seasonal changes in a Mediterranean region | Terminal-restriction fragment Length polymorphism (T-RFLP) | Primer pair for the bacterial 16S rDNA gene: Universal bacterial primers P0 and P6 63F (5′-AGGCCTAACACATGCAAGTC-3′) 518R (5′-ATTACCGCGGCTGCTGG-3′) | Bevivino et al. [19] |
| Organic farming induces changes in soil microbiota that affect agroecosystem functions | Amplicon sequencing of the V1–V3 regions of the bacterial 16S rRNA gene (520 bp) and a portion of the eukaryotic 18S rRNA gene region (436 bp) using Roche 454-pyrosequencing | Universal primers for the V1–V3 regions of the 16S rRNA gene Primer pairs for the 18S rRNA gene portion: 580F (5′-ATTCCAKCTCCAAKAGCG-3′) 997R (5′-GACTACGAYGGTATCTIATC-3′) | Bonanomi et al. [26] |
| Organic amendment type and application frequency affect crop yields, soil, fertility, and microbiome composition | Amplicon sequencing of the V1–V3 regions of the bacterial 16S rRNA gene and a portion of the eukaryotic 18S rRNA gene region using Roche 454-pyrosequencing | Universal primers for the V1–V3 regions of the 16S rRNA gene Primer pairs for the 18S rRNA gene portion: 580F (5′-ATTCCAKCTCCAAKAGCG-3′) 997R (5′-GACTACGAYGGTATCTIATC-3′) | Cesarano et al. [42] |
| Rhizosphere microbiome recruited from a suppressive compost improves plant fitness and increases protection against vascular wilt pathogens of tomato | T-RFLP | Universal primer pairs for the fungal rDNA ITS gene region: ITS1F (5′-TCCGTAGGTGAACCTGCGG-3′) ITS4R (5′-TCCTCCGCTTATTGATATGA-3′) Primer pairs for the bacterial 16S rDNA gene: 27F (5′-AGAGTTTGATCMTGGCTCAG-3′) 907R (5′-CCGTCAATTCMTTTRAGTTT-3′) | Antoniou et al. [6] |
| Suppression of soil-borne *Fusarium* pathogens of peanut by intercropping with the medicinal herb *Atractylodes lancea* | Amplicon sequencing of the hypervariable V4 region of the bacterial 16S rRNA gene and the fungal ITS1 gene region using Roche 454-pyrosequencing | Universal primer pairs: ITS5F/ITS4R (for fungi) 515F/806R (for bacteria) | Li et al. [134] |
| Activating Biochar by manipulating the bacterial and fungal microbiome through pre-conditioning | Amplicon sequencing of the bacterial 16S rRNA gene and the fungal ITS1 gene region using Illumina MiSeq sequencing | Universal primer pair 515F/806R for bacteria Universal primer pair ITS1F/ITS2R for fungi | Jaiswal et al. [104] |
| Long-term coffee monoculture alters soil chemical properties and microbial communities | Amplicon sequencing of the V4 region of the bacterial 16S rRNA gene and the fungal ITS1 gene region using Illumina MiSeq sequencing | Universal primer pair for bacteria: 520F (5′-AYTGGGYDTAAAGNG-3′) 802R (5′-TACNVGGGTATCTAATCC-3′) Universal primer pair for fungi: ITS1F (5′-CTTGGTCATTTAGAGGAAGTAA-3′) ITS2R (5′-GCTGCGTTCTTCATCGATGC-3′) | Zhao et al. [241] |
| Fungal community profiles in agricultural soils of a long-term field trial under different tillage, fertilization and crop rotation conditions Analyzed by high-throughput its-amplicon Sequencing | Amplicon sequencing of the fungal ITS1 and ITS2 gene regions using Illumina MiSeq sequencing | Primer pair sets for the ITS1 region: ITS1F (5′-TAGAGGAAGTAAAAGTCGTAA-3′) and -ITS86R (5′-TTCAAAGATTCGATGATTCAC-3′) Primer pair sets for ITS2 region: ITS86F (5′-GTGAATCATCGAATCTTTGAA-3′) and ITS4 (5′-TCCTCCGCTTATTGATATGC-3′) | Sommermann et al. [199] |
| Response of fungal communities and co-occurrence network patterns to compost amendment in black soil of Northeast China | Amplicon sequencing of the fungal ITS2 gene region using Illumina MiSeq sequencing | Forward primer gITS7F containing a unique 12 nt barcode at the 5′ end for Miseq sequencing detection Reverse primer ITS4R | Yang et al. [234] |

**Table 4 (continued)**

| Research work | Amplicon sequencing platform | Primer | References |
|---|---|---|---|
| Long-term organic farming manipulated rhizospheric microbiome and *Bacillus* antagonism against pepper blight (*Phytophthora capsici*) | Amplicon sequencing of the bacterial 16S rRNA gene using Illumina HiSeq 2500 sequencing | Universal primer pair:<br>515F (5′-GTGCCAGCMGCCGCGGTAA-3′)<br>909R (5′-CCCCGYCAATTCMTTTRAGT-3′)<br>with a 12 nt unique barcode | Li et al. [133] |
| Soil acidification in continuously cropped tobacco alters bacterial community structure and diversity via the accumulation of phenolic acids | Amplicon sequencing of the V4 region of the bacterial 16S rDNA gene using Illumina HiSeq 2500 sequencing | Universal primer pair:<br>515F (5′-GTGCCAGCMGCCGCGG-3′)<br>806R (5′-GGACTACHVGGGTWTCTAAT-3′) | Bai et al. [12] |
| Decoding wheat endosphere–rhizosphere microbiomes in *Rhizoctonia solani*-infested soils challenged by *Streptomyces* biocontrol agents | Amplicon sequencing of the V3–V4 regions of the bacterial 16S rRNA gene and the fungal ITS1 gene region using Illumina MiSeq sequencing | Universal primer pair:<br>341F/806R (for bacterial community)<br>ITS1F/ITS2 (for fungal community) | Araujo et al. [7] |
| Impacts of long-term plant residue management on soil organic matter quality, *Pseudomonas* community structure, and disease suppressiveness | Amplicon sequencing of the bacterial 16S rRNA gene fragments by a nested PCR using Illumina MiSeq sequencing | Primer pair for the first nested PCR:<br>F311Ps (5′-CTGGTCTGAGAGGATGATCAGT-3′)<br>R1459Ps (5′-AATCACTCCGTGGTAACCGT-3′)<br>Primer pair for the second nested PCR:<br>341F (5′-CCTAYGGGRBGCASCAG-3′)<br>and 806R (5′-GGACTACNNGGGTATCTAAT-3′) | Dignam et al. [65] |
| Deciphering differences in the chemical and microbial characteristics of healthy and fusarium wilt-infected watermelon rhizosphere soils | Amplicon sequencing of the V4 region of the bacterial 16S rRNA gene and the fungal ITS gene region using Illumina MiSeq sequencing | Universal primer pairs:<br>515F/907R (for bacterial community)<br>ITS1/ITS2 (for fungal community) | Meng et al. [158] |
| Rhizosphere bacteria assembly derived from fumigation and organic amendment triggers the direct and indirect suppression of tomato bacterial wilt disease | Amplicon sequencing of the V4 region of the bacterial 16S rRNA gene and the fungal ITS1 gene region using Illumina MiSeq sequencing | Universal primer pairs:<br>520F/802R (for bacteria)<br>ITS1f/ITS2 (for fungi) | Deng et al. [61] |

## The best agronomical practices for increasing soil disease suppression by the new microbiome-assisted strategies

To the best agronomical practices for increasing soil disease suppression under the light of the new microbiome-assisted strategies, the underlying soil management items seemed to be the most reliable.

### Soil management by amendment with disease-suppressive compost

Soil management by amendment with tailored disease-suppressive composts from green wastes resulted to be a consolidated strategy that induces significant shifts of the soil microbiota toward beneficial consortia for effectively controlling soil-borne pathogens [45, 54, 149, 154]. This paper focusses its interest on the most recent findings related to a next-generation composts' collection (Table 2) coming from green sources (plant wastes, agro-industrial residues and agro-wastes) and wet biomass wastes (municipal organic solid waste and co-composted animal manure with household waste).

De Corato et al. [55] have determined abundance, richness and diversity, as well as relationships among the fungal and bacterial communities of composts by amplicon sequencing (Table 3). In general, differences in the taxonomic structure were related to feedstock composition. In particular, green composts from agro-wastes and agro-industrial co/by-products provided the most varied and complex microbiomes related to suppression of Rhizoctonia damping-off of bean and pea, Verticillium wilt of eggplant, Pythium damping-off of cucumber and melon, and Phytophthora root rot of tomato and azalea. Composts from differentiated municipal organic solid waste and co-composted cow manure with household waste were instead prevalently colonized by microbiota related to suppression of Fusarium wilt of melon, tomato and basil. The amplicons resulted affiliated to the genus *Trichoderma* in suppressing *R. solani* damping-off of bean and pea; *Aspergillus*, *Penicillium*, *Streptomyces* and fluorescent *Pseudomonas* in suppressing *F. oxysporum* wilt of melon, tomato and basil; *Bacillus* and fluorescent *Pseudomonas* in suppressing *V. dahliae* wilt of eggplant. Suppression of Pythium damping-off of cucumber and melon, and Phytophthora root rot of tomato and azalea was instead strictly correlated to the increased biological activity of the composts determined by the increased abundance, richness and diversity of the microbial consortia identified at *phylum* level (Fig. 1a, b). This study has demonstrated that amplicon sequencing resulted to be a reliable and faster approach for characterizing the fungal and bacterial microbiomes up to species level (only for certain genus) into a collection of disease-suppressive composts. In this study, fungal amplicons (Fig. 2a, b) were related to suppression of restrict groups of soil-borne pathogenic fungi. In particular, the increased population of *Trichoderma* identified sequencing the ITS1-5.8S-ITS2 gene regions of the rDNA [225] resulted to be consistent in green composts, as well as populations of *T. harzianum*, *T. asperellum* and *Trichoderma atroviride* identified by amplification of the chitinase gene region [4, 121]. Moreover, the increased population of *Mortierella* sp. was noticeable in the microbial communities associated with the suppression of Fusarium wilt of melon, tomato and basil. This finding was confirmed by previous molecular-based studies performed by Illumina revealing that Fusarium wilt of vanilla was predominantly suppressed by a significant abundance of *Mortierella* in soil [228]. The genus *Mortierella* has recently been considered as a key biotic factor for fusaria wilt suppression where the order *Mortierellales* is known as the primary indicator of disease suppression in vanilla [228]. Likely, bacterial amplicons (Fig. 2c) were related to suppression of specific soil-borne pathogenic fungi. Abundance of key taxa such as *Pseudomonadales* (overall fluorescent pseudomonads), *Bacillales* (overall species of *Bacillus* and *Paenibacillus*) and *Streptomycetales* (overall species of *Streptomyces*) conferring a stronger suppressiveness against phytopathogens resulted was consistent with composts. Amplicon sequencing was also used to evaluate abundance (Fig. 3a), richness (Fig. 3b) and diversity (Fig. 3c) of the fungal and bacterial communities in composts acting in synergism against soil-borne phytopathogens. A very rich and diversified microbiome, overall if compared to those revealed by microbial culture-based enrichment methods [57], was found in green compost.

Blaya et al. [22] have instead evaluated the microbial structure of disease-suppressive composts from green wastes (Table 2) showing different suppressiveness degrees to *P. nicotianae* in pepper using Ion Torrent sequencing (Table 3). Unlikely to the findings of De Corato et al. [55], although the microbiota of these disease-suppressive green composts has been identified up to genus level, at the most, it showed however higher correlations with the suppression attributes than traditional composts.

### Soil management by pre-fumigation combined with supplementation of OAs and bio-fertilizers

Soil management by pre-fumigation with eco-friendly molecules in combination with fortified bio-organic fertilizers (Table 4) is considered an innovative strategy that can trigger significant microbiota changes for effectively controlling soil-borne pathogens [61]. These authors have questioned that any efficient method was widely recognized for controlling and/or preventing bacteria wilt of

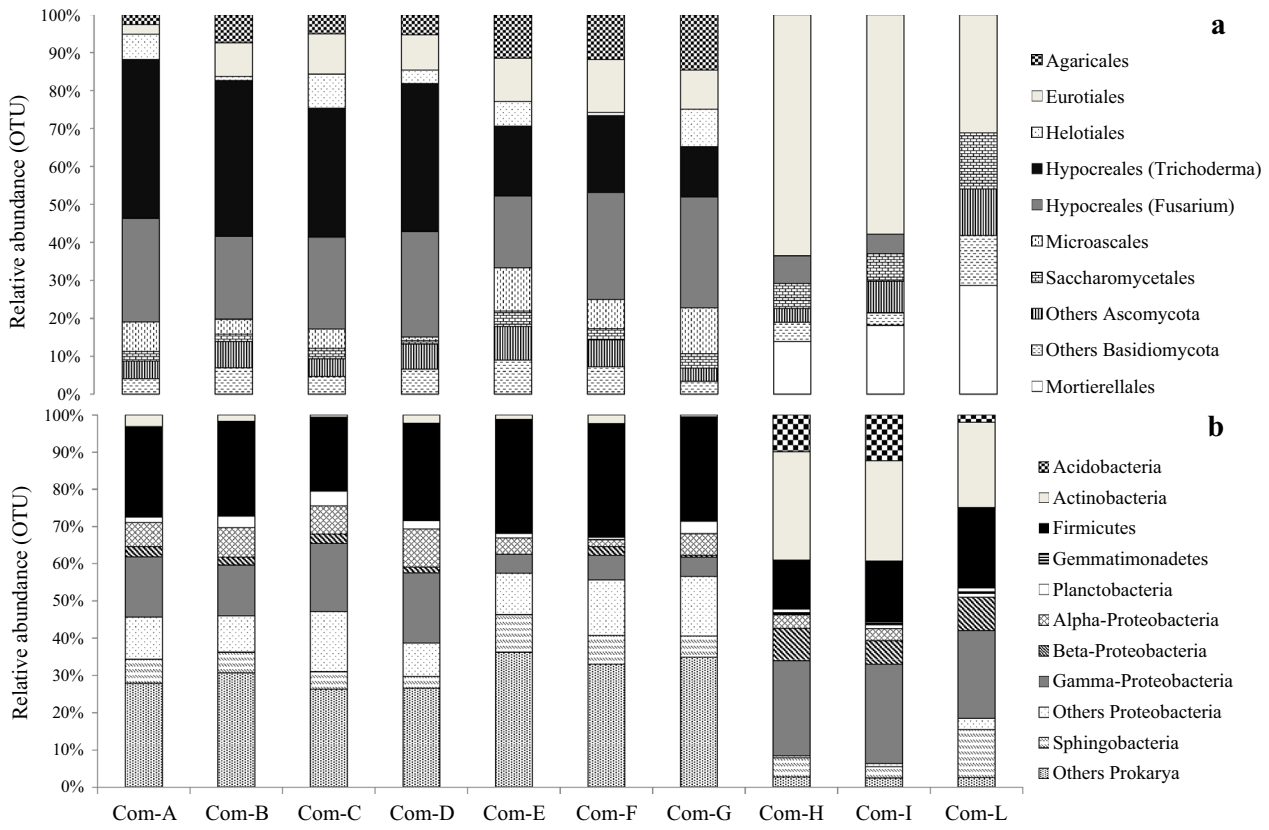


**Fig. 1** Typical compositional bars plot showing the relative abundance of **a** fungi and **b** bacteria, expressed as operational taxonomic units (OTUs) percentage, identified in 10 suppressive composts[a] at *phylum* and order levels (for fungi) and *phylum* and class levels (for bacteria) using amplicon sequencing of the ITS rDNA gene region and 16S rDNA gene, respectively (only abundances > 1% are displayed). [a]See Table 2 (source: De Corato et al. [55])

tomato caused by *Ralstonia solanacearum*. Treating of soil in a tomato field naturally affected by Ralstonia wilt using four types of treatment, and then evaluating the outcomes of disease incidence and severity in response to the treatments, these authors effectively control wilt disease without use of synthetic fumigants. All treatments had one of two bio-organic fertilizers, each with or without soil pre-fumigation. These authors found that soil pre-fumigation resulted in a very strong reduction of severity and incidence of the wilt disease. Afterward, they have gone through on the amplicon sequencing patterns to evaluate the soil microbial community structures before and after treatment using Illumina MiSeq sequencing. Basing on their findings, they presented an interesting hypothesis on how soil pre-fumigation, if combined with OAs, resulted in a microbiota restructuring by two main steps. In the first one, pre-fumigation destroys the wild microbiota; afterward, setting the further stages of soil colonization by use of OAs and bio-organic fertilizers, it can be reached more benefit for soil-supplying beneficial microbiota to suppress bacteria wilt. This study provides new insights based on the combined use of soil pre-fumigation with an eco-friendly nitrogen-based substance (ammonium bicarbonate) and compost-fortified bio-organic fertilizers to reduce disease incidence and severity of Ralstonia wilt. This combined strategy effectively controls tomato bacterial wilt disease despite a high abundance of *R. solanacearum* in soil. The impact of treatments on the soil microbiomes as well as the mechanism leading to disease suppression were both investigated. The combined treatment of pre-fumigation by ammonium bicarbonate with compost-fortified bio-organic fertilizers has led to significant change in the soil bacterial and fungal communities. Fumigation and organic amendment equally affected the microbiome variation in the rhizosphere at harvest time. Further, the shifts of the bacterial community in rhizosphere acted as a key factor for controlling Ralstonia wilt of tomato. In addition, the bacterial genera *Rhodanobacter*, *Terrimonas* and *Chitinophaga* identified in rhizosphere after

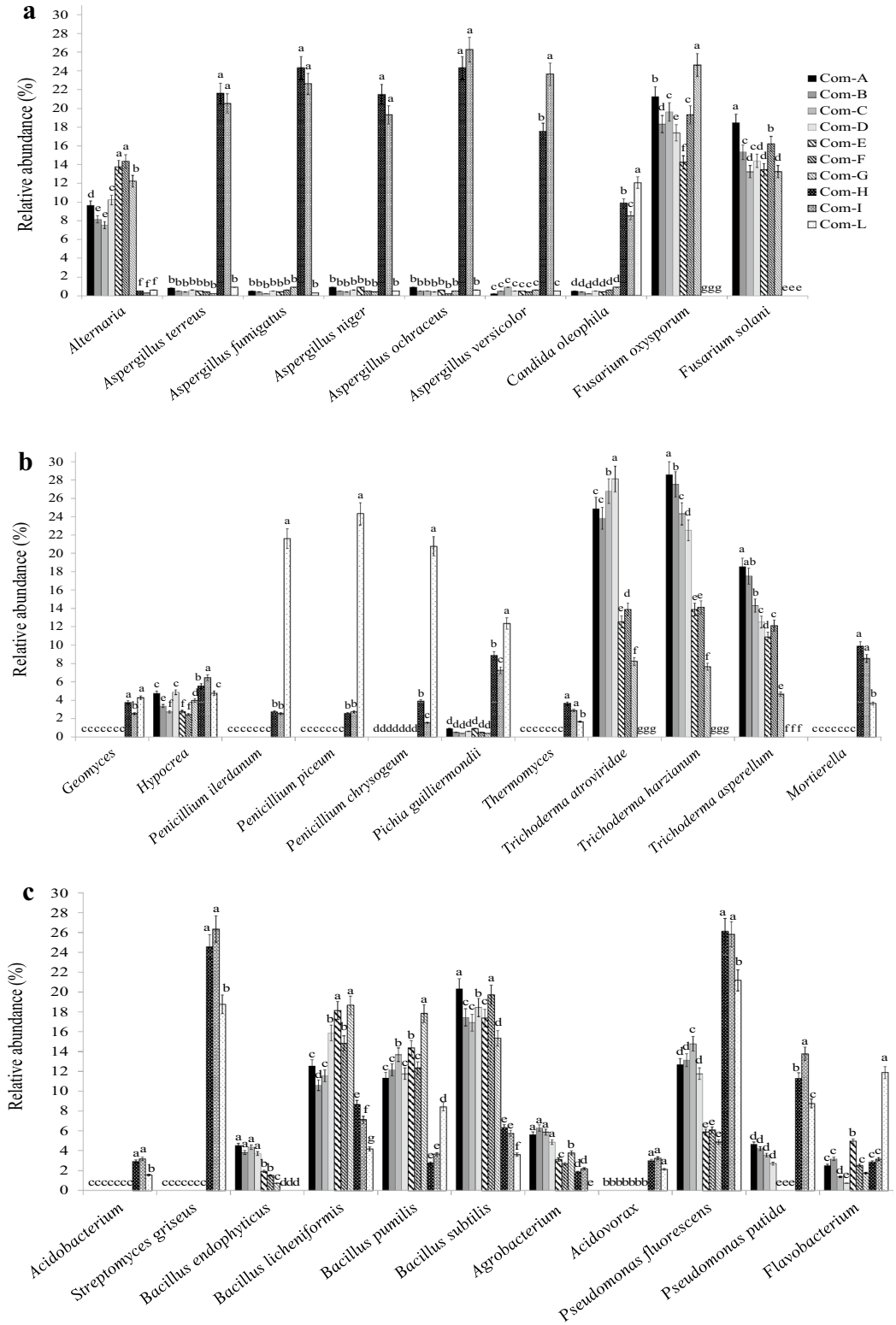


**Fig. 2** Typical bars chart showing the relative abundance of **a**, **b** fungi and **c** bacteria (expressed as high-quality sequences percentage) identified in 10 suppressive composts[a] at genus and species levels using amplicon sequencing of the ITS rDNA gene region and 16S rDNA gene, respectively (only abundances > 0.1% are displayed). [a]See Table 2 (source: De Corato et al. [55])

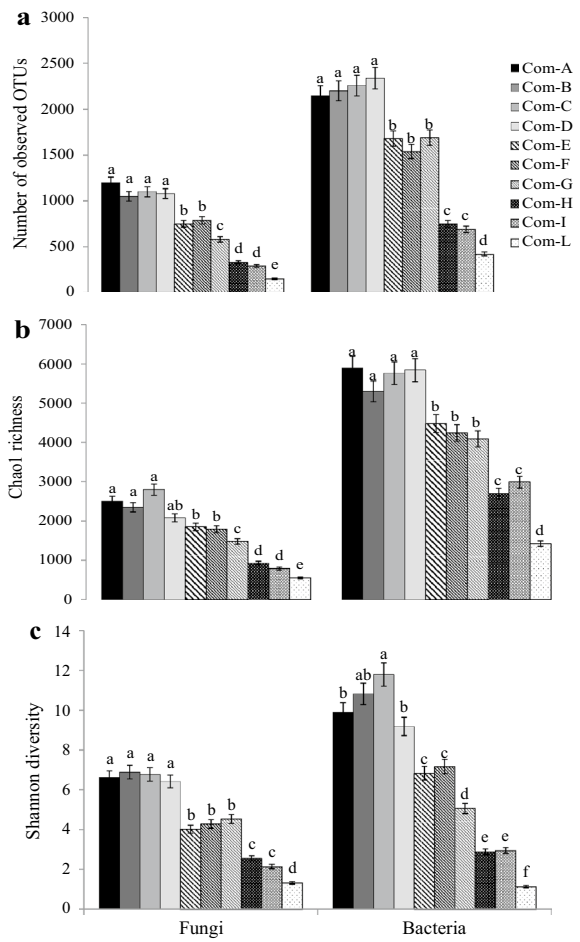


**Fig. 3** Typical bars chart showing the alpha-diversity indices of the fungal and bacterial communities in 10 suppressive composts[a] indicating **a** the number of observed OTUs, **b** Chao1 richness and **c** Shannon diversity using amplicon sequencing of the ITS rDNA gene region and 16S rDNA gene, respectively. [a]See Table 2 (source: De Corato et al. [55])

soil treatments were associated to new potential key taxa related to suppression of pathogenic soil-borne bacteria. Thus, fumigation and organic amendment determined disease suppression either directly, decreasing the abundance of *R. solanacearum* in soil, or indirectly, altering bacterial composition with the increased growth of bacterial taxa [61].

Despite these encouraging findings, other studies that employed BCAs, OAs and fortified bio-fertilizers to plant seeds and/or roots showed that these beneficial microorganisms do not last for long time (months or years) in the rhizosphere or within the plant microbiome, but only lasting for some weeks, at the least. The two main questions that should be raised by the users are the following: (i) Can any strategies be used to preserve relevant BCAs' abundance in the rhizosphere for longer times even if added artificially in multiple times? (ii) Can the protective effects against soil diseases persist for months, or even years, without further amendments? These are the two fundamental questions that should be taken account before adopting this integrated strategy on large scale according to Bonanomi et al. [24].

### Soil management by crop rotation and intercropping

Soil management by crop rotation and intercropping was both considered suitable strategies for effectively controlling soil-borne pathogens. More studies on the detrimental effects of monoculture-based systems on the microbiome patterns have been performed using Illumina MiSeq sequencing (Table 4). In this regard, authors have investigated how long-term coffee monoculture both affects the soil chemical properties and microbiota composition determining serious economic losses in China [241]. They found that a severe inhibition of the coffee plant growth and a significant yield decreasing were related with the increased abundance of fusaria wilts and fusaria-related pathogens, overall with the reduced abundance and diversity of the soil fungal and bacterial communities. Other authors have studied how long-term tobacco monocultures induced soil acidification due to accumulation of phenolic acids and severe alterations of the beneficial bacterial community in terms of abundance, structure and diversity using Illumina HiSeq sequencing [12]. In fact, it is well known that increasing the plant pathogens populations and decreasing the beneficial soil-derived microbes populations have determined severe detrimental effects in many soils managed under monoculture systems [135, 142, 146, 166].

Crop rotation can help to mitigate disease incidence and severity in many cropping systems by changing the soil fungal community structure along the rhizosphere profile [229]. Authors have studied, for example, the beneficial effects of the crop rotation cherry tomato-durum wheat vs. tomato monoculture on Fusarium wilt suppression and tomato shoot growth in an Italian tomato cropping system under open field condition by supplementation of disease-suppressive compost [54]. Overall analyzing abundance, composition, richness and diversity of fungal and bacterial communities by Illumina MiSeq sequencing including the understanding of the relationships among soil chemical parameters, disease suppression and the microbiomes, it has been established that certain microorganisms associated to biocontrol of *F. oxysporum* of tomato can consistently increase at the end of rotation period carried out for at least 4 consecutive years with durum wheat. Fluctuations of the soil microbial communities during the rotation tomato-wheat on Fusarium wilt suppression were consistently detected. The microbiome

shifts primarily depend on the adopted crop rotation system that may have a great potential for enrichment (or preservation) of the saprophytic microbial consortia supplied by compost and related to fusaria-related wilts suppression such as bacteria (*Bacillus, Paenibacillus* and *Pseudomonas*), actinomycetes (*Streptomyces*) and filamentous fungi (*Aspergillus*, *Penicillium* and *Mortierella*). These findings (unpublished observations) are in agreement with those of Liu et al. [137] in a Chinese cropping system based on the cherry tomato–rice rotation. Other authors have confirmed a significant decrease in incidence and severity of fusaria-related wilts for soils managed under different crop rotation systems. A relevant amount of data are available to well understand how the fungal and bacterial communities can operate in synergism to suppress diseases by several mechanisms [31, 140, 240]. Among them, the most accredited hypotheses about the beneficial effects of the crop rotation on, for example, soil suppression of *F. oxysporum* of tomato were related to their modulatory effects provoked by the tillage-crop rotations on the shifts of certain beneficial soil-derived bacteria and fungi associate to the roots of the host [108, 163, 205, 218, 230, 236].

Likely to crop rotation, intercropping can also help to mitigate disease incidence and severity in some cropping systems by changing the soil microbiome structure. Li et al. [133] have studied the suppressive role of volatiles and exudates from rhizome and root of the medicinal herb *Atractylodes lancea* on fungal and bacterial communities in controlling Fusarium root rot of peanut using Roche 454-pyrosequencing (Table 4). Intercropping peanut with *A. lancea* was significantly enhanced the richness and diversity of the fungal community in the peanut rhizosphere that coincided with the decline of Fusarium root rot and improvement of peanut growth in comparison to peanut monoculture. The authors suggested that intercropping peanut with *A. lancea* becomes effectively suppressed Fusarium diseases of peanut resulting in the increased peanut yield. They highlighted that *A. lancea* altered the fungal community composition in the peanut rhizosphere more than the bacterial community. Volatiles originating from *A. lancea* rhizome had more stimulating effects on the beneficial fungal community than those bacterial, thus Fusarium root rot of peanut was significantly suppressed. Exudates originating from *A. lancea* root had instead no apparent inhibitory effect on Fusarium root rot of peanut.

## Critical comparison and advancements of NGS technology for characterizating soil microbiota in agriculture

Comparing the amplicon HTS platforms in relation to the findings aforementioned, those of 1st and 2nd generation have given a series of processing data that allowed larger genomes sequencing in shorter time than traditional amplicon sequencing. In the "new era" of the MiSeq and HiSeq platforms, Illumina seemed to be more performing than Roche 454-pyrosequencing because it processes more operations (clonal amplification, genomic DNA sequencing and data analysis with base calling, alignment, variant calling and reporting) in a single sequencing run. However, a critical comparison of Illumina vs. Roche 454-pyrosequencing is done. A review study [143] concluded that the Roche 454 FLX + Titanium system has higher error rate in homo-polymer regions (three or more consecutive identical DNA bases) caused by accumulated light intensity variance than the Illumina Genome Analyzer (GA) II system [148, 182]. Moreover, up to 15% of the resulting sequences are represented by artifacts and false-positives [74]. Despite the substantial differences in read length and sequencing protocols, the two platforms provided a comparable overview of the community sampled [143]. In addition, more information concluded that Illumina is a better option vs. 454-pyrosequencing for different reasons (unpublished observations). First, although Illumina costs more to run the machine, the number of sequences processed by it is much greater vs. Roche 454. In fact, Illumina costs over 2–3 times Roche 454, but it gives an amount of data for over 10 times than Roche 454. Second, the quality filtering data in Illumina are simpler than Roche 454 and do not need worry about the artifacts coming from the homo-polymer runs. Third, if doing amplicon sequencing, the getting overlap between your forward and reverse sequences allows for a more stringent quality control. Fourth, Roche 454-pyrosequencing is discontinued from 2016. Thus, if researchers are looking for a long-term platform, Roche 454 should not be a better option; if researchers think to only need for a short time period of sequencing, Illumina should not be the best option because it requires a relevant amount of investment in getting laboratory protocols optimized in shorter time; if researcher groups are planning to do weekly or monthly a very much lot of amplicon sequencing runs, Illumina should be more long-lasting option. As last consideration, it can notice that an improved dual-indexing approach for multiplex 16S rRNA gene sequencing is available by Illumina MiSeq platform [76].

The third- and fourth-generation sequencing platforms have been developed for agricultural purposes only in the recent years. For soil microbiome studies, ion semiconductor sequencing performed by the Ion Torrent/Ion Proton platforms is a method of DNA sequencing-based on the detection of hydrogen ions (protons) that are released during the polymerization of DNA. Likely to Illumina, Ion Torrent is a method of "sequencing by synthesis" during which a complementary strand is built

based on the sequence of a template strand. This technology differs from Illumina in that no modified nucleotides or optics are used. Ion semiconductor sequencing includes different platforms as Ion Torrent sequencing, pH-mediated sequencing, silicon sequencing and semiconductor sequencing. Also, for soil microbiome studies, the Oxford Nanopore platform by mini flow cells (MinIon™) and PacBio are both based on ionic readings that potentially could become competitive due to their high capability to sequence up to 1000 kilobases per millisecond without the need of DNA amplification [30, 197]. Although these novel platforms at high-resolution level of phylogenetic microbial community profiling are potentially promising since they combine their easy use and portability with a massive data production, nonetheless they are less used than others because they still have too many sequencing errors. This could be a reason why they are not currently useful for metagenomics studies (personal communications). Table 5 provides a summary of the most commonly used HTS platforms for characterizing the soil microbiomes. Despite encouraging advancements, the researcher which currently uses Illumina and Ion Torrent can determine just the family and genus levels of microbiota, at the most, so excluding from their issues the species and strain levels. Nonetheless, Illumina seems to be the fastest approach for identifying fungal and bacterial consortia from soil, rhizosphere, compost, OAs, bio-fertilizer and biochar.

A recent work evaluated the possibility of sequencing the 16S rRNA gene for bacterial species and strain-level in microbiome analysis [109]. This study aimed at critically re-evaluating the potential use of the 16S gene to provide the highest taxonomic resolutions at species and strain levels. These authors demonstrated that targeting the 16S variable regions with short-read sequencing platforms cannot be achieved the same taxonomic resolution afforded by sequencing the entire gene. They affirmed that full-length sequencing platforms are sufficiently accurate to resolve subtle nucleotide substitutions (but not insertions or deletions) that exist between intragenomic copies of the 16S gene. They concluded that modern analysis approaches must necessarily account for intra-genomic variation between 16S gene copies. In particular, they demonstrated that appropriate treatment of full-length 16S intra-genomic copy variants has the potential to provide a better taxonomic resolution of bacterial communities at species and strain levels.

Moreover, it is due to underline that there are multiple primers at high coverage that cover a 100% similarity from different microbial species due to the lack of diversity in the partial gene sequence. For instance, there are conservative fragments in bacterial 16S rRNA genes and primers designed for 16S rDNA amplicons in metagenomics studies [220]. Researchers use multiple primer pairs that cover different area of the 16S in Illumina sequencing analysis of soil bacterial communities. The 16S rDNA gene has been amplified in many studies using the 8F/120R, F388/R534, F968/R1073 and 8F/R361 primer pairs for giving a better taxonomic resolution of the bacterial community at species level [6, 201]. Also, a better taxonomic resolution of fungal communities has been reached sequencing the ITS1 gene region by the ITS1/ITS4, ITS2/ITS5 and ITS3/ITS4 primer pairs that provided higher taxonomic resolution up to species level for characterizing fungal community [6, 225]. Moreover, ITS primers with an improved specificity for

**Table 5 Comparison of the most commonly used high-throughput sequencing platforms for characterizing the soil microbiomes. Source: Jagadeesan et al. [103]**

| Platform[a] | Generation | Sequencing technology | Read length | Output/run | Error rate | Example of use | Type of instrument and run time | Taxonomic resolution level |
|---|---|---|---|---|---|---|---|---|
| Illumina | Second generation | Sequencing by synthesis | Short reads 1 × 36 bp – 2 × 300 bp | 0.3–1000 Gb | Low | Variant calling | Benchtop 2–29 h | Low-resolution |
| Ion Torrent | Third generation | Sequencing by synthesis | Short reads 200–400 bp | 0.6–15 Gb | Low | Variant calling | Benchtop 2–4 h | Low-resolution |
| PacBio | Fourth generation | Single molecule sequencing by synthesis | Long reads up to 60 kb | 0.5–10 Gb | High | De novo assembly of small bacterial genomes and large genome finishing | Large scale 0.5–4 h | High-resolution |
| Oxford Nanopore | Fourth generation | Single molecule | Long reads up to 100 kb | 0.1–20 Gb | High | Complete genome of isolates and metagenomics | Portable 1 min–48 h | High-resolution |

[a] Roche 454-pyrosequencing (First-generation platform) is discontinued from 2016

basidiomycetes (overall mycorrhizae and rusts) are yet available since 1990s [79].

To fully describe role and functionality of the soil microbiota, it must be recalled that amplicon sequencing is not itself enough to understand the complex biological processes that take place within the soil [21]. The phylogenetic characterization of prokaryotic cells based on DNA extraction from soil does not reflect the real activity of soil microbiome since DNA may be extracted from dead or inactive cells. Moreover, the provided information did not strongly contribute to our understanding of the impact of different microbiomes in agroecosystems for various reasons. These main limitations can be summarized as follows: (i) higher cost for soil analyses and complex bioinformatics pipelines; (ii) huge heterogeneity in space and the complex statistical techniques required to grasp this variation; (iii) temporal dynamics of soil microbiome; (iv) concentration of products/substrates of the target process that often overlooks the levels of these compounds in soil that may depend on the biotic/abiotic processes; and (v) taking into account that data generated by HTS do not provide any information on the total abundances of the identified clades. Thus, general recommendations and current guidelines for soil microbiome analyses should be available worldwide [131, 165].

## Concluding remarks

Agroecosystems management is fundamental to ensure long-term persistence of ecosystem services under detrimental condition of the soils. Microbiota can increase the natural soil suppressiveness against soil-borne pathogens whenever soil properties and crop yields are progressively declining. Intensive cropping systems characterized by higher input of synthetic chemicals, lower SOM accumulation, scarce humification degree and frequent soil tillage are the primary reasons for soil depletion. Soil microbiota associated to BCAs is the key factor for plant health where more studies on soil microbiota disturbance by OAs, tailored microbe-based formulations, and BCAs' selected species/strains were reported since 2000s. Instead, very little attention has been paid on the ecological impact of beneficial microbial consortia recruited from compost, overall if associated with supplementation of exogenous BCAs of unknown origin. As well, little attention has been paid on the impact of crop rotation and intercropping, either alone or in combination with the soil pre-fumigation and compost/biochar supplementation. In this regard, the ecological roles of soil microbiota should be more in-depth elucidated in relation to a better understanding of the microbial community network inhabiting the soils.

Insights indicating what agronomical practices seemed to be the best approach to design novel cropping systems for increasing soil suppressiveness by microbiome-assisted management supported by NGS have been presented and critically discussed in this paper. The best agronomical practices for improving soil disease suppression under the light of new cropping systems can be implemented by use of tailored OAs and composts/biochar, and fortified bio-fertilizers that can shift wild microbiota of the soil toward beneficial microbial consortia based on disease suppression. In this regard, it can conclude that adopting tailored multi-suppressive composts in intensive horticultural cropping systems, if overall combined by crop rotation and intercropping with suitable crops (i.e., herbaceous medicinal species, rapeseed, rice, wheat, etc.) and soil pre-fumigation by eco-friendly molecules (i.e., ammonium bicarbonate or other nitrogen derivatives), can be reach the challenges in suppressing soil-borne diseases in sustainable agroecosystems.

The remaining open questions to a better understanding of the abundance, composition, richness, evenness and diversity of the biocontrol-based microbiota could be answered developing the best HTS platforms and bioinformatics pipelines basing on standardized analyses of the soil microbiomes. If the soil microbiomes can be quickly screened, more reliably characterized at the highest taxonomic resolution levels, and finally quantified in abundance, richness and diversity in shorter time, will be given in the near future useful ecosystem services for responding, at least partly, to the first three questions raised above. If from one hand it can conclude that Illumina can be still considered the best option for identifying soil microbial communities under disturbance of their microbiomes, on the other hand it can affirm that standardized procedures, recommendations and general guidelines for soil microbiome analyses should be urgently implemented. This review also aims to promote the use of NGS in organic agriculture highlighting the knowledge gaps and future research directions that need to augment the added-value generated from the application of NGS technology.

Concluding, it should be recalled again that the phylogenetic characterization of microbiota based on DNA analyses does not reflect the real biological activity of microbial community. In this perspective, the omics sciences combining the metagenomics, metatranscriptomics, meta-proteomics and metabolomics approaches provide an accurate understanding of the

whole microbial activities and the real physiological potential of the soil to suppress plant disease by plant-associated microbiota.

**Abbreviations**
AMF: Arbuscular mycorrhizal fungi; BCAs: Biological control agents; EMP: Earth microbiome project; GSC: Genomic standards consortium; HTS: High-throughput sequencing; ITS: Internal transcribed spacer; NCBI: National Centre for Biotechnology Information; NGS: Next-generation sequencing; OAs: Organic amendments; OTUs: Operational taxonomic units; PGPR: Plant Growth-Promoting Rhizobacteria; SOM: Soil organic matter; SRA: Sequence read archive; T-RFLP: Terminal-restriction fragment length polymorphism.

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## Publisher's Note