Chapter 18
Global Scenario of Soil Microbiome Research: Current Trends and Future Prospects

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Abstract The current chapter is focused on the microbiome investigations that have been used to understand the linkages between soil microbiota and their environments. Advanced molecular "Omic techniques" such as metagenomics, metatranscriptomics, metaproteomics and metabolomics have been employed to understand in situ microbiomes and their interactions with soil-ecosystem services at micro-scales. The potential advances in "Omics approaches" are facilitated by high-throughput next-generation sequencing techniques and the current work discussed upon implementation of these technologies in soil microbiome research at global scale. In this chapter, we have summarized recent advancements and the current state of knowledge in soil microbial diversity and soil-ecosystem functioning. Different high-throughput sequencing technologies, molecular "Omic techniques" and their limitations in soil microbiome research have been addressed. Genome-centric metagenomic approach was highlighted over gene-centric approach to understand soil microbiomes and their functions hitherto. Impacts of different physical, chemical and biological factors on soil microbial communities were reviewed in the current chapter. It is suggested that soil microbiomes can be exploited to alleviate the negative impacts of environmental changes for increased crop production.

Keywords Climate change · Ecosystem function · High-throughput sequencing technologies · Omic techniques, metatranscriptomics · Soil ecological engineering · Soil microbiome

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18.1 Introduction

Soil is one of the most complex ecosystems that harbor billion of microbiota. Soil microbial communities perform crucial roles in the elemental cycling of micro and macronutrients which are vital for the functioning of the above-ground ecosystem (Prasad et al. 2021). Nevertheless, systemic understanding of the soil microbial ecology is difficult due to the high degree of spatial heterogeneity that is present at micro-scales (Raynaud and Nunan 2014). DNA-based microbial taxonomy using phylogenetic markers (ribosomal RNA gene, ITS, etc.) were enumerated around 10^6 different archaeal and bacterial species and approximately 1 billion microbial cells in 10 g of soil (Roesch et al. 2007; Schloss and Handelsman 2006). Further, Trevors 2010 estimated around 10^{-9} genomes and 10^{-12} prokaryotic genes in a gram of soil. Recent metatranscriptomics and subsequent taxonomic annotation of agricultural soils revealed complex microbiota from the diverse origin, in the following order: Viruses < Eukaryotes < Archaea < Bacteria (Sharma and Sharma 2018).

It is said that only 1% of soil bacteria are cultivable in the laboratory and is known as a great plate count anomaly. The major fraction (99%) of soil microbiomes is uncultivable in nature. Therefore, understanding the factors driving soil microbiome structure and their interactions (physical, chemical, biological, etc.) across a contrasting ecological gradient is difficult by using conventional microbiological tools. Recent advancements in high-throughput sequencing technologies enlightened the previously unknown soil microbiome compositions without the necessity for cultivation and enable us to study complex soil microbiomes in detail using metagenomics/transcriptomics (Thompson et al. 2017a, b). In this approach, genomic material DNA or RNA will be extracted from the microbiota of soil sample of interest followed by high-throughput sequencing of gene or transcript. Later the data will be accurately annotated and corresponding cellular or ecological functions will be precisely identified (Prosser 2015). The inferences drawn in these studies could be implemented in sustainable agriculture and other land-use management practices (Fig. 18.1).

According to Prosser (2015) "metagenomics and metatranscriptomics are defined as the characterization of all genes and RNA transcripts, respectively, in a given soil/environment sample". Further, he has pointed that "single-gene/amplicon-specific high-throughput sequencing studies are sometimes described as "metagenomics" but include data for only one gene and, therefore, do not encompass the holistic element of the omics". During the past decade, many "omics" studies have been conducted to elucidate the soil microbiomes in a wide variety of environments. In this chapter, we especially highlighted the importance of omic approaches to address the soil microbiomes and ecosystem function. Different high-throughput sequencing technologies and their characteristics have been well summarized in Table 18.1. Further rhizospheric microbiomes and the effect of different environmental perturbations on soil microbial diversity and activity have been discussed (Fig. 18.2 and Table 18.2). Potential opportunities available in soil microbiome research are highlighted at the end (Fig. 18.3).

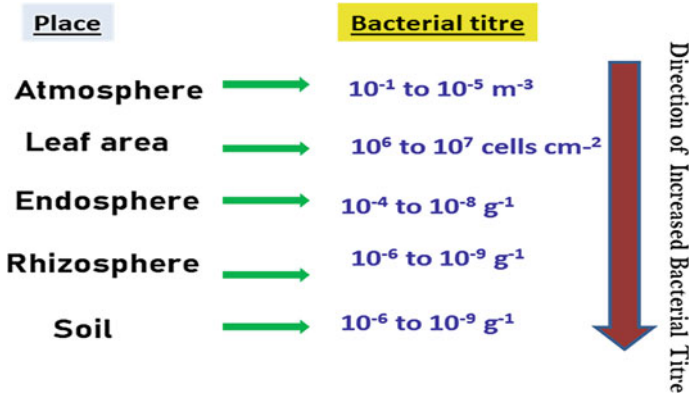

Fig. 18.1 Bacterial counts per unit in different habitats

18.2 Soil Microbiome Research in the "Omics" Era

Recent advancements in sequencing technologies along with increased computational power, including a significant reduction in sequencing costs have facilitated a substantial number of soil microbiome studies (Table 18.3, Jansson and Hofmockel 2018; Kang et al. 2019; Gans 2005; Wu et al. 2011; Prosser 2015; Fierer 2017). Further, high-throughput sequencing studies have succeeded in enlightening the previously unknown microbial diversity of soil microbial communities across a wide variety of soil habitats (Thompson et al. 2017a, b).

The global scenario of soil microbiome research commonly involves three different kinds of sequencing strategies: (1) high-throughput amplicon-based metataxonomic sequencing studies, which involves amplification of targeted regions of phylogenetic markers such as "intergenic spacer region" for Eukaryotes and 16S ribosomal RNA gene (16S rRNA) for archaea and bacteria (2) metagenomics/metatranscriptomics which involves high-throughput sequencing of the metagenome or transcriptome in a specific soil (3) metaproteomics which focuses on the detection of fragmented and separated proteins followed by sequencing with the combination of liquid chromatography-mass spectrometry (LC-MS), and (4) metabolomics wherein detection of metabolites through nuclear magnetic resonance spectroscopy (NMR) or mass spectrometry (LC-MS). Applications of different advanced technologies used in the soil microbiome research were comprehensively summarized in Table 18.3. These molecular approaches unraveled the physiological mechanisms behind unculturability and identified the factors suitable for growth promotion of previously uncultivable microorganisms in the laboratory (Stewart 2012; Biswas and Sarkar 2018; Yadav et al. 2015).

DNA-based high-throughput sequencing of 16S rRNA gene (V3–V4 region) demonstrated that dominant bacterial taxa in agriculture soils were found to be *Actinobacteria, Gemmatimonadetes, Proteobacteria, Acidobacteria* and *Chloroflexi*. pH

Table 18.1 Characteristics of different next-generation sequencing platforms used in soil microbiome research

Platform	Year of establishment	Maximum Sequencing length/yield	Runtime	Specific feature	Technology	Error rate
Second-generation sequencing technologies						
Illumina	2006	150 bp/2–600 Gb	27–11 days	Highest throughput Signal interference among Long-/short-run times, low capital cost, low-cost per Mb	Cleavable dye terminators (Reversible terminators)	10^{-2} to 10^{-3}
Roche-454	2005	200–700 bp/700 Mb	24 h	Long read lengths	emPCR, pyrosequencing	10^{-3} to 10^{-4}
Ion torrent	2010	200 bp/200 Mb	2 h	Stable sequence quality, better sequencing GC depth distribution	emPCR, H+ detection	3×10^{-2}
SOLiD/ABI Life technologies	2006	35–50 bp/120 Gb	7–8 days	High-throughput, highest accuracy two-base encoding provides inherent error correction	emPCR, ligation with cleavable dye terminators	10^{-2} to 10^{-3}
Third generation sequencing technologies						
Pacific biosciences	2010	1500 bp/100 Mb	2 h	Single-Molecule Real-Time (SMRT) sequencing technologies	Adding hairpin adapters legated on each end of the linear DNA molecule, to create a "SMRTbell" template. Sequencing dyes are phospholinked to the nucleotide	1.5×10^{1}

(continued)

Table 18.1 (continued)

Platform	Year of establishment	Maximum Sequencing length/yield	Runtime	Specific feature	Technology	Error rate
Helicos™ biosciences Ω	2007	25–55 bp/35 Gb	3–6 days	Very small amounts of starting material. Overcoming the limitations of short read length. sequence the same segment of DNA multiple times for highly accurate sequences	Single-molecule specific Sequencing. Single base, reversible dye terminator extension reactions	0.2%
Nanopore/Oxford Nanopore Technologies/1 Gb	2007	>5000 bp/6 × 10^4	48–72 h	Strand sequencing wherein intact DNA is ratcheted through the nanopore base-by-base	Real-time Single-molecule sequencing	34%

Ω: Thompson and Steinmann (2010)

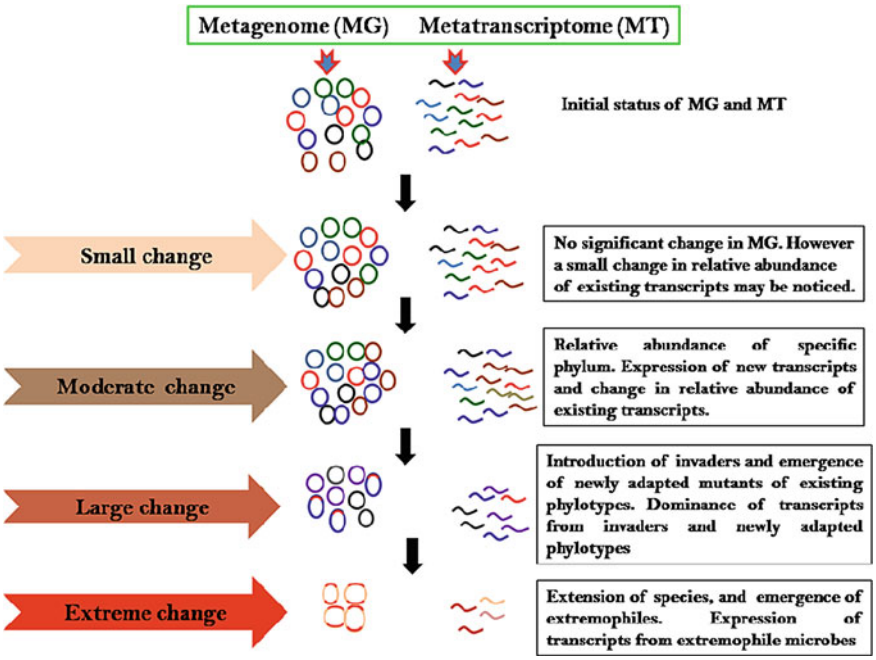

Fig. 18.2 Effect of a change in environmental condition on the response of soil microbiomes as revealed by metagenomics and metatranscriptomics. The concept illustrated in this figure was adopted, modified and redrawn from Prosser (2015)

was found to be one of the major soil characteristics that confer bacterial communities in agriculture soils. A significant positive correlation was found between soil pH, soil bacterial α-diversity and abundance of operational taxonomic units. Results demonstrated that soil pH is a relatively more important factor than nutrients in shaping soil bacterial communities in agricultural soils.

Metatranscriptomics revealed that the diversity of the rhizosphere microbiome has differed from bulk soil and in between plant species, for example, Pea had a stronger effect on the rhizosphere microbiome than wheat and oat resulted in a different rhizosphere community. A comprehensive understanding of the microbial communities of the paddy soils driving methane metabolism via the formation hydrogen and acetate has been established by RNA-based metatranscriptomics (Masuda et al. 2018). Deep metatranscriptomics analysis revealed that in the anoxic layer, *Deltaproteobacteria, Planctomycete, Acidobacteria* actively generated hydrogen; Further, *Acidobacteria, Betaproteobacteria, Alphaproteobacteria* and *Deltaproteobacteria* generated acetate; Utilizing both hydrogen and acetate as substrates for methanogenesis, the archaeal genera such as *Methanoregula, Methanocella* and *Methanosaeta* actively produced methane in anoxic layers. Subsequently, in the oxic layer, methanotrophs related to *Methylogaea* and *Methylocystis* readily oxidized methane (Masuda et al. 2018).

Table 18.2 Effect of various environmental changes or disturbances on soil microbiome

Environmental change/disturbance	Techniques used	Soil microbiome response	References
Inorganic and organic contaminants into agriculture soils for 90 days	*16S rRNA* amplicon sequencing and shotgun metagenomics	Resilience and succession patterns of soil microbial diversity and community structure in response to chemical contamination	Jiao et al. (2019)
Land-use patterns and system restoration activities	High-throughput sequencing of V3–V4 region of bacterial *16S rRNA* as well as the ITS1 region	The alpha-diversities of bacteria, fungi and *Acidobacteria* were affected by land-use change. A higher abundance of bacteria, *Acidobacteria* and fungi were noticed in the arable land and lowest in the wetland soils. The composition of soil microbiomes was altered by changing land use. This study highlights that Once the soil microbial community is altered by human activity, it might be difficult to restore the same to its original state	Sui et al. (2019)
Diesel oil and unleaded petroleum polluted soils	High-throughput sequencing of bacterial 16S rRNA gene	The petroleum pollution disturbed the soil metabolic processes and the stability of the soil microbiome. The greater negative impact was noticed with diesel oil that unleaded petroleum	Borowik et al. (2019)
Hg pollution in soils across china	Shotgun metagenomic sequencing. The high-throughput V4 region of the bacterial *16S rRNA* sequencing	Hg pollution has significant negative impacts on multiple taxonomic and functional attributes such as bacterial diversity, abundance, ecological clusters, key soil processes and functional genes. An increase in soil Hg toxicity was linked to anthropogenic activities and will lead to predictable shifts in the taxonomic and functional attributes	Liu et al. (2018)
Agriculture practices and seasonal effects	Shotgun metagenomics approach	Soil microbial communities under seasonal changes were shaped principally by water deficit, with a strong increase of Proteobacteria and Actinobacteria members in the rainy and dry seasons, respectively. In contrast, nutrient availability played a significant role in driving the microbial community in agriculture-affected soils. Soil microbiomes of preserved and agriculture practices showed differences in the genetic potential for C acquisition and nutrient cycling	Lacerda Júnior et al. (2019)
Fungicides	Next-generation sequencing (NGS) method, liquid chromatography tandem-mass spectrometry (LC-MS/MS)	Obvious negative effect of fungicides on the composition of soil microbiota and in the biochemical properties of soil by inhibiting the activity of almost all tested extracellular enzymes	Baćmaga et al. (2018)

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Table 18.2 (continued)

Environmental change/disturbance	Techniques used	Soil microbiome response	References
Soil pH and PAH contamination	High-throughput V4 region of the bacterial *16S rRNA* sequencing	pH was found to be the principal determinant of the bacterial community in arable soils, indicative of a more substantial influence of acidification than PAH pollution on bacteria-driven ecological processes. Bacterial community structure was strongly related to soil pH, with higher diversity in neutral samples and lower diversity in acidic soils	Wu et al. (2017)
Type of the ecosystem, various soil variables such as pH, OC, C/N ratio, latitude, potential evapotranspiration, temperature, etc.	DNA fingerprinting and sequencing (T-RFLP) analyses	The diversity and species richness of soil bacterial communities differed by type of the ecosystem. The differences in mcirobiome structure was largely explained by soil pH. Higher bacterial diversity was observed in neutral soils and lower diversity was noticed in acidic soils. Results suggested that microbial biogeography is primarily controlled by edaphic variables which is different from the biogeography of "macro" organisms	Fierer and Jackson (2006)
Different levels of N deposition and seasonal changes; Soil properties	High-throughput sequencing of V4 region of the bacterial *16S rRNA*; and ITS regions of Fungal 18S rRNA	Responses of soil microbial community to N addition are significantly varied in different seasons. The abundance and diversity of soil microbial communities were significantly affected by N addition and seasonal changes. Particular response of specific microorganisms to different N deposition was observed. Results indicate that specific microbial taxa could be used as biomarkers/biological indicators for microbial responses to the N addition and seasonal changes. pH, dissolved organic carbon, dissolved organic N and Total N was likely to be key variables for soil microbial community	Yan et al. (2017)
Heavy metals Cu and As	Metagenomics of *amoA* gene	Soil ammonia-oxidizing microbes were vulnerable to the stress of heavy metals Cu and As in acidic alfisols. The effect of As and Cu on the community structure of ammonia-oxidizing archaea (AOA) was not significantly different from unpolluted soil. Phylogenetic analysis of *amoA* gene revealed that the Thaumarchaeal-AOA group 1.1b plays an important role in nitrification in oligotrophic acidic soils and provide further importance of this group in ammonia oxidation in heavy metal polluted soils. Results suggested that soil contamination by Cu and As may have a significant negative impact on soil potential nitrification rates and soil fertility	Subrahmanyam et al. (2014a)

(continued)

Table 18.2 (continued)

Environmental change/disturbance	Techniques used	Soil microbiome response	References
Industrial effluent pollution (IWE)	Molecular fingerprinting of soil microbiome by DGGE, cloning and sequencing analysis of phylogenetic and functional gene markers	The apparent deleterious effect of industrial waste effluent (IWE) on soil microbial activity, diversity and soil function was observed. Bacterial community shift in the IWE-affected soils were observed. Bacterial genera such as *Acidobacteria, Firmicutes* and *Actinobacteria* were predominant members in polluted soils indicating bacterial tolerance to pollutants. The study proposed specific bacterial phyla along with soil enzyme activities that can be used as relevant biological indicators for assessing long-term pollution of soils. Further, Ammonia-oxidizing bacteria (AOB) was more abundant than Ammonia-oxidizing archaea (AOA) in the highly contaminated soil. However, predominance of AOA was noticed in uncontaminated and moderately contaminated fields. Reduced diversity accompanied by apparent community shifts of both AOB and AOA populations was detected in highly polluted soils	Subrahmanyam et al. (2014c, 2016)
Soil pH	High-throughput sequencing of V4 region of the bacterial *16S rRNA*	pH was found to be the main soil parameter that determined microbial diversity, composition and biomass in the Park Grass experiment soil (PGE). This could be due to the mechanism of the pH for mediation of nutrient availability in the soil. Bacterial genera such as *Bradyrhizobium, Bacteroides*, *Clostridium*, *Mycobacterium, Paenibacillus*, *Rhodoplanes* and *Ruminococcus* were abundant in the soil. The addition of nitrogen decreased the soil pH through increased nitrification and soil C/N ratio	Zhalnina et al. (2015)

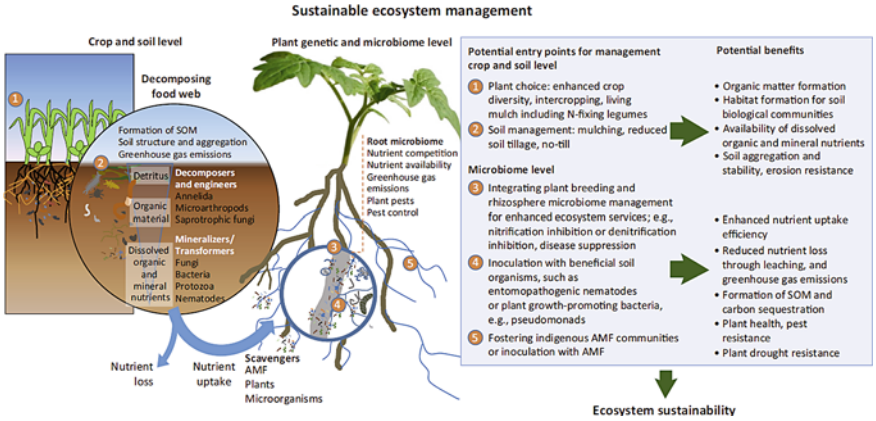

Fig. 18.3 Different soils ecological engineering approaches for local ecosystem management. The figure was adopted from Bender et al. (2016)

In a study, Sharma et al. (2019) demonstrated a high expression of microbial transcripts in agricultural and organic soils with diversified metabolic functions. This study provided insights about certain molecular markers which are indicative of metal and pesticide contamination in soil. It was observed that Archaea had relatively a greater role than bacteria in the soil nitrification process of polluted environments. Particularly, over-expression of aromatic hydrocarbon-degrading transcripts indicates the importance of soil microbiomes in the biodegradation of pollutants in agroecosystems (Sharma et al. 2019).

Community shifts in the structure and composition of the soil microbiomes are considered as biological indicators for assessing long-term pollution of soils (Subrahmanyam et al. 2011, 2014b, 2016; Ros et al. 2020; Liu et al. 2018; Kumar et al. 2020a, b, c, 2021). RNA-based metatranscriptomics of agriculture soils indicated that higher expression of transcripts related to heavy metals bioremediation (e.g., thioredoxin reductase, mercuric ion reductase, cobalt-zinc-cadmium resistance protein, etc.). Enhanced RNA transcripts in soils were related to soil C, N, P and S cycles (e.g., PstA, PstB SoxX, SoxD, SoxA, SoxB, etc.). Large quantity of the transcripts involved in soil denitrification suggesting its key role in the loss of nitrogen in agriculture soils. Transcripts of sulfur metabolic pathways demonstrated a higher expression of alkane sulfonate monooxygenase, arysulfatase and sulfonate monooxygenases. This is indicative of active sulfur metabolism wherein microbiomes in these ecosystems were able to acquire sulfur from organosulfur substances. Higher abundance of pesticides and heavy metal degrading bacteria such as *Pseudomonas*, *Streptomyces Achromobact*er, *Bacillus*, *Sphingobium*, *Serratia*, *Micrococcus*, *Desulfobulbus*, *Ralstonia*, *Acinetobacter*, *Desulfobacterium*, *Thiobacillus Rhodospirillum* and *Arthrobacter* were noticed in agricultural soils (Sharma and Sharma 2018; Yadav et al. 2020).

Table 18.3 Advanced molecular "omic techniques" used to establish soil microbiomes and ecosystem function

Soil	Source of sample	Technique/Tools	Observation	References
Agricultural soil, Norwich, UK pH 7.49	Rhizosphere of wheat, Oat, Pea and an Oat mutant	RNA-based metatranscriptomics	The diversity of rhizosphere microbiomes were differed from bulk soil and between plant species. Pea had a stronger effect on the rhizosphere microbiome than wheat and oat resulted in a different rhizospheric community. The relative abundance of eukaryotes in the Oat and Pea rhizospheres was fivefold higher than in the bulk soil or in the wheat rhizosphere. Cereals such as wheat and oat rhizospheres were enriched with cellulose degraders, whereas a legume rhizosphere was enriched for hydrogen oxidizing microbes	Turner et al. (2013)
Cd-contaminated soil, Sichuan province, China Soil pH 6.6 to 6.7	Soils were obtained from private land and Cd-contaminated site next to the sewage outlet of three phosphate rock chemical plants	DNA-based Metagenomics followed by COG and KEGG annotation	Cd pollution decreases both the diversity and function of soil microbial communities. It is observed that *Sulfuricella, Nitrosospira* and *Nitrososphaera* were abundant in Cd polluted soils where as *Candidatus Solibacte, Candidatus Koribacter* and *Bradyrhizobium* were the dominant genera in unpolluted soil. The relative abundance of dominant metabolic (KEGG) pathways increased in the Cd polluted soil. The enriched pathways cd polluted soils were biosynthesis and degradation of fatty acids, amino acids, and nucleotides	Feng et al. (2018)
Pristine soil, agriculture and Organic soils. Agriculture soil had pH of 7.5 to 8.0; soil was acidic and had pH of 6.5, Punjab, India	Agriculture field and a site free from agriculture	RNA-based metatranscriptomics	Proteobacteria are the dominant bacterial phyla in both pristine and agricultural soils. The top three abundant microbial phyla in agriculture soil was in the order of Proteobacteria > Ascomycota > Firmicutes, whereas in organic soils the order was Proteobacteria > Cyanobacteria > Actinobacteria Several soil microbial RNA transcripts which are related to ammonification, nitrification, stress response, and alternate carbon fixation pathways were overexpressed in agricultural soil. Further, transcripts of archaeal origin had high expression in agricultural soils than in organic soils. This indicates the active role of Archaea in metal- and pesticide-contaminated environment. It was observed that the nitrification process was dominated by Archaea as compared to bacteria in metal and pesticide polluted soils	Sharma et al. (2019)
Paddy field in Niigata Agricultural Research Institute, Japan	Paddy soil	RNA-based metatranscriptomics (Both rRNA seq and mRNA seq analysis)	Transcriptional profiles of genes encoding the enzymes that catalyze the formation of hydrogen, acetate and methane in paddy fields were comprehensively established. Deep metatranscriptomics analysis revealed that in the anoxic layer, *Deltaproteobacteria, Planctomycete, Acidobacteria* actively generate hydrogen; Further, *Acidobacteria, Deltaproteobacteria Betaproteobacteria*, and *Alphaproteobacteria* generate acetate; Utilizing both hydrogen and acetate as substrates for methanogenesis, the archaeal genera such as *Methanoregula, Methanocella* and *Methanosaeta* actively produce methane in anoxic layers. Subsequently, in the oxic layer, methanotrophs related to *Methylogaea* and *Methylocystis* oxidize methane	Masuda et al. (2018)

(continued)

Table 18.3 (continued)

Soil	Source of sample	Technique/Tools	Observation	References
Soil samples from wheat fields treated with suppressive and non-suppressive (soilborne fungal pathogen *R. solani* AG8). Lithocalcic Calcarosol	Rhizosphere of Wheat	RNA-based metatranscriptomics followed by COG, KEGG, and SEED functions	In response to the infection of wheat roots by R. solani, both suppressive and non-suppersive soils had a different expression of functional genes. Suppressive samples had higher expression of a terpenoid biosynthesis gene i.e. polyketide cyclase and other cold shock proteins. Non-suppressive samples showed greater expression of antibiotic genes which is involve in pyrrolnitrin synthesis (e.g., Chloroperoxidase) and phenazine and its transcriptional activator proteins Further, genes involved in detoxifying superoxide radicals (ahp, cat, gpx1, bcp, trx, sod, etc.) and reactive oxygen species were expressed in the non-suppressive wheat rhizosphere samples	Hayden et al. (2018)
Soil from New Caledonia, a biodiversity hotspot located in the southwest Pacific	Surface serpentine soils (Depth 10 cm)	DNA-based metagenomics and high-throughput sequencing	Microbial species abundance, composition, and richness were linked to the surface vegetation type and the dominant plant species. Each plant possesses its own microbial community resulting from multiple interactions between abiotic and biotic factors. Soil fungal and bacterial communities are affected by diverse edaphic parameters and also site-specific	Gourmelon et al. (2016)
200 soil samples from Arctic region	Top soil (15 cm depth)	DNA-based metagenomics and high-throughput sequencing	Spatial and edaphic factors played an important role in the structure of Arctic soil bacterial communities. It was elucidated that pH as the key environmental driver shaping Arctic soil bacterial communities. The core microbiome of all the 200 samples composed of 13 OTUs, mainly affiliated to *Proteobacteria* and *Acidobacteria.* The *Alphaproteobacteria*, especially the *Bradyrhizobiaceae* family, was most abundant in acidic soils and decreased along with increasing pH, whereas *Betaproteobacteria,* especially the *Comamonadaceae* family decreased along with decreasing pH	Malard et al. (2019)
Soils collected from Arabidopsis, pine, corn and potato growing fields, USA		Metabolomics with GC-MS analysis; DNA-based pyrosequencing	Plant growth patterns, as well as leaf metabolome composition, have been differentially affected by soil microbiomes GC-MS analyses revealed that soil microbiomes applied in the rhizosphere of *Arabidopsis thaliana* were able to modulate leaf metabolome and plant growth	Badri et al. (2013)

(continued)

Table 18.3 (continued)

Soil	Source of sample	Technique/Tools	Observation	References
Soils collected from agriculture field Punjab, India	Bulk soil (top 10 cm)	RNA-based metatranscriptomics	Studies indicated that higher expression of genes involved in the transformations of heavy metal (e.g., Thioredoxin reductase, mercuric ion reductase, Cobalt-zinc-cadmium resistance protein, etc.). Increased number of transcripts related to C, N, P and S cycles (e.g., PstA, PstB SoxX, SoxD, SoxA, SoxB, etc). Higher abundance of the transcripts linked to the denitrification process suggests its major role in process of nitrogen loss in the soils Transcripts of sulfur metabolic pathways demonstrated that higher expression of alkane sulfonate monooxygenase, arysulfatase, sulfonate monooxygenases, etc. This is an indication of active sulfur metabolism wherein microbes in this ecosystems acquiring sulfur from organosulfonated substances Higher abundance of pesticides and heavy metal degrading bacteria (e.g., *Pseudomonas*, *Streptomyces Achromobacter*, *Bacillus*, *Sphingobium*, *Serratia*, *Micrococcus*, *Desulfobulbus*, *Ralstonia*, *Acinetobacter*, *Desulfobacterium*, *Thiobacillus Rhodospirillum, Arthrobacter*) were noticed in agricultural soils	Sharma and Sharma (2018)
Soils collected from the Tea (*Camellia sinensis*) growing experimental station, Fujian China	Rhizosphere of *Camellia sinensis* fields treated with organic fertilizers	DNA-based high-throughput amplicon sequencing	The use of organic fertilizer (OF) positively increased beneficial bacteria such as *Nitrospirales*, *Streptomycetales*, *Burkholderiales*, *Gemmatimonadales*, *Ktedonobacterales*, *Myxococcales*, *Acidobacteriales* and *Solibacterales* in the rhizosphere of *Camellia sinensis* Results demonstrate that soil microbiome composition and recruitment of beneficial bacteria into the rhizosphere of tea were influenced by organic fertilizer amendment. Further, OF improved tea quality and substantially decreased heavy metals in the rhizosphere and in tea leaves	Lin et al. (2019)
Tropical forest, Yucatan Peninsula Mexico	Surface soil ata depth of 10 cm in the we	DNA-based high-throughput sequencing of 16S rRNA gene V3-to-V4 region	Soil heterogeneity and rainfall seasonality were the main factors that correlate well with soil bacterial community structure and function (e.g., potential nitrification and denitrification.) in this tropical forest	Pajares et al. (2018)
The experimental region, Jiangsu Province, China	Soil were collected from dry lands and paddy fields at a depth of 0–20 cm	DNA-based high-throughput sequencing of bacterial V3–V4 region and Fungal ITS region	Bacterial phyla *Firmicutes* and *Actinobacteria* and were dominant in paddy field and dry land and respectively. *Ascomycota* was a dominant member in fungal communities of both paddy field and dry land. Conversion of dry lands to paddy field showed an impact on diversity and molecular ecological networks in soil microbiomes. Interspecific relationships and molecular interaction networks among bacterial and fungal populations in paddy soils were relatively simpler and unstable than in dry lands. Results conclude that large-scale conversion of dry land-to-paddy fields may reduce the ecological stability of regional soil. A significant correlation ($p < 0.05$) between change in soil environmental factors, such as electrical conductivity, organic matter, pH, and available potassium directly affected the soil microbiome come community structure	Li et al. (2020)

(continued)

Table 18.3 (continued)

Soil	Source of sample	Technique/Tools	Observation	References
Composts derived from different by-products and sludge from vegetable and fruit processing Industries rationing the Region of Murcia	Matured Compost	Metaproteomics and DNA-based high-throughput sequencing of bacterial V3–V4 region	Microbiomes of suppressive and non-suppressive compost vary at the phylogenetic levels. The proteins identified were assigned to the functions affiliated to the cell wall structure, carbohydrate and inorganic ion transport and metabolism. The study proposed a phyla Proteobacteria could be used as a bio-indicator for detection of *Phytophthora nicotianae* suppression in the compost	Ros et al. (2020)
sugarcane rhizospheric soil	Rhizospheeric soil	Metaproteomics	The comparative soil metaproteomics analysis deciphered that sugarcane ratooning induced changes in the expression patterns of soil proteins originated from microbes, plants, and fauna. A majority of upregulated plant proteins were affiliated to stress response, amino acid and carbohydrate metabolism whereas most of the upregulated microbial proteins were affiliated to signal transduction and membrane transport mechanisms. In conclusion, sugarcane ratooning practice negatively impacted soil enzyme activities involved in carbon, nitrogen and phosphorus cycles. Catabolic diversity of the microbial community and the expression level of metaproteome were significantly reduced by rationing of sugar cane in agriculture soil	Lin et al. (2013)
Agriculture soils from 206 locations at Jilin province, China	Topsoil at a depth of 0–30 cm	DNA-based high-throughput sequencing of V3–V4 of the 16S rRNA Gene	The dominant taxa in agriculture soils were found to be *Actinobacteria, Gemmatimonadetes, Proteobacteria. Acidobacteria* and *Chloroflexi.* pH was found to be the major soil characteristic that confers bacterial communities in agriculture soils. A significant positive correlation was found between soil pH, soil bacterial α-diversity and abundance of operational taxonomic units. Results demonstrate that soil pH is a relatively more important factor than nutrients in shaping soil bacterial communities in agricultural soils. Biogeographic distribution of microbes and soil ecological functions are directly influenced by soil pH	Wang et al. (2019)
Different rhizospheric soils, China	Rhizosphere of rice, sugar cane, and tobacco	Metaproteomics	Most of the proteins (1/3rd) could not be identified by existing MALDI-TOF/TOF/MS. Very complex interactions were observed between microbiomes and plants in a crop rhizosphere. Functional analysis proteins revealed various metabolic pathways and signal transductions involved in the soil biotic community	Wang et al. (2011)
Copper mine tailings, Upper Peninsula, Michigan, USA	Copper mine soil in the pot experiment	Metabolomics and metaproteomics	Maize metabolomic analysis revealed that plant growth-promoting bacteria inoculation upregulated hormone biosynthesis, photosynthesis and TCA cycle metabolites. The metaproteomic analysis identified the upregulation of several proteins related to plant development and stress response. The ability of plant growth-promoting bacteria to modulate and interconnected metabolic pathways could be exploited to enhance crop productivity in polluted soils	Li et al. (2014)

Metabolomics has the potential to characterize the plant–soil biochemical interactions in the soil ecosystem. Metabolomics has advantages over conventional "Omic technologies" by determining key metabolites which are utilized by both plants and microbes. However, only a few metabolomics studies were conducted in soil microbiome research (Li et al. 2014). Maize metabolomic analysis revealed that inoculation of plant growth-promoting bacteria upregulated the hormone biosynthesis, photosynthesis and TCA cycle metabolites. The ability of plant growth-promoting bacteria to transform soil metabolic pathways could be utilized to enhance production and productivity of agriculture crops in polluted soils (Li et al. 2014).

Metaproteomics indicated that proteins expressed in the agriculture crops rhizosphere are unique and are not identified by existing MS/MALDI-TOF. Very complex interactions were observed between microbiomes and plants in a crop rhizosphere. Functional analysis of proteins revealed several pathways and metabolic signal transductions involved in the soil biotic community (Wang et al. 2011). Metaproteomics of maize soils identified the upregulation of several proteins related to plant development and stress response (Li et al. 2014). Applications of omic techniques in soil microbiome research were comprehensively reviewed by many authors (Biswas and Sarkar 2018; Krishna et al. 2019).

18.3 Different Sequencing Technologies in Soil Microbiome Research

Although Sanger sequencing has been used for decades in soil microbial ecology, it has certain limitations such as time consuming, not economic and is not a high-throughput technology. Consequently, it is essential to develop economic high-throughput sequencing methodologies that will provide information on the soil microbiomes and their functions in different realms. In the recent past, new sequencing technologies were evolved and subsequently commercialized by different firm's viz. Applied Biosystems, Thermo Fisher Scientific, Roche Life Sciences and Illumina (Table 18.1). Generally, these methods were referred to as next-generation (NGS) or second-generation sequencing technologies which revolutionized soil microbiome research. Many sequencing platforms employing NGS have been developed, including Illumina/Solexa platform, Ion Torrent technology, SOLiD and pyrosequencing (Krishna et al. 2019), PacBio etc. Comprehensive details for different sequencing platforms were summarized in Table 18.1. Different sequencing technologies and their chemistry have been reviewed by previous authors (Ambardar et al. 2016; Thompson and Steinmann 2010; Krishna et al. 2019).

18.3.1 *"Gene-centric" Versus "Genome-centric" Metagenomics*

Molecular analysis and investigation of individual target genes obtained from metagenomes are known as "Gene-centric" metagenomics. Most of the soil microbiome research at the global scale involves a gene-centric approach. It mainly targets amplicon-specific sequencing of phylogenetic markers such as 16 rRNA, ITS, etc. So that it could not be possible to establish the origin of the genes like which genes originated from which genome. Therefore, it is difficult to establish a link between soil function and microbial phylogeny based on the taxonomic genes. Subsequently, it is difficult to reestablish interrelated metabolic pathways operating in complex soil microbiomes with the help of gene-centric metagenomics. The main technical limitation in the sequencing of single-cell genome is difficulty in annotating a full coverage of genome assembly. These limitations can be addressed with genome-centric metagenomics.

In contrast to gene-centric' metagenomics, "genome-centric" metagenomics is considered to be a holistic approach as it aims to obtain complete sequences of genomes in a given soil sample through single-cell genomics or the Denovo assembly of individual genes. Few disadvantages of genome-centric' metagenomics involve the risk of formation of chimeras during genome assembly, in which segments of other microbial genomes are assembled. These limitations can be minimized by bioinformatics and technological advancements. Kougias et al. (2018) employed a genome-centric metagenomics approach and reported a spatial distribution of lignocellulose degrading microbiota with diverse metabolic functions. Most recently "genome-centric metagnemics" were employed to resolve microbial diversity of denitrification pathways, coral reefs and the response of bacteria to operational disturbances in activated sludge (Gao et al. 2019; Pérez et al. 2019; Glasl et al. 2020). A detailed account of Gene-centric' versus "genome-centric" metagenomics was discussed by Prosser (2015).

Metatranscriptomics provide us to understand the functional roles of microorganisms in soil-ecosystem services. Nevertheless, the diversity and composition of microbiomes in diverse soils are rarely addressed owing to enormous habitat complexity and micro-scale heterogeneity. Furthermore, recent advancements in computational biology and the development of algorithms such as Check-M, MetaBAT and MaxBin, etc., facilitate us to reconstruct metabolic pathways of microbial genomes in complex soil microbiomes (Kang et al. 2019; Wu et al. 2011).

18.3.2 *Functional Potential of Soil Microbiomes to Environmental Changes/Disturbances*

Understanding soil microbiomes and their potential multifunctionality under contrasting environmental factors such as nutrient availability, pH, temperature,

moisture, etc., is a complex subject in soil ecology (Yadav et al. 2020). It is essential to understand the dynamic responses of global soil microbiomes to physical, chemical, biological changes including soil-plant-microbe interactions for developing/predicting long-term soil-ecosystem models. However, small numbers of investigations have employed multi-omics technologies to decipher the impact of soil contamination/environmental changes at functional and taxonomic levels in the soil microbiome (Jiao et al. 2019). Identifying the factors for microbial community stability such as "resilience (the degree of rate of recovery after disturbance) and resistance (inherent capacity of insensitivity to disturbance)" is of paramount importance for forecasting microbiome response to environmental stress. Comprehensive details on concepts of microbiome resilience and resistance were reviewed by Shade et al. (2012). Measuring the soil microbiome response to a disturbance has been a subject of interest for many decades.

Agricultural ecosystems are currently facing various anthropogenic and environmental perturbations such as climate change, pollutants, heavy metals, antibiotics pesticides, fertilizers and organic residues (Trenberth et al. 2014; Callaway et al. 2011, Subrahmanyam et al. 2014a, c; Prasad et al. 2012; Singh et al. 2020) (Table 18.2). Soil microbes play significant roles in driving the global biogeochemical cycles (C, N, P, S, Fe, etc.) and recycling of organic and inorganic elements (Falkowski et al. 2008; Subrahmanyam et al. 2014b). Since microbes plays a crucible in soil-ecosystem functioning, it is imperative to elucidate spatio-temporal dynamics of soil microbiomes and their diversity under contrasting disturbances. This information is required to mitigate environmental pollution and mitigate agro-ecosystem contamination.

Metatranscriptomics is considered to be advanced technology to capture functional gene expression patterns in soil microbiomes and subsequently investigates their responses to environmental perturbations. The effect of a change in environmental condition/disturbance on the response of soil microbiomes as revealed by metagenomics and metatranscriptomics was comprehensively illustrated in Fig. 18.2. A small change in the soil environment (temperature, pH or any disturbance) is unlikely to change any significant soil microbiome community composition. This could be due to physiological plasticity and flexibility within the prevailing microbiome (Terzaghi and O'Hara 1990; Prosser 2015). However, a little environmental change in the soil-ecosystem could lead to a subtle change in both metabolic profiling and activity which can be reflected in metatranscriptomics. Such type of responses would not be traced in metagenomes as discussed earlier (Prosser 2015); A moderate environmental impact could lead to a change in the distribution of the different phylotypes at the metagenomics level. However, at the metatranscriptomics stage, one can notice a relative change in the expression of new genes which belong to phylotypes adapted to environmental disturbance. A change in the relative expression of existing transcripts was also noticed at the metatranscriptomics level. Large and extreme changes in the soil environment could possibly make either expression of new RNA transcripts (At metatranscriptomics level) or extinction of susceptible phylotype or the invasion of new species at metagenomics level. Extreme changes in the soil-ecosystem may also induce mutations/adaptations in existing phenotypes

subsequently expression of new genes contributes to a different kind of metatranscriptome. Table 18.2 summarizes the important observations in microbiome research with response to soil physical, chemical and biological disturbances.

The diversity and species richness of soil bacterial communities differed by type of the ecosystem (Table 18.2; Fierer et al. 2009, Fierer and Jackson 2006). The differences in microbiome structure were largely explained by soil pH. Higher bacterial diversity was observed in neutral soils whereas lower bacterial diversity was noticed in acidic soils (Wu et al. 2017). Results suggested that microbial biogeography is primarily controlled by edaphic variables which are different from the biogeography of "macro" organisms (Fierer and Jackson 2006). The abundance and composition of soil microbiomes were greatly influenced by soil pH. This could be due to the mechanism of the pH for mediation of nutrient availability in the soil. Bacterial genera such as *Bradyrhizobium, Bacteroides*, *Clostridium*, *Mycobacterium*, *Paenibacillus*, *Rhodoplanes* and *Ruminococcus* were abundant in the soil (Zhalnina et al. 2015; Wu et al. 2017).

Land-use patterns and system restoration activities showed a greater effect on soil microbiomes (Sui et al. 2019). The diversities of fungi, bacteria, and *Acidobacteria* were influenced by the change in land-use patterns. A low abundance of bacteria, *Acidobacteria* and fungi were noticed in the wetlands and their abundance was substantially increased in arable land (Sui et al. 2019). The composition of soil microbiomes was altered by changing land use. The community structure of soil microbiomes was influenced by seasons and the diversity was shaped principally by water scarcity. A higher abundance of *Proteobacteria* and *Actinobacteria* were noticed in the rainy and dry seasons, respectively. In addition to this, the availability of nutrients also showed a significant role in shaping the microbiome assemblages in soils under agriculture management. Soil microbiomes were greatly influenced by agriculture practices and showed contrasting genetic potential for C acquisition and biogeochemical cycling (Lacerda Júnior et al. 2019).

18.4 Limitations of Soil Metagenomics/Metatranscriptomics

Soil metagenomics and metatranscriptomics have certain limitations and biases as like as in any other molecular techniques. These limitations are mainly confined to protocols that are related to lysis of microbial cells, genomic DNA/RNA extraction along with sequencing errors (Lombard et al. 2011). The stability of the extracted nucleic acids (DNA or RNA) has also posed a major problem in soil metagenomic studies. There are certain main limitations found in absolute quantification and accurate annotation of sequenced genes. Therefore, complete soil metagenome or metatranscriptome coverage is very difficult to achieve; for instance, Howe et al. (2014) in a study reported that deep coverage of the majority of a soil microbiomes was not accomplished, even after processing 398 billion base pairs of sequence

data. It was highlighted that sixty percent of proteins predicted in sequencing data were not matched with existing databases indicating the limitations of the existing databases, for example, Genomes Orthology database and Kyoto Encyclopedia of Genes. Further, they suggested that more deep sequencing data are required to characterize the functional content of soil microbial communities. More importantly "Omic techniques" require substantial computational resources to annotate and predict the genes obtained through De novo metagenomic assembly.

Functional gene identification in a metagenomics library is not a substantiated proof of its expression at the RNA level or its activity at the protein level. The qualitative presence of functional gene may be cryptic in nature and the gene transcript could not be translated or the host organism may be inactive or dormant. One should be noted that the prevailing environmental conditions such as temperature, pH, water availability and substrate concentra-tion may likely inhibit the activity of the functional gene product. The amount of a particular enzyme in the soil may be accurately reflected by quantitative soil metagenomic data, but it would not deliver much information about the process rate/metabolic flux. It is a well-known phenomenon that the cellular flux of metabolites in a metabolic pathway relies on the available quantities of other co-enzymes and enzymes of the same metabolic pathway (Kacser 1983). Accordingly, the potential metabolic flux of the related pathway could not be sensitive to different quantities of the encoding gene. Prosser et al. (2015) opinioned that metagenomics may not provide complete information related to physiological characters, for example, susceptibility to predation, optimum pH and temperature for growth, minimum and maximum specific growth rates, saturation constants, etc. A small change in a soil environment (temperature, pH or any disturbance) is unlikely to induce any change in soil microbiome community composition. This could be due to plasticity and flexibility within the prevailing microbiome (Terzaghi and O'Hara 1990; Prosser 2015). However, it is noticed that a small change in soil environment may lead to subtle changes in metabolic profiling and activity. Such type of responses would not be traced in metagenomes (Prosser 2015).

Drawing correlations between soil physicochemical characteristics and metagenomic data for obtaining meaningful information is difficult. This could be due to temporal and spatial heterogeneity of soil matrix which will separate substrates physically from cells that contain a functional gene involved in the metabolism of those substrates (Prosser 2012; Schimel and Schaeffer 2012). The fundamental quest in soil microbiome research is how soil microbial diversity is produced and maintained. Conventionally, the fundamental processes that are responsible for inducing genetic diversity in species are defined as evolutionary processes which include genetic drift, gene flow, mutation, and selection (Hartl and Clark 2007). Conversely, the fundamental forces that are driving diversity among species are in general referred to as ecological processes which include ecological drift, selection, speciation and dispersal (Vellend 2010; Zhou and Ning 2017). Metagenomics, or metatranscriptomics may not deliver much information to understand these fundamental ecological mechanisms that are driving soil microbial communities.

Although metagenomic sequencing can provide certain information on great plate count anomaly, it is fundamentally difficult to understand the functionality

of metabolic pathways of uncultivable microbes in soil (Stewart 2012). Cultivation of uncultivable soil microbiota in the laboratory is necessary to understand complete physiology and their functional roles in soil microbial ecology and host plant improvement. Stewart (2012) discussed advancements made in co-culture technique suitable for growing uncultivable microbes in the laboratory by providing in situ environment. Further, a novel "micro-cultivation technology" to increase more resolution and exploit rare microbial species from the complex environment was highlighted in the same study.

18.5 Future Prospects in Soil Microbiome Research

18.5.1 Biodiversity and Biogeography

Six distinct biogeographical regions are found on the Earth's surface (Lomolino et al. 2006). The biogeographic regions are defined as land surface areas that harbor distinctive plants, animals and other biota. The distribution of specialized biotas is hypothesized to exist due to evolutionary events such as vicariance, separation and dispersal of species by various barriers (Womack et al. 2010). Much emphasis was given to the distribution of microbiota and the corresponding ecosystem processes that underlie species distribution. Gourmelon et al. (2016) inferred that microbial species distribution, abundance, richness were related to the type of surface vegetation and the prevailing plant species. Each plant possesses its specialized microbiome because of multifactorial linkages between abiotic and biotic factors in contrasting geographical regions (Gourmelon et al. 2016). Dispersal limitation in the context of the biogeographical-island theory proposed by MacArthur and Wilson (1963), can explain differences in microbiomes of various geographical locations (Gourmelon et al. 2016). Similar observations were reported by Malard et al. (2019) wherein spatial and edaphic factors played an important role in the structure of Arctic soil bacterial communities. It was elucidated that pH as the key environmental driver shaping Arctic soil bacterial communities. However, still, our understanding of the different processes of the biosphere is limited. Therefore, polyphasic studies should be carried out to understand the biosphere, one that links knowledge about biodiversity and biogeography in the atmosphere, hydrosphere and lithosphere (Hanson et al. 2012; Womack et al. 2010).

Gaston (2000) described that species richness is found to be higher in the tropics and gradually declines toward the poles. Molecular studies focused on the continental scale distribution and diversity of soil microbiomes revealed a lot of uncertainty in the global biogeography of soil biota due to a lack of data on patterns. Unraveling the factors that regulate soil microbiomes, biogeographical distribution, succession and functions are poorly understood in soil microbiology. Stochastic processes are thought to have minimal roles in driving soil microbiomes and their functions in the ecosystem process (Zhou and Ning 2017). It is believed that heterogeneous selection

by different biotic and abiotic environmental conditions making for more dissimilar and more diversified microbial structures among microbiomes. This type of selection is known as variable selection (Zhou and Ning 2017) and we anticipate that variable selection is one of the major underlying forces in leading diversified microbiomes in soils at the global scale. It is demonstrated that biodiversity is of paramount importance for ecosystem functioning (Cardinale 2012; Knelman and Nemergut 2014; Bardgett and Van Der Putten 2014), but the underlying forces driving the relationships between microbial communities and ecosystem functioning are still not clear. A few studies indicate that stochastic processes are important for regulating both microbial community structure and corresponding ecosystem functions (Fukami et al. 2010; Zhou et al. 2013). Nevertheless, systematic studies across diverse ecosystems are necessary to understand whether stochastic community assembly processes affect ecosystem functioning or not.

18.5.2 Sustainable Soil-Ecosystem Management

Recent studies unraveled that soil biodiversity is crucial to support several ecosystem functions simultaneously (Delgado-Baquerizo et al. 2016; Wagg et al. 2014). It is observed that intensive management of agricultural practices, for example, indiscriminate use of pesticides, fertilizers, soil tillage and monocropping have adverse effects on soil biota consequently reduce overall soil microbial biomass and diversity (McDaniel et al. 2014). An apparent microbial community shift in soil microbiomes was observed because of intensive land-use management practices (Tardy et al. 2015). Similarly, Philippot et al. (2013) emphasized that the loss in microbial diversity affects nitrogen cycling and other terrestrial ecosystem process. Therefore, soil microbial diversity has to be enhanced and maintained for the proper functioning of agro-ecosystem. It is proposed that sustainability in agricultural soils can be maintained by regulating internal ecosystem processes (Hota et al. 2021; Bender et al. 2016; Kumar et al. 2019a, b; Kumari et al. 2020; Rai et al. 2020). Recently, soil ecological engineering has gained a lot of momentum and is considered to be an important concept to enhance sustainable productivity in human land-use systems (Bender et al. 2016).

Soil ecological engineering is a comprehensive approach wherein soil biological processes are maximized for sustainable ecosystem functioning. This is one of the holistic approaches to minimize negative environmental impacts in agro-ecosystems and provide global food security. Figure 18.3 illustrates different soil ecological engineering approaches for local ecosystem management. Bender et al. (2016) comprehensively reviewed soil ecological engineering and biodiversity for sustainable agriculture/human land-use systems.

Agro-ecosystems are generally characterized into extensive and intensive systems with a different rate of productivities. The extensive agro-system is accompanied by high biodiversity, low resource output and inputs, low level of productivity and

enhanced internal soil regulatory processes. While the intensive agro-system is characterized by depleted biodiversity, high resource inputs-losses, high rate of productivity and decreased internal soil regulatory processes. Both of these systems have merits and demerits in terms of productivity and internal soil regulatory processes. Therefore, the ecological intensification approach needs to be implemented to bring sustainability in ecosystem multifunctionality. Bender et al. (2016) describe that the ecological intensification approach combines both traits (extensive and intensive agrosystems) and leads to an ideal sustainable agro-ecosystem that comprised rich biodiversity, moderate resource inputs/low nutrient losses, higher productivity and enhanced internal soil regulatory process. The ecological intensification approach further maximizes agro-ecosystem multifunctionality.

18.5.3 Rhizosphere Microbiome—Plant Health

Rhizosphere microbiomes that are assembled near roots can harbor up to 10^{-11} microbial cells and approximately 30,000 different microbial species per gram of root (Sharaff et al. 2020; Egamberdieva et al. 2008). Rhizosphere microbiomes are considered to be one of the complex-ecosystems on the Earth (Kour et al. 2019; Subrahmanyam et al. 2020; Weinert et al. 2011; Raaijmakers et al. 2009). Rhizosphere microbiomes utilize a diverse array of metabolites released by plant roots (Lu et al. 2018). Microbiomes of the rhizosphere are rich in diverse plant growth-promoting fungi and bacteria (Subrahmanyam et al. 2018, 2020; Sharaff et al. 2020; Kour et al. 2019). The density and distribution of microbial population in the root rhizosphere are much higher than in the bulk soil and this phenomenon is known as the "rhizosphere effect." Increased plant growth is associated with enhanced plant defense mechanisms. Root microbiome plays important role in conferring host plant health (Berendsen et al. 2012). It is evidenced that the plant is able to recruit a wide variety of microbial populations as its microbiome by secreting root exudates (Ahemad and Kibret 2014; Rana et al. 2020; Subrahmanyam et al. 2020).

Several abiotic and biotic factors are found to be critical for rhizosphere microbiome diversity and species richness. Abiotic factors, such as seasonal variation, pH, soil temperature, root exudates/chemical substances and biotic factors such as developmental stages of host plants, root architecture, cultivars and host plant genotypes act as chemical messengers for heterogeneous soil microbiota and subsequently influence the microbiome structure and function (Lakshmanan et al. 2014; Kumar et al. 2019a, b; Verma et al. 2016; Verma et al. 2017; Yadav et al. 2019). The rhizospheric microbes can induce a series of plant defense mechanisms for host plant growth and health. Induced systemic resistance (ISR) is one of the defense mechanisms of plants induced by PGPR to increase vigor and the health of their host plant against invading pathogen (Pieterse et al. 2014). Recently, excellent reviews on rhizospheric microbiomes, plant growth-promoting characteristics and their potential agricultural applications are published (Berendsen et al. 2012; Subrahmanyam et al. 2020; Sharaff et al. 2020).

Rhizosphere microbiomes harbors both useful and harmful microbiota and can control host plant physiology, growth and development (Subrahmanyam et al. 2020; Subrahmanyam et al. 2018; Sharaff et al. 2020). Further, the healthy mcirobiomes can prevent plant infection by controlling the pathogen colonization by either competing or producing antimicrobial compounds such as siderophores, 2,4-diacetylphloroglucinol, polymyxin, colistin, etc. (Maksimov et al. 2011). The regulation of the plant defense system is generally involved by different phytohormones such as ethylene, jasmonic acid and salicylic acid (Pieterse et al. 2014). Beneficial rhizospheric microbes' triggers induced systemic resistance by modulating salicylic acid.

The key functions of rhizosphere microbiome include protection against plant pathogen infection, nutrient acquisition and abiotic stress tolerance in host plants. Therefore, it is essential to understand the molecular signaling mechanisms between host plant and microbiome assembly in the rhizosphere by using functional metagenomics and transcriptomics. This information can be exploited to develop soil management practices for increasing plant productivity, designing healthy rhizomicrobiomes and introduction of novel biocontrol and bio-fertilizer microbes in sustainable agricultural strategies. Unraveling the mechanisms such as how plants recruit their selective microbiome and how the rhizosphere microbiome controls host plant health will open new avenues to increase crop productivity.

18.5.4 Climate Change and Soil Microbiomes

Soil microbiomes perform crucial functions in the elemental cycling of micro and macronutrients which are vital for the functioning of the above-ground ecosystem. Nevertheless, still we do not have a general framework at a global scale for predicting microbiome responses and their ecosystem services to climate change. Recently, Jansson and Hofmockel (2020) comprehensively reviewed the effect of climate change on soil microbiomes in diverse soil ecosystems. Mekala and Polepongu (2019) highlighted the effects of climate change viz. elevated temperature, precipitation, drought and atmospheric CO_2 on beneficial plant–microorganism interactions. Further, they have emphasized that k-strategist or oligotrophic microbial groups and their abundance are increased under high temperature or drought and their abundance significantly decreased with elevated CO_2. In contrast, r-strategist or copiotrophic microbial groups shown potential resilience after the disturbance or stress has ended. Studies on climate change have shown both negative and positive impacts on soil microbial communities (Mekala and Polepongu 2019). In arid grasslands, Yu et al. (2018) observed increased expression of functional genes involved in carbon fixation, nitrogen fixation, CH_4 metabolism, decomposition, denitrification, and nitrogen mineralization under elevated atmospheric CO_2 levels.

It is observed that soil respiration, soil organic matter decomposition and microbial biomass content were increased with increased temperature (Bradford et al.

2008). Long-term experiments on the elevated temperature at Harvard Forest Ecological Research Station revealed microbial community reorganization, diversity shift toward oligotrophic communities, rapid loss of carbon through respiration in the heated plots than in control soils. A change in microbiome community structure followed by reduced recalcitrant carbon pools was observed in the same study (Melillo et al. 2017). Multiyear field experiments and Mesocosm studies revealed that draught had a more negative impact on bacteria than fungi in grasslands (Upton et al. 2018; de Vries et al. 2018).

The residential soil microbiomes can either adapt and or dormant or extinct in response to climate change. Depending on their physiological and genetic potential, soil microbiomes respond to environmental disturbances in contrasting ways (Schimel et al. 2007). For example, Hayden et al. (2012) reported community shifts of fungi, archaea and specific bacterial groups under elevated CO_2 in Australian grasslands. Mekala and Polepongu (2019) proposed that specific functional genes involved in the N and C cycles can be used to predict the consequences of climate changes on soil microbial community composition in soil functioning.

Around 30% of the land surface area is occupied by forests and forest soil ecosystems are the major potential sinks for atmospheric carbon as a stable soil organic matter (Llado et al. 2017). However, it is predicted that because of increasing global temperature and severity of drought, these forest ecosystems may get converted from net carbon sinks to net carbon sources globally in the coming future (Kirschbaum 2000). This could be due to increased soil organic matter degradation by microbial activity (Kirschbaum 2000). A similar kind of observations was made with grasslands which occupy approximately 26% of the earth surface land area and store around 20% of total soil carbon (Ramankutty et al. 2008; Malyan et al. 2019). Therefore, potential ways and strategies for predicting the response of soil microbial activity and diversity to climate change needed to be developed and accordingly soil microbiomes may be exploited to mitigate the negative impacts of climate change.

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