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Review article

High-throughput molecular technologies for unraveling the mystery of soil microbial community: challenges and future prospects

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ABSTRACT

Soil microbial communities play a crucial role in soil fertility, sustainability, and plant health. However, intensive agriculture with increasing chemical inputs and changing environments have influenced native soil microbial communities. Approaches have been developed to study the structure, diversity, and activity of soil microbes to better understand the biology and plant-microbe interactions in soils. Unfortunately, a good understanding of soil microbial community remains a challenge due to the complexity of community composition, interactions of the soil environment, and limitations of technologies, especially related to the functionality of some taxa rarely detected using conventional techniques. Culture-based methods have been shown unable and sometimes are biased for assessing soil microbial communities. To gain further knowledge, culture-independent methods relying on direct analysis of nucleic acids, proteins, and lipids are worth exploring. In recent years, metagenomics, metaproteomics, metatranscriptomics, and proteogenomics have been increasingly used in studying microbial ecology. In this review, we examined the importance of microbial community to soil quality, the mystery of rhizosphere and plant-microbe interactions, and the biodiversity and multi-trophic interactions that influence the soil structure and functionality. The impact of the cropping system and climate change on the soil microbial community was also explored. Importantly, progresses in molecular biology, especially in the development of high-throughput biotechnological tools, were extensively assessed for potential uses to decipher the diversity and dynamics of soil microbial communities, with the highlighted advantages/limitations.

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1. Introduction

Microbes, which have populated the Earth for over 3.5 billion years, are the most dominant living entities in nature, with the biosphere containing an estimated 4–6 $\times$ 10^{30} prokaryotic cells (Whitman et al., 1998). This microbial wealth is still poorly explored, and it is highly desired to better understand the biodiversity and ecology of soil microbial communities (Ahmad et al., 2011).

Bacterial populations have been frequently studied using various molecular biology methods. Indeed, the study through the isolation of bacterial strains using culture media, commonly known as *culturomics*, allows the identification of a very small proportion of bacterial species present in a given soil sample (Sarhan et al., 2019). Better knowledge of the microbial community is important to improve our understanding of the ecosystem, but it is also a challenging endeavor due to the difficulties of cultivating or directly observing some of the soil microorganisms. Consequently, many of these microbial communities are not yet well characterized (Jo et al., 2020).

Several studies have attempted to characterize the microbiome from agricultural ecosystems for a better understanding of soil microbial biodiversity. Since the composition of soil microbial community is influenced mainly by plant species and soil types, the interactions in the soil environment are highly complex, especially between plants and soil microbes (Wei et al., 2018).

Microorganisms play an important role in soil structure and organic matter recycling (Ahmad et al., 2011). The secretion of root exudates modulates the structure of the microbial community and its enzymatic activities, which provide important nutrients for plants through degradation and mineralization of soil organic matter (Andrianarisoa et al., 2010; Jacoby et al., 2017). Moreover, soil microorganisms are the main mediators of these chemical transformations during nutrient recycling, playing a fundamental role in the biogeochemical process (Dong et al., 2017; Falkowski et al., 2008).

The use of molecular technologies in microbial ecology research may be linked to the development of molecular phylogeny in the late '60s (Falkowski et al., 2008). Methods used for diversity analysis of microbial communities such as traditional cultural and non-cultural methods (i.e. Random Amplified Polymorphic DNA, RAPD; Real-Time Polymerase Chain Reaction, RT-PCR; Restriction Fragment Length Polymorphism, RFLP; Denaturing Gradient Gel Electrophoresis, DGGE) provided preliminary knowledge of these communities (Feinstein et al., 2009) but would often be insufficient for a comprehensive taxonomic assessment (Rastogi and Sani, 2011).

Metagenomic approaches can explore both the functional and structural diversity of soil microbial communities (Dubey et al., 2020). Next-Generation Sequencing (NGS) or High-Throughput Sequencing (HTS) has shown a great potential to reveal the hidden diversity of these communities. HTS allows investigations to a specific habitat, with relatively low cost and high accuracy, radically changing the methodology of research and generating a huge amount of data (Wei et al., 2018).

This review attempts to summarize the evolution of HTS tools and highlight the progress made during the last decades to study soil microbial communities. It will also look at the biodiversity and plant-microbe/microbe-microbe interactions in soils, the importance of soil microbiome, and factors that affect the soil microbial community. The strength and weaknesses of different techniques and approaches used for HTS in this field will also be discussed.

2. Importance of microbial community to soil fertility and sustainability

Global food production needs to be increased by 70% for the needs to feed the world population by 2050 (Hunter et al., 2017). The increased crop production may be achieved by both land clearing and intensive use of existing croplands (Godfray et al., 2010). However, intensive agriculture has depleted the nutrient reserves in certain regions (Kraaijvanger and Veldkamp, 2015), which is defined as a physico-chemical and biological deterioration of soil environment through anthropogenic activities, thus resulting in a serious decline in soil productivity and fertility (Dregne, 2002; Prăvălie et al., 2021). Furthermore, some agricultural practices are less ecologically sustainable (Roell and Zurbriggen, 2020), and food production is projected to decline due to many abiotic and biotic stresses, a situation that may be exacerbated by climate change (Myers et al., 2017).

Harnessing microorganisms allied with crop species has been considered one of the environmentally sustainable approaches to address some of the above-mentioned challenges for increased food security. Soil microorganisms help maintain the soil health in crop agriculture systems; soil microbiome shows a range of organisms although bacteria, fungi, and archaea have attracted much greater research attention (Lee et al., 2019; Mishra et al., 2016; Odelade and Babalola, 2019; Spence and Bais, 2013). The plant-associated bacteria and fungi have a broad range of trophic/living habits with either detrimental or beneficial, saprophytic, or symbiotic association to plants. Some of them reside in rhizosphere or rhizoplane, while a small subpopulation collectively called endophytes can colonize plant tissues (Porras-Alfaro and Bayman 2011; Hardoim and van Elsas, 2013; Brader et al., 2014; Mercado-Blanco 2015). Soil microbial communities can be affected by many factors, including plant species, soil type, and agricultural practices.

The global demand for fertilizers (N, P, K, and other macronutrients) reached more than 208 million tons in 2018, according to FAO (2012), with fertilizer manufacturers consuming a huge amount of non-renewable resources of energy. The extensive use of chemical fertilizers has also contributed to soil and air pollution as well as water eutrophication. Hence, more economically and environmentally sustainable solutions are desired to meet the need of modern crop agriculture. In this context, microbes (i.e., bacteria and fungi), which exist naturally in the soil or are supplied as bio-fertilizers, may represent a new option for improved soil structure and fertility. Bacterial and fungal inocula and soil organic matter (SOM) modifications could be considered for incorporating degraded soils into crop integrated nutrient management (Chaer et al., 2011); these inocula may be introduced to exploit, translocate, mineralize and mobilize soil P, K, Fe reserves, boost SOM and/or fix N, making resources more available to plants (Ahemad and Kibret, 2014; Leifheit et al., 2014; Nguyen and Bruns, 2015; Owen et al., 2014). According to van der Heijden et *al.* (2015), arbuscular mycorrhizal (AM) fungi and biological N-fixing bacteria contribute 5–20 % of the annual total N demand in grassland and savannah. The contribution of AM fungi to the soil fertility in temperate and boreal forests is 80% while the total P acquired by plants through bacteria and fungi is about 75%. Similarly, the N-fixing bacteria have been shown to be an effective and sustainable tool for a two-fold decrease in the recommended dose of mineral N fertilizer and the management of the Egyptian henbane nutrition in a more environmentally sustainable way (Nassar et al., 2020). The basic mechanisms by which bacteria and fungi promote the availability of nutrients include N fixation, P, K, and Fe mobilization by organic acids and siderophores (Menendez and Garcia-Fraile, 2017; Nguyen and Bruns, 2015; Owen et al., 2015; Stevens et al., 2014). Protection against plant pathogens and abiotic stresses are also among the mechanisms exerted by soil bacteria (Menendez and Garcia-Fraile, 2017). Organo-polysaccharides and proteins (golmaline, mucilages, and hydrophobins) produced by these soil microbes, mainly bacteria and AM fungi, also help enhance soil aggregates (Nguyen and Bruns, 2015; Owen et al., 2015; Stevens et al., 2014). Rhizobium bacteria form a symbiotic relationship with roots of legume crop that results in N fixation, as well as increased uptake of P and macronutrients by the plant and reduced impact of stress factors (Nadeem et al., 2009). Symbiotic bacteria may also promote plant growth by supplying additional N through atmospheric N_2 fixation, producing phytohormones (auxins, cytokinins, and gibberellins), and releasing anti-microbial molecules to shield crops from diseases (Afkhami et al., 2021; Akinola and Babalola, 2020; Barka et al., 2016; Díez-Méndez and Menéndez, 2021; Flores-Félix et al., 2019;

Khan, 2005; Lindstrom and Mousavi, 2019; Menendez and Paço, 2020; Mupambwa et al., 2018; Murali et al., 2021; Siqueira et al., 2020). In the past, farmers have widely used earthworms and organic fertilizers to boost soil productivity (Rashid et al., 2013, 2014a, 2014b, 2016; Shah et al., 2013), and these practices have proven to be beneficial to agro-ecosystems. Earthworms, however, may increase greenhouse gas emissions (Lubbers et al., 2013). The high maintenance costs of such systems would also have a direct bearing on crop prices.

Microorganisms play significant roles in the decomposition of SOM and the biogeochemical cycling of soil nutrients in ecosystems (Cusack et al., 2011; Leininger et al., 2006). The soil microbial diversity is also important for soil health (Fierer et al., 2021; Garbeva et al., 2004; Janvier et al., 2007). Diverse microbial communities are required for the decomposition of different crop residues. For instance, bacteria often dominate in the initial stages whereas fungi would dominate in later stages of crop residues decomposition (Marschner et al., 2011; Paterson et al., 2008). Also, saprotrophic fungi are an important source of oxidative enzymes in the soil (Cusack et al., 2011). The composition of soil microbial communities can also be affected by crop management activities (Ai et al., 2012; He et al., 2007; Navarro-Noya et al., 2013). Long-term use of organic fertilizer has been shown to increase total microbial biomass and fungal abundance, while decreasing bacterial abundance in alluvial soils of Northern China (Ai et al., 2012; Zhao et al., 2016). No-tillage activity in Northeast China also raised soil fungal abundance (Zhang et al., 2012). Retention of crop residues greatly increased the prevalence of Bacteroidetes, Beta-proteobacteria, and Gemmatimonadates in Central Mexico (Navarro-Noya et al., 2013). Changes in the structure of microbial communities can affect the transformation of C and N in soil ecosystems (Cusack et al., 2011; Grandy et al., 2013); some microbial species that inhabit root zones promote plant growth by participating in nitrogen fixation and phosphorus solubilization (Bargaz et al., 2018). Therefore, it may be possible to use soil microbes to balance crop production and biosphere protection. Many approaches have or are being explored for more efficient use of beneficial microbial resources, including low-input biotechnologies, to support sustainable crop agriculture, with increased use of soil microbiome information for improved nutrient supply and plant defense (Esmaeel et al., 2018; Raaijmakers and Lugtenberg, 2013; Singh et al., 2020).

Plant stress may be caused by salinity, drought, nutrient deficits, pollution, diseases and insect pests, etc. The use of agrochemicals to control the biotic stresses and nutrient deficiencies may also impose a negative impact on ecosystems and even human health. Ultimately, these limitations may cause losses in agricultural and forestry productivity, soil degradation, water deficit, reduced biodiversity, and destruction of certain valuable landscapes (Berg et al., 2020; Hirsch et al., 2013; Stegen et al., 2018). Because the soil microbial community can be affected by many ecological and agronomic factors, it is reasonable to consider the effect of the environment, especially with global warming, for optimal management of the soil microbiome (Jacoby et al., 2017; Veen et al., 2021; Zolla et al., 2013).

3. Soil as a complex environment and reservoir of biodiversity with multi-trophic interactions

Soil biodiversity plays a crucial role in soil health and fertility in both agricultural and natural ecosystems for functioning Earth's ecosystems (Wall and Knox, 2014), and the knowledge is essential to maintaining both environment and agricultural productivity (Colwell, 1997). It reflects the variety of living organisms, such as microorganisms (bacteria, fungi, algae, cyanobacteria, yeasts, actinomycetes, and myxomycetes), microfauna (nematodes, mites, collembola, and protozoa), and mesofauna (springtails, mites, diplura, proturaenchytraids) (Ruiz et al., 2008). These organisms are responsible for a range of vital functions, including nutrient cycling, regulation of soil hydrological cycle, suppression of pests and diseases, decomposition of SOM, maintenance of soil structure, carbon sequestration, and soil detoxication. The ecology, activity, and dynamics of microorganisms in the soil are affected by several environmental factors, including mineral nutrients, carbon, energy sources, available water, aeration, pH, electromagnetic radiation, genetics of microorganisms, and interactions among them (Berg et al., 2020; Nannipieri et al., 2017).

Soil biota plays an important role in soil food webs and contributes to regulating a broad suite of essential soil processes, including recycling of carbon (C) and nutrients, decomposition of organic materials that includes sequestration and mineralization of C, pollutant degradation, disease prevention, and soil structure improvements (Nielsen et al., 2015). Several studies have shown the crucial impact of soil fauna on soil ecosystems, which makes organically bound nutrients available for eventual processing through the decomposition of SOM (Su et al., 2020; Wei et al., 2019).

3.1. Soil fungi

Soil fungi are among the most important biological components of soil, playing an essential role in several ecological processes (Rosas-Medina et al., 2020). Some of them can significantly affect soil and plant health, with great ecological significance (Ritz, 2005). The diversity of soil fungi is affected by various abiotic factors such as soil, pH, salinity, temperature, and moisture (Frąc et al., 2015; Rouphael et al., 2015).

Tedersoo *et al.* (2014) reported a high diversity of soil fungi in soils with around 80 to 500 operational taxonomic units worldwide. These soil fungi perform vital functions in agricultural systems, with a wide range of meditative and integrative functions at physiological, metabolic, and ecological levels (Figure 1). They are extremely diverse and can be classified into three groups according to Swift (2005) and Gardi and Jeffery (2009): i) those participating in SOM decomposition; ii) biological controllers; and iii) ecosystem regulators. Several studies have reported multi-functionality with these soil fungi, including protection against drought and root pathogens (Baum et al., 2015; El Komy et al., 2015).

Other fungi like *Trichoderma* spp., which are free-living species found commonly in soils, can establish endophytic associations with part of the plant such as roots and have shown great ability and economical value with their production of secondary metabolites used in medicine, biotechnology, and agriculture. These microbes exert directly or indirectly benefit to plants against diseases (Contreras-Cornejo et al., 2020). However, other species may not be as plant-friendly, such as *Rhizoctonia* sp. that causes extensive soil-borne diseases on many crops (Brown et al., 2021; Parveen et al., 2020).

3.2. Arbuscular mycorrhizal fungi

Arbuscular mycorrhizal fungi (AMF) also play an important role by altering plant interactions with other biotas in soil ecosystems, including the uptake and transfer of nutrients, improvement of plant growth, and modification of soil environment (Köhl et al., 2016; Powell and Rillig, 2018). They are obligatory soil fungi, which colonize the roots of most crops. Numerous studies stated the benefit of applying AMF to agricultural soils (Delavaux et al., 2017; Gosling et al., 2016; Köhl et al., 2016; van der Heijden et al., 2015). Additionally, they may enhance water use efficiency, stress tolerance, and protection against diseases (Chen et al., 2019a, b; Diagne et al., 2020; Jabborova et al., 2021; Wu et al., 2021). AMF also substantially affects C flow from autotrophic plants to the heterotrophic soil microbial community and nutrient cycling due to increased root exudation (Jeffries and Barea, 1994). However, almost all ecological studies have indicated that the diversity of AMF is reduced significantly upon land-use intensification due to several factors related to intensive agricultural management, including excessive tillage, fertilization, fallow, and crop rotations (Jansa et al., 2006). Whilst the abundance and distribution of AMF in ecosystems is influenced by

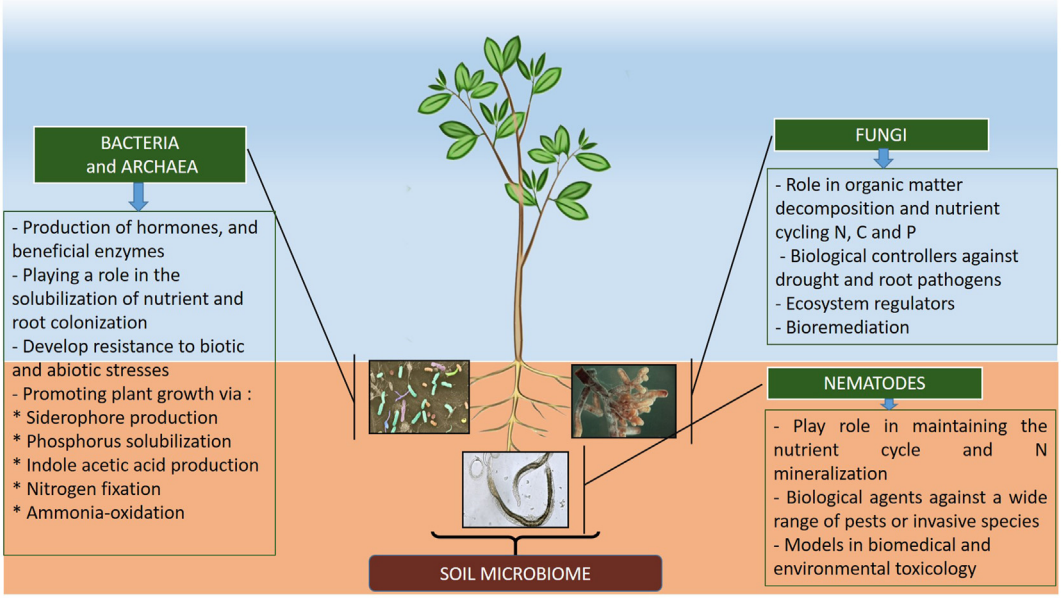

Figure 1. The roles of soil microorganisms (archaea, bacteria, nematodes, and fungi) in the maintenance of soil integrity, fertility, plant growth, and sustainable agriculture.

intrinsic properties of AMF species (extinction rates, dispersal capabilities), soil disturbance regimes, as well as vegetation type, edaphic properties, and climate, can also play a role (Carvalho et al., 2003). Effects of AMF on host plant growth and soil health have been recognized for sustainable agricultural systems (Bethlenfalvay and Schüepp, 1994; Hooker and Black, 1995) and the positive relationship between AMF colonization and plant diversity has been extensively reported (Brígido et al., 2017; Campos et al., 2018; Igiehon and Babalola, 2017; Ryan and Graham, 2018; Van Der Heijden et al., 1998).

3.3. Nematodes

Nematodes occupy different functional links within the edaphic trophic network. They can be classified into four functional groups based on their feeding habits, and the most common groups of nematodes in agricultural soils are the fungivores and bacterivores, which feed on fungi and bacteria, respectively, regulating microbe population and participating in the nutrient cycle and N mineralization (Akpheokhai and Oribhabor, 2016; Bongers, 1999; van den Hoogen et al., 2019). Plant-parasitic nematodes (PPN) feed mostly on roots, causing significant damage to crops, such as root-knot nematodes *Meloidogyne* spp. and cyst nematodes *Heterodera* and *Globodera* (Bongers, 1999; Jones et al., 2013). Predators and omnivores which feed on other edaphic organisms (including other nematodes) can be used as biological agents (Campos-Herrera et al., 2008). Nematodes have also been used as environmental indicators since the 1970s, with *Caenorhabditis elegans* Maupas being a model for biomedical and environmental toxicology. Several trophic network indices have been developed, which allowed inferring the ecological role of soil nematodes in a more general framework of an edaphic trophic network (Sánchez-Moreno and Talavera, 2013). Soil nematode communities can also provide genera or species, which are highly tolerant or sensitive to the impact of certain agricultural practices, as biomarkers of certain land use (Melakeberhan et al., 2021; Neher, 2001). The selection of key taxa as bioindicators should be exercised with caution since agricultural practices often employ a combination of chemicals and agronomical measures that may produce differential effects on nematode communities. A series of taxa has been suggested for biomonitoring (Fiscus and Neher, 2002; Hodda et al., 1999; Lazarova et al., 2021).

3.4. Bacteria and Archaea

Plant-microbe interaction in soils helps plant growth via a wide range of processes and microbes improve plant growth and recycle crop residues in the soil (Rajkumar et al., 2013; Dubey et al., 2019). The biological traits of soil can be affected by the diversity of microbes (Gryta and Frąc, 2020). Bacteria and Archaea are also dominant microorganisms in soils that play a major role in biogeochemical cycling (Feng et al., 2019). Microbes help sustain the equilibrium and integrity of the biosphere (Dubey et al., 2019).

Plant growth-promoting rhizobacteria (PGPR) constitute a diverse group of microbes with an important ability to produce a variety of chemicals that protect the plant from pathogens besides promoting plants growth (Dubey et al., 2019; Lugtenberg and Kamilova, 2009). PGPR have gained much interest due to the production of hormones and enzymes that help to solubilize nutrients. Improved knowledge will help to understand the mechanisms of PGPR for sustainable agriculture (Dubey et al., 2019; Lugtenberg and Kamilova, 2009).

Archaea, present in a wide range of habitats (Alori et al., 2020), contribute mainly to promoting plant growth via improved nutrient uptake and protection of plants against abiotic stresses (Alori et al., 2020). They may promote plant growth via siderophores, phosphorus solubilization, indole acetic acids, nitrogen fixation, ammonia-oxidation, and sulfur cycling. Archaea also contribute to the functions of vegetation/ecosystem via participation in nutrient cycling, phytohormone biosynthesis, and plant stress release (Alori et al., 2020; Taffner et al., 2018).

4. The mystery of plant-microbe interaction in rhizosphere

Lorenz Hiltner coined the term *rhizosphere* more than 100 years ago as the soil surrounding plant roots where microbes interact actively (Hartmann et al., 2008). This concept has had a tremendous impact on soil microbial ecology, remaining as a milestone until this date for our understanding of plant-microbe interactions in soils. Rhizosphere communities are highly complex, not only in terms of species composition (e.g. bacteria, fungi, nematodes, and invertebrates) but also their interactions (Bakker et al., 2013). Within the rhizosphere, microbes can occupy different niches such as the rhizoplane (root surface) or endosphere

(inside roots). The diversity in these niches tends to be lower than that in the bulk soil (Bakker et al., 2013).

Root exudates are the major driving force of the rhizosphere community. As part of an adaptative strategy, plants use the exudation of rich-carbon compounds (e.g. mucilage, low- and high-molecular-weight molecules like amino acids or complex carbohydrates) to selectively recruit beneficial microbes in the rhizosphere for nutrient acquisition and disease-fighting (Badri and Vivanco, 2009; Bakker et al., 2018). PGPR are well-known for increasing plant biomass and nutrient intake, as well as disease resistance and/or abiotic stress tolerance (Glick, 2020). One of the best examples may be the symbiotic relationship between nitrogen-fixing rhizobia and legumes; certain signaling molecules in root exudates (i.e. flavonoids) attract the free-living rhizobia towards the root, triggering an infection and nodulation process (Poole et al., 2018), which provides substantial nitrogen to the plant in the form of nitrate (Lindström and Mousavi, 2019; Poole et al., 2018). Another example is the symbiotic association of plants with AMF. As rhizobia, AMF are also attracted to signaling molecules (i.e. strigolactones) in root exudates. Ultimately, AMF will colonize the roots intracellularly, acting as effective extensions of the root system and increasing the plant's ability to take up water and nutrients from the soil (Glick, 2020).

Like other sessile organisms, plants have to rely on their innate immunity (reviewed by Jones and Dangl (2006) and Zhou and Zhang (2020)) and selective microbiota to protect themselves against pathogens (Yu et al., 2019). Plant pathogens, including bacteria, fungi, nematodes, or oomycetes, also are drawn to root exudations (Mendes et al., 2013). For example, PPN can sense host root exudates, migrating towards the rhizoplane to feed on the host (Liu et al., 2020; van Dam and Bouwmeester, 2016). In response, plants may rely on specific root microbiota as a line of defense against PPN (Hussain et al., 2018). Similar responses have been reported in plant defense against *Fusarium oxysporum* Schltdl. or *Rhizoctonia solani* Kühn. Indeed, certain antagonistic microbes were selectively enriched in the rhizosphere (Bakker et al., 2018), which reduced the impact of the pathogens. To provide benefits, the beneficial bacteria need to be highly competitive in the rhizosphere and can successfully colonize roots to suppress the pathogen. The production of secondary metabolites, antibiotics, or lytic enzymes are examples of antagonists that render the competitiveness of these bacteria (Berendsen et al., 2012; Yu et al., 2019). Other microbes may modulate plant defenses incrementally via induced systemic resistance (ISR). ISR is often regulated by the phytohormones jasmonic acid (JA) and ethylene (ET) *via* JA/ET pathways and also salicylic acid (SA) pathways (Mendes et al., 2013). The rhizobacteria *Pseudomonas putida* LSW17S confers resistance against *Pseudomonas syringae* DC3000 by eliciting ISR and triggering cellular/molecular defense responses, including hydrogen peroxide accumulation, callose deposition, and expression of defense-related genes (i.e. JA/ET) (Ahn et al., 2007).

Communications in the rhizosphere play a vital role in multitrophic interactions, shaping the microbial community and its impact on plants. Different signaling may occur: i) among microbes as quorum-sensing (QS) regulates population behaviors, growth, and activities, ii) from plants to microbes (Lira et al., 2015), and iii) from microbes to plants that affect plant gene expression, root structure and defense responses (Venturi and Keel, 2016). Complementing the short-distance effect of QS signaling molecules, volatile organic compounds (VOCs) from microbes are perceived as long-distance messengers in intra- and inter-kingdom interactions (Schulz-Bohm et al., 2018). The low molecular mass and high vapor pressure make it easy for VOCs to evaporate and diffuse in the rhizosphere (Schulz-Bohm et al., 2018), and VOCs emitted by rhizobacteria can affect the growth and gene expression of phylogenetically and physically distant organisms (Garbeva et al., 2014). Using assembled soil communities containing common soil bacteria, bacterial pathogens, and host plants, Raza et *al.* (2020) found that interactions among bacteria affected VOCs production, resulting in VOCs-mediated disease suppression and plant growth promotion.

Plant-microbe interactions in the rhizosphere make up part of a highly complex network of molecular exchanges under strong selective pressure (Bakker et al., 2013), which are also affected by edaphic (e.g. nutrients, pH, carbon and energy sources) and environmental (water, temperature, and aeration) factors. Vegetation type and land management practices (Cheng et al., 2019) augment the intricacy of the ecosystem. HTS approaches coupled with cutting-edge analytical techniques are expected to help shed light on these interactions for the development of more sustainable crop production (van Dam and Bouwmeester, 2016).

5. Impact of cropping systems and climate change on soil microbial communities

Sustainable agriculture aims at meeting the needs of the present generation without endangering the resource base for future generations, based on sound ecological considerations that optimize the benefit of organisms in the environment. It often refers to an integrated system for plant and animal production with a site-specific application that will last over time. Cropping systems include cropping patterns interacting with resources and available technologies, with common systems such as intercropping, mixed cropping, and sequence cropping. Spatial patterns of microorganisms should be considered in these systems for optimized management strategies and agricultural productivity (Cavigelli et al., 2005). When spatial patterns of denitrifying bacteria were detected at the farm level, the information helped the identification of resource-based niches for denitrifiers relevant to land management and cropping practices (Enwall et al., 2010; Rashid et al., 2016). Continuous cropping may reduce the bacterial population in the soil while increasing the relative proportion of fungi. This may decrease the buffering capability to biotic and abiotic stress, increasing the disease pressure (Mo et al., 2016; Wang et al., 2011; Xiong et al., 2016). Cropping systems that leave crop residues behind may increase SOM and microbial activities, as well as reducing soil erosion. Reduced tillage may also increase soil microbial activities and protect the quality of soil, water, and air (Benitez et al., 2017; Tian et al., 2015; Wang et al., 2015). Clostridia and other archaea, as well as anaerobic bacteria, have been found in only no-till systems (Luo et al., 2016). Crop rotation can also influence soil fertility and microbial communities (Benitez et al., 2017). In this regard, cropping systems with winter cover crops and/or rotation of cotton with a high-biomass crop like sorghum showed positive results in key soil-quality parameters related to SOM, nutrient cycling, and C sequestration relative to alternative systems (Acosta-martinez et al., 2011; Cotton et al., 2013). Studies in semiarid regions, however, have shown the challenge of enhancing soil microbial communities in dryland cropping systems with low levels of biomass production under limited rainfall and extreme temperature conditions (Liebig et al., 2006).

The assessment of soil health and quality under different cropping systems may be based on soil bacterial assemblages (Song et al., 2018). Using vetch and rye as cover crops increased soil microbial biomass in the rhizosphere of tomato (Buyer et al., 2010). Decomposition of roots and rhizosphere exudation leached from cover-crop biomass can form gradients in soil texture and pH (Fernandez et al., 2016), which further showed the impact of the microbial process on soils. Bowles et *al.* (2014) showed that microbially-based functions in soil could be manipulated to boost nutrient cycling, which may be used to guide nutrient management for optimized soil microbial communities. Jing et *al.* (2015) pointed out that the richness of plant species and soil microbial biodiversity together may explain more variability in ecosystem multifunctionality (42%) than did by the soil microbial biodiversity alone (32%), as the microbial diversity may vary temporally to crop rotation and various stress factors. In this regard, Ashworth et *al.* (2017) believed that microbial diversity would increase with judicious nutrient management (inorganic fertilizers *vs*. animal manure), legume cover crops, greater crop rotations, and richness in crop species. These findings corroborate the linkage between microbial communities and cropping system management.

Climatic change such as increased atmospheric CO_2, global warming, and altered precipitation may have direct (Auffret et al., 2016; Bintanja, 2018; Gao et al., 2018; Zhang et al., 2018) and indirect (Charubin and Papoutsakis, 2019; Dubey et al., 2019; Muleta, 2017; Orozco-Mosqueda et al., 2018; Sharma and Prasad, 2017) impact on soil microbial communities (Castro et al., 2010; Classen et al., 2015; Mandal and Sathyaseelan, 2012). Fungal and bacterial abundance may respond variably to temperature and CO_2 changes (Bagri et al., 2018; Cavicchioli et al., 2019; Hashem et al., 2019). The response of microbiota and ecosystem to climatic change may affect agricultural sustainability (Dubey et al., 2020). Few studies have identified specific factors that would influence the spatial pattern of soil microbial community on large scales and our understanding of the key habitat-selective factors is still limited. Lauber et *al.* (2009) illustrated that the composition of soil bacteria could be predicted by pH on a large scale. This notion is supported by several additional studies (Enwall et al., 2005; Tan et al., 2019; Wakelin et al., 2008), although soil type is another complex factor often associated (Buckley and Schmidt, 2001; Cavigelli et al., 2005; Girvan et al., 2003). In many studies of microbial ecology, not enough attention has been directed to carbon and nitrogen pools likely due to the challenges of measuring them accurately (Kong et al., 2011). Human activities that increase greenhouse gas emissions (CO_2, CH_4, and N_2O) and other environmental pollution, agriculture activities, and population growth, may accelerate climate change, further affecting soil microbial communities (Cavicchioli et al., 2019; Nisbet et al., 2019).

6. Functional microbial communities in the soil

Soil microbial communities are a complex network with multifunctional interactions influenced by many factors. Changes or shifts in the soil community and biodiversity may compromise the functionality and sustainability of the ecosystem (Wagg et al., 2014). Losses in diversity generally reduce the functionality, impacting negatively soil fertility and productivity (Delgado-Baquerizo et al., 2018). A low diversity, especially when some of the special microbial taxa are lacking (Xun et al., 2019), can be problematic to an ecosystem. Bacteria, archaea, and fungi play a key role in soil functionality; they manage biogeochemical cycles and regulate SOM decomposition. This microbial community may vary substantially in response to N in the soil (Zheng et al., 2019); increases in N availability may change microbial C dynamics, which leads to further shifts in community composition, structure, and metabolic functions (Fierer et al., 2012).

6.1. Factors affecting soil microbial communities

6.1.1. Fertilizers

Adding fertilizers can affect soil microbial communities. Chen et *al.* (2020) found a correlation between microbial diversity and multifunctionality, and some of the rare microbial taxa seem to play a key role in defining this functionality in agricultural soils with a long history of fertilization. Microbial adaptation is a key factor, and some rare bacterial taxa (<1% abundance) can even adapt to saline and metal-contaminated soils (Wang et al., 2019). Partial replacement of chemical fertilizers with manure or vermicompost may produce a significant short-term effect on the community structure and functions, mostly related to P uptake. In the longer term, there could be a more positive effect on crops (Lazcano et al., 2013); organic fertilizers generally result in soil microbial communities with greater diversity (Chen et al., 2020), which can further influence the functionality of the ecosystem. Other agricultural practices and land use also affect the soil microbial diversity and functions.

6.1.2. Land uses

Intensive agriculture tends to reduce biodiversity in general (Tsiafouli et al., 2015). Different land uses and management practices may lead to changes in microbial communities over time (Lauber et al., 2013), although the functionality may somewhat be maintained (Bissett et al., 2011). Agricultural land with less microbial diversity may still reserve some basic functions, including the degradation of cellulose or lignin from plants and soil contaminants (Griffiths and Philippot, 2013). In the Amazon ecosystem, for example, where the forest-to-agriculture conversion resulted in reduced soil microbial community and biochemical activities, the key functions related to N cycling remained (Merloti et al., 2019). Plant richness may also have an effect (Lamb et al., 2011). Garau et *al.* (2019) found differences in metabolic traits in the community influenced by the type of tree species. Despite these observations, many believed that land uses would have a stronger effect on the soil microbial community than plant species and soil types (Jangid et al., 2011).

6.1.3. Pesticides

Several studies showed that glyphosate application reduced the abundance of some important rhizospheric taxa involved in biogeochemical cycling, thus affecting soil nutrient dynamics, fertility, and productivity (Barriuso and Mellado, 2012; Newman et al., 2016). However, Kepler et *al.* (2020) found no effect of glyphosate on soil microbial communities in association with glyphosate-tolerant varieties of corn and soybean crops. Interestingly, Barriuso & Mellado (2012) found that the impact would depend on the soil type and texture for the community associated with glyphosate-tolerant cotton. The fungicides triazole also reduced the microbial communities (Satapute et al., 2019), but many other pesticides, including azadirachtin and trifloxystrobin, showed no deleterious effect (Suciu et al., 2019). Interestingly, neonicotinoids (insecticide) shifted the soil microbial functionality by enhancing the taxa promoting nitrogen metabolism (Yu et al., 2020), and deltamethrin (synthetic pyrethroid insecticide) is degraded by several taxa present in agricultural soils (Bragança et al., 2019).

Undoubtedly, understanding the microbial community and interactions within it can be a challenging task due to difficulties in cultivating and observing some of the microbes involved. The results of biodiversity in such complex ecosystems can be biased due to a lack of sensitive indicators when conventional techniques such as plating and microscopy were used. These techniques can be overly selective and prone to inhibitors in the environment. Molecular tools may be considered to improve such studies (Jo et al., 2020; Martin-laurent et al., 2001).

6.2. New tools to understand functions of soil microbial communities

Most studies relied only on a single technique or tool to investigate the composition or function of soil microbial communities, and some of them provided only theoretical extrapolations with limited data. In the past decade, NGS tools have been increasingly used in such studies with the advances in technologies from the 454 Roche and MiSeq Illumina to Nanopore and SMRT PacBio sequencing platforms. In a critical assessment, Nkongolo and Narendrula-Kotha (2020) compared those non-culturing-dependent tools and concluded that NGS could be used with PLFA (PhosphoLipid Fatty-acid Analysis) to obtain the picture of the entire microbial community in a given soil, structurally and functionally. Moreover, Nannipieri et *al.* (2020) proposed that a combination of metagenomics, gene expression, and classical culturomics would be the most accurate approach to study the function of the soil microbial community.

In a semi-arid grassland soil, Chen et *al.* (2019a, b) used PFLA profiling and DNA-based analyses and found shifts in microbial composition and function related to soil nutrient dynamics after precipitations. Stable isotope probing, micro autoradiography, isotope array, metaproteomics, proteogenomics (combination of metaproteomics and metagenomics), metatranscriptomics are the technologies that may identify the structural taxa associated with certain functionalities displayed by a microbial community (Rastogi and Sani, 2011).

7. Caution when using molecular tools in studying soil microbial communities

Culture-independent molecular methods used in studying soil microbial biomass, diversity, and activity (Rincon-Florez et al., 2013) may fall into three categories: *i*) *in situ* analysis of nucleic acids, *ii*) direct analysis of extracted DNA/RNA, and *iii*) analysis of PCR-amplified segments of DNA molecules (Thies, 2007). The key objective is to describe the microbial community based on the taxon richness and evenness. However, intrinsic features of soil samples could impede the accuracy of the results (Rincon-Florez et al., 2013), which could occur during the extraction of nucleic acids from soil samples or PCR amplification (Thies, 2007; Sipos et al., 2010). Commonly cited problems with nucleic-acid extraction include: *i*) presence of enzyme-inhibiting organic compounds, such as humic and fulvic acids in the soil, and *ii*) low extraction yields due to bonding of nucleic acids to soil particles, incomplete cell lysis, and DNase and RNase contamination (Rincon-Florez et al., 2013). Since soil types can influence the efficiency of DNA/RNA extraction (Thies, 2007), commercial soil DNA/RNA extraction and purification protocols generally use a bead-beating step to facilitate the extraction from humic acid-rich soil samples to ensure maximum cell lysis (Lakay et al., 2007; Wang et al., 2008). Using molecular tools may require extra caution during sample collection, handling, and processing because errors in preceding steps could be multiplied as PCR is based on an exponential magnified over original templates (Thies, 2007; Sipos et al., 2010). Additional indicators may be considered to verify the data provided with PCR. To minimize intermediate changes before molecular analysis, soil samples should be frozen immediately at -20 °C for the short-term and -80 °C for long-term storage (Thies, 2007).

8. Molecular tools to evaluate soil microbial communities

8.1. Genetic fingerprinting and other classical techniques

Many PCR-based fingerprinting methods are useful for tracking dominant members in the soil microbial community. One of the common critics of this approach is the underestimation of biodiversity (Rincon--Florez et al., 2013; Smalla et al., 2007), which is related to the fact that PCR can generate a bias in favor of more stable microbes due to the ease of extracting short fragments with low GC contents from them (McGrath et al., 2008; Suzuki and Giovannoni, 1996).

Some genetic fingerprinting techniques were used for profiling soil microbial communities: i) Denaturing Gradient Gel Electrophoresis (DGGE) and Temperature Gradient Gel Electrophoresis (TGGE), ii) Terminal Restriction Fragment Length Polymorphism (T- RFLP); and iii) Length Heterogeneity PCR (LH-PCR), amongst others. Those techniques were also commonly used to monitor soil microbial communities' dynamics, diversity, and richness in different kinds of soils (Changey et al., 2020; Hussein, 2021; Mucsi et al., 2020). One of the major problems associated with these methods lies in the fact that they can only detect the most abundant species present in the soil (Rincon-Florez et al., 2013), while those of low abundance, known as the “rare biosphere”, are largely inaccessible with these techniques (Shade et al., 2012). This is mainly due to differential 16S rRNA gene amplification by primers (Al-Awadhi et al., 2013). The use of universal primers may neglect minor constituents in PCR detection (Al-Mailem et al., 2017). Other approaches have shown successes in overcoming the underestimation of the rare biosphere, such as the use of taxon-specific primers with nested PCR (Gomes et al., 2001; Rincon-Florez et al., 2013).

Automated Ribosomal Intergenic Spacer Analysis (ARISA) is a commonly used method that provides estimates of soil microbial richness and diversity (Kovacs et al., 2010). This is an automated process that replaces the previous polyacrylamide gel electrophoresis and DNA detection by silver staining (Fisher and Triplett, 1999). ARISA is a robust technique due to its high resolution and reproducibility of results, making it a sensitive tool for studying complex bacterial communities at various spatial scales (Ranjard et al., 2001). This technique, however, may over-, as well as under-estimate the species richness due to multiple operons within a single genome with variable spacer lengths and unrelated microbes with spacer regions of identical length (Kovacs et al., 2010). Several approaches were considered to address this issue, including the analysis of particular taxonomic groups rather than entire communities for less complex fragment patterns, and the use of several primers targeting different taxa (Fisher and Triplett, 1999).

Length Heterogeneity PCR (LH-PCR) is another method to measure microbial changes in soil (Moreno et al., 2011). This method helps provide insights into the community organization without recoursing to the construction of clone libraries and DNA sequencing analysis, which are both laborious and costly (Mills et al., 2007). LH-PCR tends to underestimate the diversity, as phylogenetically unrelated organisms could produce the same-length amplicons, indistinguishable from each other in the profile (Mills et al., 2003, 2007). This tool may be more suitable for the preliminary assessment of a soil microbial community. LH-PCR analysis may be improved by using more specific primers or including a restriction digestion step (Ritchie et al., 2000).

8.2. Quantitative PCR

qPCR (Quantitative PCR), also called real-time PCR, has been used to measure the abundance and expression of taxonomic and functional gene markers in the environment (Bustin et al., 2005; Fierer et al., 2005; Smith and Osborn, 2009). It may overestimate the target, especially when SYBR green detection is used (Andreote et al., 2009), which can bind to all double-stranded DNA (Smith and Osborn, 2009). High specificity and optimized concentration of primers used in SYBR green qPCR assays may help minimize the false detection (Andreote et al., 2009; Smith and Osborn, 2009). Furthermore, a post-PCR melting curve analysis should be done to confirm that the fluorescence signal is produced only from the target templates (Smith and Osborn, 2009). Relative to SYBR green-based qPCR, TaqMan-based assays are intrinsically less prone to nonspecific amplification (Brankatschk et al., 2012).

8.3. FISH

Fluorescence *In Situ* Hybridization (FISH) allows simultaneous visualization, identification, enumeration, and localization of individual microbial cells. This method can overestimate the biodiversity in soil (Moter and Göbel, 2000) due to its high sensitivity based on the detection of low amounts of rRNA (Zarda et al., 1997) and lack of oligonucleotide probe specificity (Moter and Göbel, 2000). Non-specific binding of these probes to either soil organic matter (Christensen et al., 1999) or non-target organisms (Moter and Göbel, 2000) may also result in non-specific fluorescence. Therefore, careful design and evaluation of new probes are crucial to address this issue with FISH, with both positive and negative controls used in experiments. Closely related strains harboring target sequences with few mismatches to respective probes should be used as negative controls (Moter and Göbel, 2000).

Despite meticulous design and testing, the binding of probes to non-target organisms is difficult to rule out definitively, especially to those whose sequences have not been retrieved and, consequently, considered during probe design. A way around this dilemma is the use of two or more specific probes targeting different positions of the 16S rRNA labeled with distinct fluorochromes because the chances for coincidental false-positive detection by two probes against independent and variable target sites will be low. In these cases, only the cells detected by both probes and exhibit double fluorescence will be considered as the target organism (Neef et al., 1996). In general, the application of FISH in soil microbe study is still restricted by limited target sequences available (Moter and Göbel, 2000).

8.4. Lipid analysis

Phospholipid fatty acid (PLFA) analysis is one of the most popular methods used in studying soil microbial communities due to the rapidity and sensitivity of assay that enables monitoring of the population (Frostegård et al., 2011; Veum et al., 2019). As with all other popular methods, PLFA has its own biases stemmed from sample storage conditions and handling procedures that could affect PLFA microbial group designation based on biomarkers (Frostegård et al., 2011). A better understanding of how these conditions/procedures affect the quantification of PLFA biomarkers and interpretation of PLFA profile may help (Veum et al., 2019). For example, G+ bacteria are favored more by dry and cold storage (4 °C or -20 °C), relative to G-bacteria (Lee et al., 2007).

8.5. HTS molecular methods

HTS encompass several culture-free methods to analyze the genetic and functional diversity of microbial communities in soils and rhizosphere (Barret et al., 2013; Chauhan et al., 2013; Hirsch et al., 2013; Hu et al., 2014; Schreiter et al., 2015; Zhu et al., 2018). Although these tools were first available 20 years ago, they have been more widely used in the past decade due to their ability to quickly identify relevant compounds in the soil microbial community. HTS is also a multiparametric technique that analyzes various parameters quantitatively, including target molecules in cells/localization, cell motility, and morphological information, based on high-throughput fluorescence or luminescence measurements of samples. A rapid and sensitive assay based on HTS chemical libraries has been developed recently for analyses of soil microbial communities (Murray et al., 2019).

8.5.1. Illumina sequencing

Illumina sequencing technology, released in 2006, is based on fluorescence-based readouts of millions of immobilized DNA fragment libraries that are formerly constructed by sequencing-by-synthesis using reversible dye-termination nucleotides. Illumina-based 16S rRNA sequencing is a valid alternative to other 16S-based sequencing methods (Lazarevic et al., 2009), with the advantage of fluorophore detection.

This technology offers a range of platforms, including HiSeq 2500, HiSeq 2000, Genome Analyzer IIx, and MiSeq platform genome, NextSeq 550 series, Iseq 100, and MiniSeq (Table 1), with HiSeq 2500 being most powerful and delivering up to 600 Gb of data at up to six billion reads per run (at approximately 2 × 100 bp read length) (Jeon et al., 2021; Modi

Table 1. Summary of high-throughput molecular screening tools.

Platform	Manufacture	No of units on sequencing support	Run condition and read length	Run time	Maximum data output/run
Roche	454 FLX+	1 PTP with gaskets to separate 2, 4, 8 or 16 regions	FLX (modal 450 bp, max. 600 bp)	10h	450 Mb
			FLX+ (modal 700 bp, max. 1000 bp)	23 h	700 Mb
	454 GS Junior Titanium	1 PTP	~ 450 bp	10h	35 Mb
Illumina	HiSeq 2000/2500 (High output mode) V3 kits	8 lanes per flow cell, 1 or 2 flow cells per run	36 bp	2 days	95–105 GB
			2 × 50 bp	5.5 days	270–300 GB
			100 bp	5 days	270–300 GB
	HiSeq 2000/2500 (High output mode) V4 kits	8 lanes per flow cell, 1 or 2 flow cells per run	2 × 100 bp	11 days	540–600 GB
			36 bp	29 h	128–144 Gb
			2 × 50 bp	2.5 days	360–400 Gb
			2 × 100 bp	5 days	720–800 Gb
			2 × 100 bp	6 days	900–1000 Gb
	HiSeq 2500 (Rapid run mode) V3 kits	2 lanes per flow cell (not independent), 1 or 2 flow cells per run	36 bp	7 h	18–22 Gb
			2 × 50 bp	16 h	50–60 Gb
			2 × 100 bp	27 h	100–120 Gb
			2 × 150 bp	40 h	150–180 Gb
	HiSeq X ten miSeq, V2 kits	1 or 2 flow cell	2 × 150 bp	<3 days	1.6–1.8 Tb
			36 bp	4 h	540–610 Mb
		1 lane, 1 flow cell	2 × 25 bp	5.5 h	750–850 Mb
			2 × 150 bp	24 h	4.5–5.1 Gb
			2 × 250 bp	39 h	7.5–8.5 Gb
	NextSeq 500 (High output mode)	4 lanes (not independent), 1 flow cell	75 bp 2 × 75 bp 2 × 150 bp	11 h 18 h 29 h	25–30 Gb 50–60 Gb 100–120 Gb
Life technologies	SOLiD	2 × 6 lanes	75 bp	5 days	160 Gb
	5500xl		75 bp + 35 bp	8 days	220 Gb
			60 bp + 60 bp	8 days	260 Gb
	SOLiD	2 × 6 lanes	50bp	4 days	160 Gb
	5500xl W		75 bp	5 days	240 Gb
			2 × 50 bp	8 days	320 Gb
	Ion PGM,	1 Chip	200 bp mode	2.3 h	30–50 Mb
	314 chip v2		400 bp mode	3.7 h	60–100 Mb
	Ion PGM,	1 Chip	200 bp mode	4.4 h	600 Mb–1 Gb
	314 chip v2		400 bp mode	7.3 h	1.2–2.0 Gb
	Ion Proton, PI chip	1 Chip	200 bp mode	2–4 h	Upto10Gb
Pacific biosciences	PacBio RS II	Up to16 SMRT cells	C2/P4 chemistry, mean read length ~ 8000 bp	2–3 h per cell	400 Mb per cell

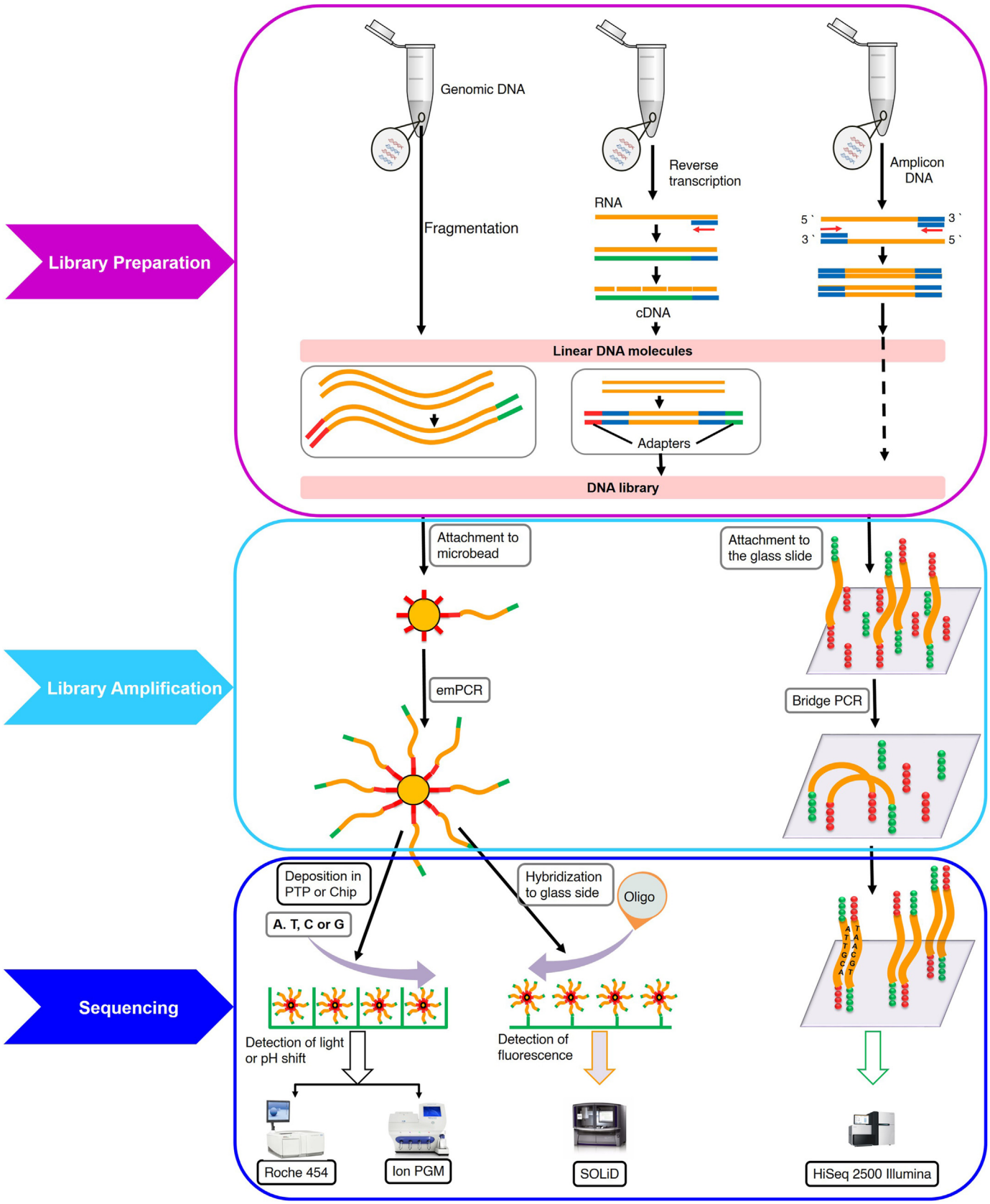

Figure 2. A schematic outlines of the library preparation, amplification, and sequencing process of the most commonly used culture-independent high-throughput screening tools to decipher the genetic diversity of soil microbial communities.

Table 2. Criteria necessary for adopting each molecular technique: advantageous and limitations.

Platform	Advantages	Limitations
Roche	Low error rate	Medium/high start-up costs
	Medium read length	Must run at a large scale
	Cheaper and faster	Relatively high costs per base
	Clonal amplification: Emulsion PCR	Difficulty in distinguishing the number of bases in a run of identical bases
Illumina	Low error rate	Must run at very large scale
	Lowest cost per base	Short read length
	Tons of data	Runs take multiple days
	Clonal amplification: Bridge	High start-up costs
SOLiD	Relatively accurate because each base is interrogated twice	Potential for error propagation across reads due to two-base encoding and sequential ligation
	High throughput and low cost per base	High instrument cost
	Clonal amplification: Emulsion PCR	Short reads (up to 50 b)
	Independent lanes can be run on 5500XL	Relatively long run time
Ion PGM	Medium/Low start-up costs	Read lengths only ~100–200 bp so far Inadequate for SNP or mutation analysis
	Low error rate	
	Fast runs (<3 h)	
	Clonal amplification: Emulsion PCR, semiconductor sequencing technology	
HeliScope	Single molecule sequencing	High error rate
		High cost
SMRT/PacBio	Can use single molecule as template	Medium/high cost per base High error rate High start-up costs
	Potential for very long reads	
	Clonal amplification: N/A single molecule	
	It has the ability to observe and capture kinetic information	

et al., 2021). The Illumina sequencers would have shorter reads with a much higher throughput, which makes them more fit for gene expression studies. This tool has enabled the characterization of organisms at low relative abundances (Fierer et al., 2012), although the short read length can affect the accuracy of taxonomic designation. Overall, Illumina sequencing is cost-effective and can yield 10 times or more sequences per sample than 454 pyrosequencing, thereby allowing the analysis of a high number of taxonomic profiles (Kozich et al., 2013; Zhu et al., 2018).

8.5.2. SOLiD sequencing

The System of Oligonucleotide Ligation and Detection (SOLiD) is a sequencer developed by Life Technologies in 2006. It uses emulsion PCR such as the 454 sequencing to produce clone libraries (Table 1, Figure 2) via DNA ligation, and a unique approach to sequence amplified DNA fragments. The high accuracy of the SOLiD allows the analysis of samples across a wide range of applications using fragment library (single DNA fragment) or mate-paired library (two DNA fragments). In both cases, DNA is sheared into a specific size, and adapters are ligated to both ends. Additionally, the template-attached beads are combined with a universal primer, ligase, and a large pool of di-based probes consisting of four fluorescence-labeled nucleotides. When a labeled probe hybridizes to its complementary sequence, DNA ligase joins the probe to the primer. Adding a subsequent DNA ligase will connect the 8-mer fluorescent oligonucleotides of the complementary probe that hybridize to the primer (Zhang et al., 2011). The technology can create billions of short sequence reads (2 × 60 bp) at once (120 Gb).

SOLiD was used to sequence the genome of the soft rot/blackleg pathogen *Pectobacterium* sp. strain SCC3193 to overcome homopolymer and assembly errors in 454 sequencings (Koskinen et al., 2012). However, the assemblage of short reads may be difficult to annotate, which is an inherent problem for using SOLiD with an Illumina platform (Table 2). Despite the high accuracy of dinucleotide-based sequencing technologies (up to 99.94%), the library preparation is time-consuming (Morozova and Marra, 2008). The technology was widely used in studies of transcriptomics and epigenomics, and its ability in exploring multiple variable regions of single target oligotyping makes it a valuable tool to study the soil biodiversity based on the abundance of relevant functional marker genes (Eren et al., 2013).

8.5.3. Ion Personal Genome Machine

Ion Personal Genome Machine (PGM) was launched in 2010. For each nucleotide base incorporated into DNA, a proton is released, which results in pH change. Instead of fluorescence, it measures the H+ ion release during the base incorporation. The pH change in an individual well is detected with an ion sensor, which transforms chemical changes into digital information on an ion PGM machine. Compared to other fluorescence-based detection systems, PGM provides shorter runtimes as no nucleotides are used (Table 2), with 400 bp reads generated in 4 h, and has been suggested as a microbial ecology-sequencing platform to assess the dynamics of bacterial and archaeal communities (Whiteley et al., 2012).

8.5.4. Helioscope single molecule sequencer

This platform offered by the Helicos Genetic Analysis System is based on the technology developed by Braslavsky et *al.* (2003), and the Oxford Nanopore Technology revolutionized it into a single-molecule DNA sequencing tool by direct sequencing of DNA/RNA fragments. No amplification or leveling is needed, and the platform instead detects a direct electrical signal (Clarke et al., 2009). The template DNA is fragmented at first and hybridized on disposable glass flow cells. The most recently developed third generation of Helicos opened the door for transcriptomics without converting RNA to cDNA (Narayanasamy et al., 2016). This system has a >1 GB data output per day and generates billions of reads per run ranging from 25 to 35 bp (Shokralla et al., 2012). Helioscope may contribute to genome biology through direct sequencing of nucleic acids. Kapranov et *al.* (2012) obtained the sequence information by counting the abundance of short RNA (sRNAs) and the discovery of new sRNAs in culture cells with these technologies. However, high error rates (3–4%) (Table 2) and higher costs relative to other platforms might have limited the popularity of this technology (Loman et al., 2012).

8.5.5. SMRT sequencing

The Single-Molecule Real-Time (SMRT) sequencing technology was developed by the Pacific Biosciences in 2010, which allowed sequencing a single stretch of DNA molecule from a single/unique cell in real-time, although genome sequencing of microbes has mainly used a large number of DNA templates extracted from a homogeneous culture of an organism rather than a single cell (Table 2). The technology is scalable with high throughput, providing long reads and high consensus accuracy without the need for prior PCR amplification. SMRT changed the paradigm of genomic analysis by delivering much longer reads and built-in flexibility (Jiménez-Gómez et al., 2020; Sevim et al., 2019; Tedersoo and Anslan, 2019).

9. Conclusions and future prospects

Terrestrial ecosystems represent 30% of the surface of our planet, and the soil is a biocenosis consisting of microorganisms, soil fauna, and plant roots with only about 20% of living things currently known. Microorganisms play a major role in the soil environment, especially in the rhizosphere; they are involved in the biogeochemical cycling of essential elements, and other interactions which influence the structure or function of soil. Yet, the identification and characterization of these organisms pose many challenges (Zhou et al., 2015). There has been substantial progress in studying soil microbial diversity, due to the advances and increased uses of molecular technologies; they helped identify, and characterize the compositional and functional traits of a range of soil microbial communities. Most of the molecular tools today are highly automated for efficiently processing a large number of samples; they have become more efficient and less expensive tools for research. Despite the progress, much of the soil ecosystem remains little unknown due to the complexity of interactions (Juzan et al., 2012). There are also technical issues related to potential bias in RNA and DNA extraction, PCR, and bioinformatics. Sometimes the true abundance and interaction of different taxa in the soil environment can be difficult to determine based solely on molecular tools (Ahmad et al., 2011).

Recently, HTS tools/platforms have been developed and used extensively to study the soil microbial community. Illumina, Roche, and other platforms of high throughput sequencing can focus on targeted genes, functional or shotgun-metagenome sequencing (Zhou et al., 2015). Substantial progress has been made in understanding soil microbial communities using these new HTS technologies, despite some challenges that remained (Tedersoo et al., 2021). Indeed, the effective application of high-throughput molecular tools in studying soil microbial communities depends on the ability to analyze and interpret massive amounts of data properly, about biodiversity, functionality, and ecosystem stability. Further progress in bioinformatics may help in face of complex soil microbial communities (Abdelfattah et al., 2018; Amarasinghe et al., 2020; Ramirez et al., 2018; Xia et al., 2018; Zhou et al., 2015).

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