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Running Title: SOIL MICROBIOME FOR SOIL REMEDIATION

Soil Microbiome: A Promising Strategy for Contaminated Soil Remediation

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ABSTRACT

Bioremediation is a process mediated by microorganisms, which is a sustainable and eco-friendly way to degrade and detoxify environmental contaminants. Soil microbiome clearly becomes a key component of bioremediation as it is more stable and efficient than pure culture, being recognized as one of the scientific frontier of soil environmental science and technology field. Recently, many progresses have been made in the investigation of remediation mechanisms by soil microbiomes and the interactions inside the microbiome. It greatly expanded our ability to characterize the remediating function of the soil microbiome and identify the factors that influence the efficiency of soil microbiome in remediation. Here, we suggest that soil microbiome is a promising strategy for soil remediation. The field is now poised to identify how we can manipulate and manage the soil microbiome to improve the remediation efficiency and increase soil fertility at the same time. Thereby, this review aimed to emphasize the importance of soil microbiome in bioremediation and promote further development of this strategy into a widely accepted technique.

Key Words: bioremediation, degradative mechanism, environmental pollution, soil microbiome

INTRODUCTION

Over the past 20 years, the rise in human population density and anthropogenic activity has led to pollution of the Earth’s surface through misuse of environmental resources and improper disposal of wastes (Imadi *et al.*, 2016; Kowalska *et al.*, 2018). Soil resources have faced unwarranted abuses and unrelenting development pressures for a long time (Li *et al.*, 2015; Teng *et al.*, 2015). Excessive use of fertilizers and pesticides, improper handling of industries’ gaseous emissions, wastewater discharges, and processing residues (abbreviated hereinafter as 3-Ws), and uncontrolled mineral exploration result in widespread environmental pollution (Lohmann *et al.*, 2007; Wiłkomirski *et al.*, 2011; Kowalska *et al.*, 2018). Besides to contemporary pollutants such as heavy metals, hydrocarbons, and pesticides, a new generation of persistent organic pollutants (POPs) such as polybrominated diphenyl ethers (PBDEs), polychlorinated naphthalenes (PCNs), and perfluorooctanoic acid (PFOA) require urgent attention (Lohmann *et al.*, 2007; Teng *et al.*, 2015). Soil pollutants not only threaten the human health but also have adverse effects on the physical chemical and biological properties of the soil. The conventional methods of waste disposables such as digging hole and dumping wastes, heat incineration, and chemical decomposition of contaminants were found to be more complex, uneconomical, and be short of public acceptance (Karigar and Rao, 2011). Bioremediation, a process mediated by microorganisms, is a sustainable way to degrade and detoxify environmental contaminants (Chakraborty *et al.*, 2012; Teng *et al.*, 2015). The key to successful bioremediation is to harness the naturally occurring catabolic capability of microbes to catalyze transformations of soil pollutants. Therefore, microbial bioremediation is an alternative, cost-effective and eco-friendly technology that provides sustainable ways to clean up contaminated soils (Gillespie and Philp, 2013; Pushpanathan *et al.*, 2014).

Microbiome is a new developing discipline that studies the relationship between microbial consortia and the environment they live in (Coyte *et al.*, 2015; Jiang *et al.*, 2017). Microbial consortium is referred to microbial community with diverse species on the basis of ecological selection principles. Meanwhile, microbiomes are intricately linked to critical ecosystem services and human health and can be applied in the fields of industry, agriculture, fishery, medicine, and so on (Kau *et al.*, 2011; Peralta *et al.*, 2014; Martiny *et al.*, 2015). A group of leading US scientists proposed a Unified Microbiome Initiative (UMI) to research almost all the microbiomes in human, plants, animals, soils, and sea (Alivisatos *et al.*, 2015; Dubilier *et al.*, 2015). Soil microbial biomass rivals the aboveground biomass of plants or animals, with soil often containing >1,000 kg of microbial biomass carbon per hectare (Serna-Chavez *et al.*, 2013). These soil microorganisms have crucial roles in decomposition, nutrient cycling, the maintenance of soil fertility, soil carbon sequestration and climate regulation, and the soil microbiome has both direct and indirect effects on the health of plants and animals in terrestrial ecosystems (Mendes *et al.*, 2015; Delgado-Baquerizo *et al.*, 2016; Fierer, 2017). Furthermore, when a soil is exposed to contaminations, the indigenous microbiome adjusts and adapts to the environmental perturbation and may metabolize external contaminants. Consequently, microbial communities in soils are essential in the degradation of contaminants (Ren *et al.*, 2015; Ren *et al.*, 2016; Fierer, 2017; Wang *et al.*, 2018).

In the past 50 years, there have been some spectacular discoveries of the types of energy-yielding reactions catalyzed by microbes, including the capacity to use insoluble metal oxides as terminal electron acceptors and anthropogenic hydrocarbons as electron acceptors (Schmidt, 2006; Gounou *et al.*, 2010; Chakraborty *et al.*, 2012). Most of these processes are accomplished by joint effort of microorganisms with different functional roles (Delgado-Baquerizo *et al.*, 2016). These microorganisms do not act as individuals but rather act as a dynamically changing microbial community, where all cells interact and communicate with one another. They influence each other’s behavior and possibly alter the biochemical phenotypes of the participating strains (Pushpanathan *et al.*, 2014; Martiny *et al.*, 2015). Since soil microbiomes contribute to degradation and transformation of soil contaminations as they are the drivers of the cycles of carbon, nitrogen, oxygen, sulphur, phosphorus and heavy metal, engineering of microbiome is developing new tools and approaches to construct microbial consortia with specialized functioning like bioremediation (Gillespie and Philp, 2013; Karen *et al.*, 2014; Lakshmanan *et al.*, 2014). The goal of engineering microbial consortia is to design and construct simple or complex artificial biological systems and engineer them to perform complicated tasks that are difficult or impossible for individual microbial species or strains (Brenner *et al.*, 2008; Song *et al.*, 2014). To apply the soil microbiome approach in bioremediation projects, we must involve the characterization of microbial community composition, cellular and molecular activities and the normal behavior of soil microbiomes which were altered by the presence of toxic pollutants. (Lakshmanan *et al.*, 2014). In this review, we summarize the principles, the instances and the contributory factors of bioremediation by soil microbiome. At the same time, we will introduce the latest findings in the field of bioremediation by soil microbiome and elucidate the potential for environmental remediation.

THE MECHANISMS OF BIOREMEDIATION BY SOIL MICROBIOME

The degradative mechanisms of POPs by soil microbes

Persistent organic pollutants (POPs) are highly lipophilic in nature and cause adverse effects to the environment and human health by biomagnification through the food chain (Chakraborty and Das, 2016). Diverse soil microorganisms have a demonstrated capacity to thrive on these toxic organic compounds in the soil, such as polycyclic aromatic hydrocarbons (PAHs), polychlorinated biphenyls (PCBs), pesticides, plastics and so on (Teng *et al.*, 2015). Gene mutation, gene rearrangement, and differential regulation of genes in microbes help in their survival in various unfavorable conditions like contaminated environment (Thomas and Nielsen, 2005). Bacterial genera include *Pseudomonas, Burkholderia, Stenotrophomonas, Corynebacterium, Staphylococcus, Micrococcus, Mycobacterium, Rhodococcus, Sphingobium, Bacillus, Aeromicrobium, Brevibacterium, Desulfotomaculum,* *Desulfovibrio, Dietzia, Escherichia, Gordonia, Methanoseata, Moraxella, Pandoraea* and *Pelatomaculum* show chemoorganotrophy for POPs degradation (Chowdhury *et al.*, 2008; Mikeskov á *et al.*, 2012; Karen *et al.*, 2014; Chakraborty and Das, 2016). At the same time, fungal genera, namely *Amorphoteca, Neosartorya, Talaromyces, Graphium* and *Irpex* were proved to be the potential organisms for POPs degradation (Gupta *et al.*, 2016; Lenoir *et al.*, 2016).

Role of the microbial enzymes and the encoding genes.

The degradation of the POPs by microbes basically relies on their catabolic enzymes. Catabolic enzymes could help catalyze the degradative process of complex molecules into simpler ones and release the chemical energy stored in the bonds of those molecules (Pushpanathan *et al.*, 2014; Gupta *et al.*, 2016). Microbes undergo numerous genetic permutation and combination to ensure a metabolically active life. In the meantime, horizontal gene transfer (HGT) is an important process in adaptation and evolution of microbiome and has, in particular, contributed to development of xenobiotic catabolism pathways (Juhas *et al.*, 2009; DeBruyn *et al.*, 2012). So understanding the evolution of catabolic pathways and their key catabolic enzymes is an effective means to determine enhanced cleanup of pollutants (Nzila, 2013).

The detoxification of toxic organic compounds by various microorganisms through oxidative coupling is mediated with oxidoreductases (Mrozik *et al.*, 2003). Microbes extract energy to cleave chemical bonds and to assist the transfer of electrons from a reduced organic substrate to another chemical compound (Karigar and Rao, 2011). The oxidoreductases were separated into three categories: oxygenases, monooxygenases, and dioxygenases based on the reactions they catalyzed. Oxygenases participate in oxidation of reduced substrates by transferring oxygen from molecular oxygen (O_2) utilizing FAD/NADH/NADPH as cosubstrates (Arora *et al.*, 2009). As reported, the degradation of many kinds of halogenated organic compounds (i.e., herbicides, insecticedes, fungicides, plasticizers, halogenated methanes, ethanes and ethylenes, etc.) could be achieved by specific oxygenases (Karigar and Rao, 2011). Monooxygenases incorporate one atom of the oxygen molecule into the substrate. P_{450} monooxygenase which is an important member of monooxygenases is a kind of hemecontaining oxygenases that exist in both eukaryotic and prokaryrotic organisms (Arora *et al.*, 2010). Dioxygenases could introduce of two oxygen atom to the substrate (aromatic compounds) which results in intradiol cleaving and extradiol cleaving with the formation of aliphatic product (Chakraborty and Das, 2016). Besides, there are some other kinds of enzymes participating in the degradation of POPs. For instance, laccases are able to catalyze oxidation, decarboxylation and demethylation of substrate like ortho and paradiphenols, polyphenols or PAHs (Zeng *et al.*, 2016). Peroxidases are ubiquitous enzymes that catalyze the oxidation of lignin and other phenolic compounds at the expense of H_2O_2 in the presence of a mediator. This kind of enzyme was reported to take part in the degradation of halogenated phenolic compounds, polycyclic aromatic compounds and other aromatic compounds (Karigar and Rao, 2011). In addition, several kinds of hydrolases (i.e., lipases, celluloses and proteases) which disrupt major chemical bonds in the toxic molecules and results in the reduction of their toxicity also play a role in biodegradation (Hiraishi, 2016).

Microbial metagenome constitutes the largest genetic reservoir with miscellaneous enzymatic activities implicated in degradation (Chakraborty and Das, 2016). The rapid exchange of specific catabolic activities occurs by the horizontal transmission of genes between microbes, frequently by broad host range plasmids. This process leads to the unique catabolic function of a single recombinant strain in biodegradation (Pushpanathan *et al.*, 2014) Extensive research is yet to be conducted to discover various microbial species from the environment having functional roles in POPs biodegradation. The major genes or gene clusters take part in biodegradation of POPs were summarized in Table I. Aromatic dioxygenases, which initiate the aerobic degradation of aromatic compounds like PAHs, biphenyls, and dioxins have been of considerable interest or bioremediation (Iwai *et al.*, 2011). *bph* and *nah* are the most common and widely existent gene clusters encoding aromatic dioxygenases in the environment, which are key genes in the degradation of PCBs and PAHs, respectively (N íChadhain *et al.*, 2006; Wang *et al.*, 2014). In addition, *alkB1B2* investigated in *Alcanivorax hongdengensis* A-11-3 were reported to play crucial roles in the degradation of alkane, while *tbc* and *tom* were related to benzenes transformation in

Burkholderia strains (Wang and Shao, 2012; Kahng *et al.*, 2001; Hendrckx *et al.*, 2006).

Degradative processes and pathways.

Polychlorinated biphenyls (PCBs) are a class of Persistent Organic Pollutants (POPs) differing in the number of chlorine atoms (1-10) attached to their biphenyl rings (Passatore *et al.*, 2014). The microbial PCB-degradation system includes two major metabolic steps: (i) anaerobic reductive dechlorination, where PCBs are transformed into less chlorinated congeners; (ii) aerobic breakdown of the biphenyl structure in lower-halogenated congeners, resulting in the production of chlorobenzoic acid, ring opening, and potentially complete mineralization (Teng *et al.*, 2015). Pathway of bacterial PCB degradation at aerobic conditions was displayed in Fig. 1a. Soil microbes transform PCBs to chlorobenzoic acids and the intermediates of the Tricarboxylic acid (TCA) cycle which could be catalyzed by several enzymes (Mackova *et al.*, 2010). Firstly, biphenyl dioxygenase catalyze the incorporation of two oxygen atoms into the aromatic ring to form cis-2,3-dihydro-2,3-dihydroxybiphenyls. Then, the products are dehydrogenated and oxygenated by dehydrogenases and dioxygenases and 2-hydroxy-6-oxo-6-(chloro)phenylhexa-2,4-dienoic acid is generated. Finally, benzoic acid and 2-hydroxypenta-2,4-dienoate is formed by ring cleavage reaction (Pieper and Seeger, 2008). The degradation of benzoic acid and 2-hydroxypenta-2,4-dienoate is called lower pathways. 2-hydroxypenta-2,4-dienoate could be catalyzed by hydratase, acetaldehyde dehydrogenase and aldolase into three carbon metabolites like pyruvates which could be degraded through TCA cycle.

PAHs are aromatic hydrocarbons with two or more fused benzene rings with natural as well as anthropogenic sources (DeBruyn *et al.*, 2012). The general base of degradative mechanism of PAHs usually begins with aromatic ring oxidation, followed by PAHs breakdown into its metabolites. Fig. 1b illustrates the major pathways involved in the mechanism of PAHs degradation by soil microorganisms. Microorganisms utilize dioxygenase enzymes to incorporate both atoms of molecular oxygen into the aromatic nucleus to form cis-dihydrodiols. Cis-dihydrodiols are stereoselectively dehydrogenated by cis-dihydrodiol dehydrogenases, which rearomatize the benzene nucleus to form dihydroxylated intermediates. Subsequent enzymatic fission of the aromatic ring by procaryotic organisms is also catalyzed by highly regio- and stereoselective dioxygenases. Fig. 1b shows the different routes of initial oxidative attack of PAHs by fungi and bacteria. The sites of enzymatic attack, mechanisms, chemical intermediates and pathways for the metabolism of several PAHs by different microorganisms are diverse (Haritash and Kaushik, 2009; Mineki *et al.*, 2015; Kuppusamy *et al.*, 2017).

Poly(ethylene terephthalate) (PET) is a kind of plastic products which accumulation in the environment. The degradation pathway of PET is shown in Fig. 1c. PETase and mono(2-hydroxyethyl) terephthalic acid hydrolase catalyze PET to terephthalic acid (TPA). Then TPA dioxygenase and protocatechuic acid dioxygenase help further degrade the metabolites to 3-Carboxy-muconic acid (Yoshida *et al.*, 2016).

The bioremediation of heavy metals by soil microbiome

The remediation of heavy metals might be impeded by their low bio-availability due to their insolubility and soil-bound properties (Teng *et al.*, 2015). Engineering indigenous microorganisms to treat heavy metal polluted soil by converting toxic heavy metals into non-hazardous forms is an efficient way of bioremediation (Gupta *et al.*, 2016).

The metabolism of some soil microbes could increase metal bioavailability in the soil through alterations in the soil pH, resulting in the release of chelators (i.e., siderophores) and organic acids capable of enhancing the complexation of metals and their mobility (Schalk *et al.*, 2011). Meanwhile, microbial volatilization is another preferred method of metal bioremoval (i.e., selenium and mercury) which could be catalyzed by some other kinds of soil bacteria (Zhang *et al.*, 2012). Based on previous studies, the metal resistance of microorganisms might be attributed to:(i) sequestration of toxic metals by cell wall components or by intracellular metal binding proteins and peptides; (ii) alteration of biochemical pathways to block metal uptake; (iii) immobilize and/or change the redox state of metals to lessen their toxicity by microbial enzymes; (iv) reduction of intracellular concentration of metals using efflux systems (Hao *et al.*, 2014; Jan *et al.*, 2014; Teng *et al.*, 2015).

Moreover, the immobilization or activation of heavy metals employed by microbes makes them valuable tools to assist phytoremediation (Ojuederie and Babalola, 2017). The plant growth-promoting microorganisms in soil employed different ways to stimulate the plant growth, including nitrogen fixation, phosphorus solubilization, phytohormone synthesis, siderophore release, and the production of indole acetic acid, 1-aninocyclopropane-1-carboxylic acid deaminase and volatile compounds (de-Bashan *et al.*, 2012; Hao *et al.*, 2014).

Furthermore, some research suggested that consortia of bacterial strains showed better effects than a single strain in the process of bioremediation of heavy metals. For instance, (Kang *et al.*, 2016) investigated the synergistic effect of bacterial consortium consisting of *Viridibacillus arenosi* B-21, *Sporosarcina soli* B-22, *Enterobacter cloacae* KJ-46 and *Enterobacter cloacae* KJ-47 on the bioremediation of Pb, Cd and Cu combined contaminated soils. They observed that the bacterial consortium had greater resistance and efficiency for the remediation of heavy metals compared to the single strain.

THE INTERACTION NETWORKS BETWEEN CELL AND CELL IN SOIL MICROBIOME

Soil environmental conditions are highly variable at the global scale. The relationship between microbial diversity and function in soil is largely unknown, but biodiversity has been assumed to influence ecosystem stability, productivity and resilience towards stress and disturbance (Torsvik and Øvreås, 2002). Studies have tried to link alterations in biodiversity to soil functioning, showing that soil functional stability is very dependent on microbial diversity (Mendes *et al.*, 2015). Some researchers predict that microbial diversity has a positive effect on nutrient cycling efficiency and contributes to increased ecosystem processes (Tardy *et al.*, 2014; Coyte *et al.*, 2015; Fierer, 2017). Therefore, higher microbial diversity increases resistance and resilience of microbial process, and microbial diversity loss affects nutrient cycling in soil (Girvan *et al.*, 2005; Tardy *et al.*, 2014). Diverse microorganisms form intricate interactive networks in the soils. The networks between cell and cell in the microbiome which comprise the quorum sensing (QS), biofilm formation, competition and cooperation make it sufficient and stable to function in the soil environments.

Quorum sensing

Quorum sensing is a cell-to-cell communication process that enables bacteria to obtain information about cell density and species composition of the vicinal community and adjust their gene expression profiles accordingly (Papenfort and Bassler, 2016; Kylilis *et al.*, 2018). This process, termed quorum sensing, allows bacteria to monitor the environment for other bacteria and to alter behavior on a population-wide scale in response to changes in the number and/or species present in a community (Waters and Bassler, 2005). The microbial cells can release some specific signal molecules and detect the change of their concentrations spontaneously, thus coordinating behaviors upon the establishment of a sufficient quorum (Sedlmayer *et al.*, 2018). Gram-positive and Gram-negative bacteria usually use autoinducing peptides (AIPs) and N-acyl-homoserine lactones (AHLs) as communication signals, respectively (Parsek and Greenberg, 2000; Williams, 2007). Bacteria also develop mechanisms to detect the presence of other species in a mixed population. The signals of AI-2 (autoinducer-2) family are used for interspecies communication (Jiang *et al.*, 2017).

Most quorum-sensing-controlled processes are unproductive when undertaken by an individual bacterium acting alone but become beneficial when carried out simultaneously by a large number of cells. Thus, quorum sensing confuses the distinction between prokaryotes and eukaryotes because it enables bacteria to act as multicellular organisms (Waters and Bassler, 2005). Quorum sensing is a key process in natural microbial interactions and plays an important role in many kinds of process in soil microbiome, such as controlling virulence factor production, biofilm formation, improving microbial stress resistance.

Biofilm

A biofilm is a group of microorganisms in which cells stick to each other and/or adhere to a surface. These adherent cells are frequently embedded within a self-produced matrix of extracellular polymeric substance (EPS) (Mah and O'Toole, 2001). Simultaneously, biofilms can consist of single or multiple species of microorganisms originating from one or more kingdoms (i.e., bacteria, fungi, algae, and archaea) and with varying environmental requirements with regard to electron acceptors/donors and nutrient concentrations (Gambino and Cappitelli, 2016; Jiang *et al.*, 2017). For example, a coculture of *Pseudomonas aeruginosa*, *Pseudomonas protegens*, and *Klebsiella pneumoniae* forms a mixed-species biofilm that collectively exhibits greater resistance to antimicrobials (tobramycin and sodium dodecyl sulfate) than do biofilms of the individual species (Fredrickson, 2015). The ability for microorganisms to congregate in sessile biofilm structures allows for many advantages compared to the free-living microorganisms: (i) protection from the surrounding environment; (ii) the capability to communicate and exchange genetic material, nutrient availability from the environment and each other; (iii) persistence in different metabolic states; (iv) providing different microenvironment for the microorganisms with special environmental requirements (i.e., different oxygen gradient) (Edwards and Kjellerup, 2013; Jiang *et al.*, 2017; Sedlmayer *et al.*, 2018).

Though indigenous bacterial communities are capable of degrading persistent organic pollutants and transforming heavy metal contaminants, their low abundance and activity often together with a lack of access to the contaminants and limitations in available nutrients in the environment (Edwards and Kjellerup, 2013).While the free-living microorganisms survival in the environment is less likely due to decreased protection, the low metabolic activity combined with low bioavailability of the pollutants in the water or soil cause insignificant transformation by the microorganisms (Martiny *et al.*, 2015). This durability and metabolic range make biofilm a very attractive actor in bioremediation. In the environment, indigenous biofilms constantly perform bioremediation, particularly in soils and sediments, which is a part of the global nutrient cycling process and a part of the global self-purification system (Johnsen and Karlson, 2004; Edwards and Kjellerup, 2013).

It has been reported that mixed biofilms achieved higher biodegradation efficiencies on mixed PAH substrates due to the increasing of solubility of PAHs (Rodriguez and Bishop, 2008). Subsequently, the pollutants transfer from recalcitrant crystals to cells for biotransformation (Johnsen and Karlson, 2004). There were also some promising studies showed enhanced ability of the biofilms to degrade PCBs and dioxins. (Yoshida *et al.*, 2009) employed *Burkholderia* sp. NK8 together with *Pseudomonas aeruginosa* PA01, showed enhanced ability of the dual species biofilms to completely degrade chlorinated benzoates. After that, Wang and Oyaizu (2011) reported that biofilms consisting of *Comamonas* sp. enhanced by their relationship with *Trifolium repens* showed significant reduction of existing dioxins in soil. In addition, extracellular polymeric substances (EPSs) of biofilm were found to play a crucial role in biosorption of heavy metals. EPSs form complexes with metal cations resulting in metal immobilization within the exopolymeric matrix and promote the bioremediation of heavy metals (Pal and Paul, 2008).

Competition and cooperation

It is clear that competition and cooperation within microbial communities is central to their stability. Understanding the principles of the intricate interactive systems that shape a microbial community is keys for microbial ecology and is also crucial for engineering synthetic microbiomes for various biotechnological applications, including bioremediation (Mee *et al.*, 2014; Coyte *et al.*, 2015).

Competition for limited natural resources within a microbial community is known as the selective force that promotes biosynthesis of antimicrobial compounds (Jiang *et al.*, 2017). Microorganisms of different species compete for the ecological niche and the nutrients for growth and metabolism in soil environment. Microorganisms use different strategies, such as secreting the antimicrobial molecules, to confront this kind of competition. Recently, it was shown that these antimicrobial molecules produced in nature are not primarily used as weapons for competition but as tools of communication that may regulate the homeostasis of microbial communities (Yim *et al.*, 2007; Hibbing *et al.*, 2010).

Whereas ecological competition is thought to be prevalent in natural microbial communities, it is commonly assumed that the functioning of microbiome communities rests upon species that engage in cooperative metabolism and provide benefits for the soil (Coyte *et al.*, 2015). Cooperation refers to benefit of two or more species to one another when living together, but both of their lives will be affected badly and even die when separated (Escalante *et al.*, 2015; Jiang *et al.*, 2017). There are numerous examples of mutualisms in the bioremediation processes with microbial consortia. Based on the knowledge of degradation products and degradation capabilities of individual microbes, a cooperation of different organisms in biodegradation of certain chemicals could be derived (Mikeskov á*et al.*, 2012).

For instance, Gurav *et al.* (2017) constructed a four-menbered consortium (consisting of *Dietzia* sp. HRJ2, *Corynebacterium variabile* HRJ4, *Dietzia cinnamea* HRJ5 and *Bacillus tequilensis* HRJ6) which showed higher degradative efficiency of total petroleum hydrocarbons, total saturated hydrocarbons, total aromatic hydrocarbons, n-alkanes and 16 PAHs than any single strain of them. Another example of cooperation within a bacterial consortium in bioremediation was achieved in diesel oil and heavy metal co-contaminated soil (Sprocati *et al.*, 2012). The remediation was performed by introducing a microbial formula composed of 12 strains, which belong to a stable population isolated from a chronic polluted soil and were both hydrocarbon degraders and heavy metal resistant. The active role of the microbial formula was pushing the entire community towards an effective bioremediation of diesel oil close to 75%. On the contrary, Festa *et al.* (2016) compared the efficiency of two different inoculation strategies, using a single strain and a consortium on phenanthrene-contaminated soil. They found that the single strain offered a better efficiency than the consortium. This may indicate that the competition between consortium and the indigenous microbes.

THE APPLICATIONS OF SOIL MICROBIOME IN BIOREMEDIATION

Biodegradation of environmentally toxic pollutants using soil microbiome has been found to be a more promising approach (Gupta *et al.*, 2016). Pure cultures of microbes are capable of degrading or transforming only a certain range of pollutants due to their complex structure. Therefore, different microbial species are assembled to form microbiome with broad enzymatic capacities to increase the removal rate of contaminates. Such mixed cultures display metabolic versatility and superiority to pure cultures (Kweon *et al.*, 2011). In addition, a microbial consortium that can synthesize the degradative enzymes for different parts of the decomposition pathway should be found to be well suited to different pollutants (Gupta *et al.*, 2016). Moreover, engineered processes relying on microbiome have been around for nearly a century. Microbial interactions are intentionally stabilized to achieve a better function by selecting the source of the microbial inoculums and by controlling environmental conditions to promote the selection of favorable microbial taxa and processes (Perez-Garcia *et al.*, 2016).

Polycyclic aromatic hydrocarbons (PAHs) are common organic pollutants which are persistent compounds in the environment due to their hydrophobic nature (Lamichhane *et al.*, 2016). Soil microbiome was widely used in the bioremediation of PAHs-contaminated soil. Tauler *et al.* (2016) developed a novel biphasic system containing mineral medium and sand coated with a biologically weathered creosote-PAH mixture to specifically enrich the high molecular weight PAH-degrading consortium from a polluted soil. The enriched consortium removed 70 % of the total PAHs and their alkyl-derivatives in 12 weeks. Similarly, Thavamani *et al.* (2012) isolated a functional microbial consortium from a former manufactured gas plant soil. The consortium could utilize high-molecular-weight PAHs such as pyrene and benzo[a]pyrene as a sole carbon source in the presence of toxic metal Cd and showed great potential for field scale bioremediation of PAHs in long term mix contaminated soils. In 2016, Wang *et al.* (2016) enriched a novel aerobic microbial consortium for the complete degradation of phenanthrene from petrochemical contaminated soil. The consortium which dominated by *Proteobacteria*, *Actinobacteria* and *Deinococcus-Thermus* could degrade more than 96% of 200 mg/L phenanthrene in a minimal salt medium in 3 days. For the bioremediation of the combined pollution, Gurav *et al.* (2017) isolated four pure cultures (*Dietzia* sp. HRJ2, *Corynebacterium variabile* HRJ4, *Dietzia cinnamea* HRJ5 and *Bacillus tequilensis* HRJ6) from oil-contaminated soil. The four member-consortium showed high efficiency on degrading n-alkanes and PAHs aerobically from heavy crude oil.

Crude oil is a complex mixture of hydrocarbons and other organic compounds, including some organo-metallo constituents, most notably complexing vanadium and nickel (Varjani and Upasani, 2017). The oil sludge can potentially be degraded by a great variety of soil microorganisms (Shankar *et al.*, 2014). Bioremediation of oil spillage in soils using consortia of microbes beckons much exploration. (Mariano *et al.*, 2008) compared biodegradation of commercial and weathered diesel oils and suggested that consortia had better biodegradation potential than pure cultures, as individual isolates may fail to exhibit degradation. In addition, Cerqueira *et al.* (2011) investigated the biodegradation capacity of aliphatic and aromatic hydrocarbons of petrochemical oily sludge by heterogeneous bacterial consortium and five pure petroleum degrading isolates. Heterogeneous bacterial consortium demonstrated best results with excellent degradation capacity. Aliphatic and aromatic fractions were reduced 90.7% and 51.8%, respectively by bacterial consortium. Similarly, Shankar *et al.* (2014) isolated 32 positive oil degrading isolates and synthesized several consortia to degrade the mixture of three common oils (petrol, diesel and engine oil). Thus, they confirmed that microbes in ‘Consortial Union’ serve as better treating agents in bioremediation of oil-contaminated soils than individual microorganisms.

Plastics with desirable properties such as durability, plasticity, and/or transparency have been industrially produced over the past century and widely incorporated into consumer products (Yoshida *et al.*, 2016). But these polymers, primarily low- and high-density polyethylene (LDPE and HDPE), accumulate in the environment and cause a grave threat to the ecology, since it is not easily degradable and persist in the environment for extended periods of time (Peters and Bratton, 2016). The use of microbial biotechnology is deemed as the most benign method, since the production of toxic end products would greatly be averted and the application of bacterial consortia for effective plastic degradation has been in use for a certain period of time (Shah *et al.*, 2008). Nowadays, the utilization of strategies such as synthesis of a consortium with diverse attributes is still gaining momentum. Skariyachan *et al.* (2017) focused on the biodegradation of two forms of plastics, LDPE and HDPE, by means of formulating novel consortia constituting different thermophiles for obtaining an effective degradation of plastic. They identified highest 75% degradation for LDPE strips for a period of 120 days by the formulated consortia. The biodegradation of another kind of plastic, poly(ethylene terephthalate) (PET), was investigated (Yoshida *et al.*, 2016). A distinct microbial consortium that formed on the PET film upon culturing and induced morphological change in the PET film was isolated. The consortium which contained a mixture of bacteria, yeast-like cells, and protozoa degraded the PET film surface at a rate of 0.13 mg cm^{-2} day^{-1} at 30 ℃, and 75% of the degraded PET film carbon was catabolized into CO_2 at 28 ℃.

Bioremediation is an eco-friendly and cost-effective method also for decontamination of heavy metal polluted soil. It has been mentioned earlier that bioremediation of heavy metal polluted soil is more efficient when the site is simultaneously growing plants (Chibuike and Obiora, 2014; Gupta *et al.*, 2016). Several soil microorganisms (i.e., *Pseudomonas*, *Bacillus*, *Escherichia*, *Enterobacter*) help in contamination of heavy metal polluted sites by performing bio-absorption and bioaccumulation (Kotaś and Stasicka, 2000). Madhaiyan *et al.* (2007) inoculated tomato plant with microbial consortium consisting of *Methylobacterium oryzae* and *Burkholderia* spp. to augment the remediation of cadmium and nickel in the soil. It is reported that an increased plant growth due to the reduction in the accumulation of cadmium and nickel in the shoot and root tissues of the plant was observed.

THE FACTORS AFFECTING BIOREMEDIATION BY SOIL MICROBIOME

Microorganisms are highly sensitive to growth environment and respond to changes in their surrounding environment (Varjani, 2017). Till now, decades of research has shown that the properties of soils, including pH, organic carbon concentration, salinity, texture and available nutrients concentration, exhibit an enormous range (Fierer, 2017). However, microbial survival and growth in the soil environment is often severely limited. There can be persistent abiotic stressors (i.e., low water availability, limited availability of organic carbon sources, acidic conditions, wide range of pollutants), a high degree of competition with other soil microbial groups, frequent disturbances (i.e., drying-rewetting and freezing-thawing events, predation by earthworms and/or other fauna), and an inequality distribution of different kinds of resources across space and time (D'Costa *et al.*, 2006; Kuzyakov and Blagodatskaya, 2015). So we broadly group the factors affecting bioremediation by soil microbiome into three interrelated classes: soil and weather-related, microbial-related, contaminant and co-contaminant-related (Kuppusamy *et al.*, 2017).

The conditions of soil environment

The soil environment, including the type of soils, aeration status, temperature, bioavailability of the nutrients, presence of other inhibitory pollutants or co-contaminants, soil moisture, water activity, and microbial competition greatly influence the efficiency and effectiveness of a remedial system (Varjani and Upasani, 2017). Proper optimization of factors is essential to enhance the remedial efficiency and ensure success at field-scale.

Temperature plays a vital role in bioremediation (Varjani *et al.*, 2014). It affects both physical state of pollutants and the microbiome (i.e., microbial growth rate, gas solubilities, soil matrix, metabolism of microbes, physical and chemical state of contaminants) (Chandra *et al.*, 2013; Varjani and Upasani, 2017). For example, Thamer *et al.* (2013) reported that 80% biodegradation of crude oil in 27 days by soil microbe could be due to environmental factors and production of emulsion materials or bacterial enzyme or availability of optimal temperature. They suggested that the temperature and nitrogen demand may be the key factors which raised the efficiency of bacteria in degradation of crude oil components. Varjani (2017) has reviewed that petroleum hydrocarbons do not contain significant amount of some nutrients required for microbial growth, such as nitrogen and phosphorous. However, urea, phosphate, ammonium and potassium salts can be used to adjust carbon/nitrogen/phosphorous/potassium (C-N-P-K) ratios. Several research demonstrated that the most adequate C:N:P to promote microbial growth is 100:10:1 (Zhao *et al.*, 2011; Dias *et al.*, 2012). Furthermore, when employers analyze a collection of soils that represent a broad range of pH values (from pH 4 to pH >8), they often find that soil pH is the best predictor of bacterial and archaeal community composition (Fierer, 2017). They suggested that soil pH was most likely to have marked effects on the variety and abundance of soil microbiome structure, which determined the soil function, including biodegradation or biotransformation of pollutants.

Bioavailability of pollutants and biosurfactant

Bioavailability can be defined as amount of a substance that is physico-chemically accessible to microorganisms (Souza *et al.*, 2014). The environmental persistence of POPs is due to their low water solubility and ability to be absorbed to soil organics, which limits their availability to degrading microbes (Chakraborty and Das, 2016). It has been reported that the same compound in different pollutants can be degraded to different extents by same organisms or consortium, due to the bioavailability of the particular compound rather than its chemical structure (Varjani, 2017). Bioavailability that is also influenced by physico-chemical properties of soil (including composition, texture, moisture pH, sorption, occlusion and ageing) strongly affects the feasibility of risk-based remediation, type of microbial transformation occurring and whether POPs will serve as a primary, secondary or co-metabolic substrate or energy source (Kuppusamy *et al.*, 2017).

Soil microorganisms could produce different products (i.e., gases, biosurfactants, biopolymers, solvents, and acids) to enhance the remediation (Varjani and Upasani, 2016). Among all such products biosurfactant is very well studied as it plays critical role to enhance hydrocarbon pollutants bioavailability (Souza *et al.*, 2014). Thus, use of biosurfactants is a more promising approach for enhancing the bioavailability of

POPs, especially PAHs (Gupta *et al.*, 2016). Surfactant activity and hydrophobicity favor interaction between microorganism and insoluble substrate, overcoming diffusion limitation during substrate transport to the cell. It has been reported that efficiency of microbial consortia composed by PAH degrading bacteria was significantly higher using surfactants (Fernando Bautista *et al.*, 2009; González *et al.*, 2011). Nevertheless, Owsianiak *et al.* (2009) found that two different kinds of surfactants altered cell surface hydrophobicity of the consortia by means of increasing the hydrophilic and decreasing the hydrophobic cultures. Their result indicated that in the surfactant-mediated biodegradation, effectiveness of surfactants depended on the specification of microorganisms but not on the type of surfactant.

Indigenous microbes

To our knowledge, exogenous microorganisms are difficult to survive and grow in the soil environment due to not only persistent abiotic stressors but also the indigenous microorganisms (Varjani and Upasani, 2017). As exemplified by the widespread occurrence of antibiotic-producing and antibiotic-resistant soil bacteria, a high degree of competition between inoculated microbes and indigenous soil microbes was tended to be exist (D'Costa *et al.*, 2006; Perez-Garcia *et al.*, 2016). Compared to application of single strain, microbial consortia showed an advantage that high diversity of microbes could help the functional exogenous microorganisms to survive in new environments (Großkopf and Soyer, 2014). Some researchers have evaluated the efficiency of the microbial consortia and pure culture on bioremediation. Sathishkumar *et al.* (2008) studied the biodegradation of crude oil using bacterial consortium made of four strains. They demonstrated that the degradation rate by consortium was 77%, which was higher than the individual strains (*Pseudomonas* sp. BPS1-8: 69%; *Bacillus* sp. IOS1-7: 64%; *Pseudomonas* sp. HPS2-5: 45%; and *Corynebacterium* sp. BPS2-6: 41%). However, Festa *et al.* (2016) offered a different opinion. They suggested that utilization of single strain as a inoculant was the best strategy to remediate the soil mainly based on the degradation efficiency. But it caused more drastic changes in indigenous microbial community than inoculation with the consortium, what can be compromising the ulterior functionality of the soil.

CONCLUSION

As soil pollution receiving considerable attention, more and more researchers focused on the bioremediation function of soil microbes. Plenty of soil microorganisms were investigated to make contribution to removal or detoxicity of different environmental pollutants (Gurav *et al.*, 2017; Ojuederie and Babalola, 2017; Varjani, 2017; Wang *et al.*, 2018; Wang *et al.*, 2018; Xu *et al.*, 2018). The subjects of the research ranged from pure culture to consortium and microbiome as several advantages of microbiome were found in the field of remediation. First of all, microbiome often shows more metabolic versatility for complex pollutants or co-occurring contaminants. The remediation process mediates by a diversity of microbes harboring different and often interconnected metabolic pathways. Secondly, microbiome offers the internal microorganisms a better micro-environment to survive in the diverse circumstances and perform a better bioremediation function. Thirdly, some microorganisms could secret products such as surfactants which may change the form or bioavailability of pollutants. This may affect the toxicity of pollutants to the degraders and increase the process of bioremediation. Thus, a microbiome is more effective to be utilized to degrade organic pollutants and transform heavy metals.

As the biological technology proceeding, DNA-based, RNA-based and protein-based analyses of the soil microbiome expanded the known about the taxonomic structure, the interactive mechanisms and the functions of soil microbial communities. At the same time, we could see that the interacting network of the microorganisms among the microbiome was complicated, including quorum sensing, cooperation, competition, induction and regulation (Fig. 2). In such an elaborate network, degraders show their capacity more stably and efficiently. However, a range of biotic and abiotic factors can influence the total amount of microbial biomass, the community structures and the emerged functions in a soil (Fig. 2).

Herein, this review provides a comprehensive framework of the potential for environmental remediation of soil microbiome (Fig. 2). The selective introduction of the soil microbiome could facilitate the accelerated removal or detoxicity of various pollutants from soils. Based on the principles and the instances, the strategy of soil microbiome towards bioremediation could be improved to an environmental-friendly, sustainable and low-cost remediation technology with high efficiency.

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TABLE I

List of the catabolic genes for POP degradation found in different bacterial genera

Pollutants	Catabolic genes	Representative strains	References
Alkane	*alkB1B2*, P450, *almA*	*Alcanivorax hongdengensis* A-11-3	(Wang and Shao, 2012)
Benzenes	*tbc2ABCDEF, tomA012345*	*Burkholderia* sp. JS150, *Burkholderia cepacia* G4	(Shields *et al.*, 1995); (Kahng *et al.*, 2001); (Hendrickx *et al.*, 2006)
PAHs	*nahAc, nagAc, nidA, phnABCHGF,* P450	*Pseudomonas putida* G7, *Burkholderia* sp. RP007, *Mycobacterium vanbaalenii* PYR-1, *Acidovorax* sp. NA3, *Irpex lacteus*	(N í Chadhain *et al.*, 2006); (Haritash and Kaushik, 2009); (Singleton *et al.*, 2009); (Kim *et al.*, 2012)
PCBs	*bphABCD, rdhA*	*Pseudomonas putida* KF715, *Dehalococcoides* sp., *Rhodococcus* sp. R04	(Hayase *et al.*, 1990); (Pieper and Seeger, 2008); (Wang *et al.*, 2014)
OPPs a)	*opdA*	*Agrobacterium radiobacter* P230	(Horne *et al.*, 2002)
OCPs b)	*linABCDE*	*Sphingobium japonicum* UT26	(Okai *et al.*, 2010)
Pyrethroids	*pytH, Pye3*	*Sphingobium* sp. JZ-1	(Wang *et al.*, 2009)

a)organic phosphorus pesticide; b)organochlorine pesticides.

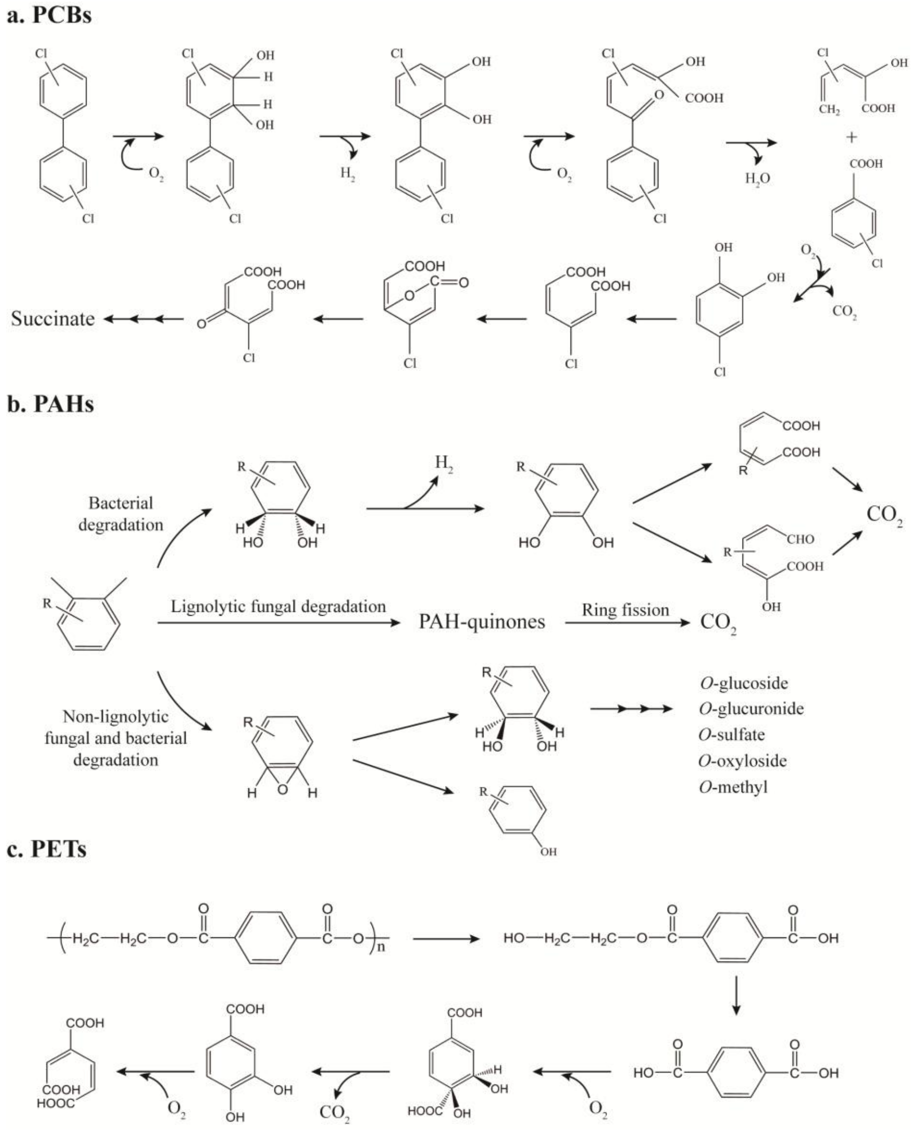

Fig. 1 Schematic representations of the proposed degradation pathways of several organic pollutants in soil microbes. Organic pollutants: a. polychlorinated biphenyls, b. polycyclic aromatic hydrocarbons, c. polyethylene terephthalates.

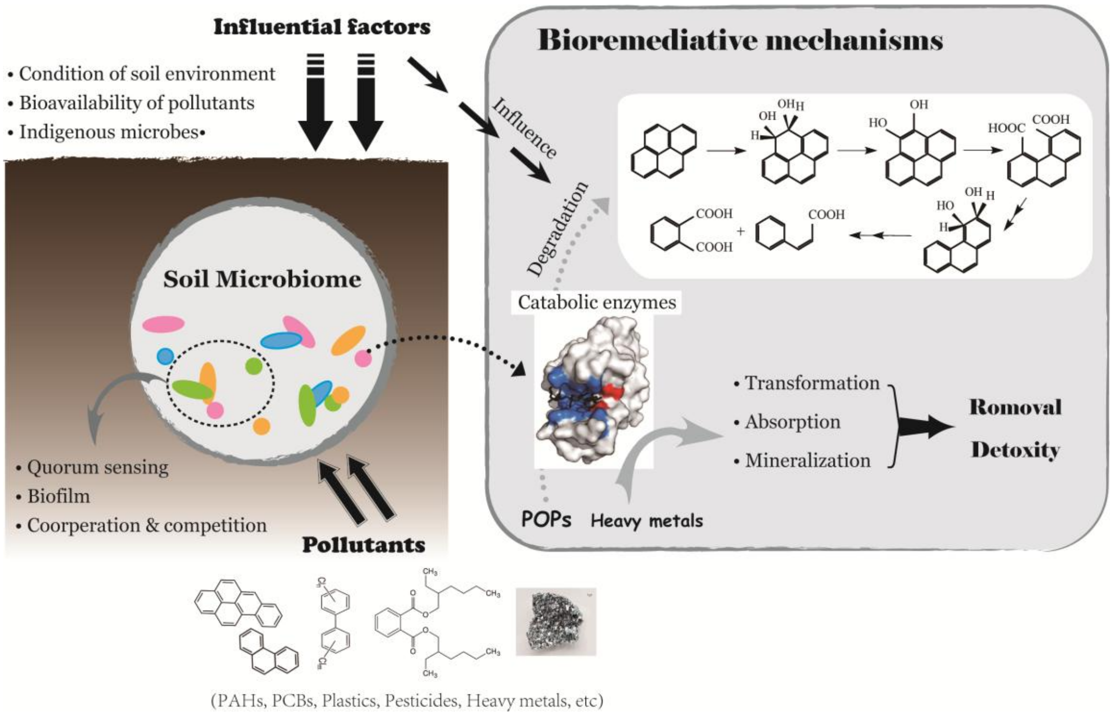

Fig. 2 The bioremediation mechanism of soil microbiome.