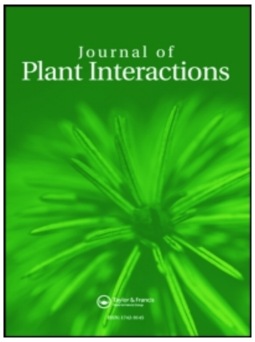

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# Harnessing plant-bacteria-fungi interactions to improve plant growth and degradation of organic pollutants

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**ABSTRACT**
Exploiting the potential of bacteria in phytoremediation for the removal of organic and inorganic pollutants from soils and (ground)water holds great promise. Besides bacteria, mycorrhizal fungi and free-living saprotrophs are well known for their strong degradative capacities and plant growth promotion effects, which makes them of high interest for use in different bioremediation strategies. To further increase the efficiency and successes of phytoremediation, interactions between plants and their associated microorganisms, both bacteria and fungi, should be further investigated, in addition to the close interactions between bacteria and fungi. Benefitting from an increased understanding of microbial community structure and assembly allows us to better understand how the holobiont can be modified to improve pollutant degradation and plant growth. In this review, we present an overview of insights in plant-bacteria-fungi interactions and the opportunities of exploiting these tripartite interactions to enhance the effectiveness of phytoremediation of organic pollutants.

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Plant-bacteria-fungi interactions; bioremediation; phytoremediation; organic pollutants

## 1. Introduction

About 20,000 plant species are unable to grow or survive without microbial symbiotic interactions (van der Heijden et al. 2008). Therefore, upon the development of every biotechnological application involving plants, plant-associated microbes should be taken into consideration. Phytoremediation is such an application where plant-associated microbes play a major role in defining its efficiency. Bacteria associated with plants as well as soil bacteria are often exploited to improve phytoremediation efficiency of organic pollutants, because of their plant growth-promoting and pollutant-degrading capacities (Weyens et al. 2009; Glick 2010; Thijs 2015). Also fungi, such as mycorrhizal fungi, but also free-living or endophytic fungi, are known for their beneficial effects on plant growth and development and their strong degradative capacities and are therefore also often applied during phytoremediation of organic pollutants (Thijs 2015; Lenoir et al. 2016; Coninx et al. 2017; Deng & Cao 2017). However, the combined application of both bacteria and fungi is less investigated. Tripartite interactions between plants, bacteria and fungi are nevertheless extensive and have major implications for the plant host and its associated microbiome. A better understanding these tripartite interactions can assist to select for, or even design, optimal phytoremediation procedures. Therefore, this review aims to describe the interactions between plants, bacteria and fungi, the effects of the interactions on the members of the association and the possibilities to exploit these tripartite interactions to improve phytoremediation of organic pollutants.

## 2. Plant–bacteria–fungi interactions

### 2.1. Physical interactions and cell-to-cell contact

#### 2.1.1. Interactions between the plant and its microbiome

Plants are well known to associate with a multitude of microorganisms, providing nutrition and residence for the microbes, while receiving several benefits like the promotion of their growth or stress reduction in return (Hardoim et al. 2008). Complex bacterial and fungal communities can be found living either on the surface of plants or inside plants.

*Bacteria and fungi on the surface of plants.* Most microorganisms living on the surface of plants are residing on the surface of the roots (rhizoplane) and the narrow zone surrounding the roots (rhizosphere) or on the surface of leaves (phyllosphere).

The rhizosphere is defined as the narrow zone of nutrient-rich soil that surrounds the plant roots and is influenced by root exudates and microbial activity (Venturi & Keel 2016). The rhizosphere can be extended to the mycorrhizosphere, which includes the extraradical mycelium of mycorrhiza, that provides a large zone for interactions with other microorganisms (Rambelli 1973). Root exudates comprise sugars, amino acids, flavonoids, proteins and fatty acids (Badri & Vivanco 2009) that passively or actively attract microorganisms that can colonize the rhizosphere and rhizoplane, where they can form microcolonies or biofilms (Compant et al. 2010). Root exudates, therefore, are the major drivers in shaping the rhizosphere and rhizoplane microbial communities. The root exudation pattern is highly dynamic and differs across space and in time (Compant et al. 2010). Rhizosphere and rhizoplane colonization might, therefore, differ across different root regions (Gamalero et al. 2004) and in function of plant growth stage and season (Musilova et al. 2016). Even though recruitment of rhizospheric and rhizoplane microbes by plants from the surrounding bulk soil is strongly dependent on the community structure of the bulk soil (Bulgarelli et al. 2012), findings of (Lundberg et al. 2012) suggest that different plant genotypes select for different rhizospheric communities, implying that genetic variation across plant species can drive differential recruitment of beneficial microbes.

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Phyllospheric bacteria and fungi are heterogeneously distributed across the plant foliage. Elements like climatic conditions, location of the leaves within the vegetation and chemical composition of the cuticle have effects on the occurrence of microorganisms (Bodenhausen et al. 2013). Also on the microscale, bacteria and fungi are heterogeneously spread over the leaves surface, where they form aggregates at the depressions formed at the joints of epidermal cells and stomata, alongside the veins and at the base of trichomes (Remus-Emsermann et al. 2012; 2014). This is connected to an increased nutrient availability caused by the presence of these leaf structures, that facilitate leaching of photoassimilates to the leaf surface (Leveau & Lindow 2001; Vorholt 2012).

*Bacteria and fungi inside the plant.* From the phyllosphere, rhizosphere and rhizoplane, microorganisms can colonize the inside of the plant. Additionally, microorganisms can be vertically transferred from generation to generation via the seeds (Truyens et al., 2015). Both bacteria and fungi are able to live inside plants. They either occupy the intercellular spaces or live intracellularly, resulting from a highly evolved mutualistic plant-microorganism interaction (Reinhold-Hurek & Hurek 2011).

Microorganisms that occupy the intercellular spaces of plants are called endophytes. Both bacterial and fungal endophytes reside inside plants. Bacterial endophytes are mostly derived from the rhizosphere, from where they enter the root epidermis and cortex through cracks occurring on side root emergence sites or at the root tip, or created by deleterious microorganisms (Hardoim et al. 2008). Bacterial endophytes can be further subdivided into three classes: (i) the passenger endophytes that become endophytic by chance and are restricted to the root cortex, (ii) opportunistic endophytes that are also restricted to specific plant tissues, like the root cortex, but show particular root colonization characteristics and (iii) competent endophytes that are able to invade specific plant tissues, like the vascular system (Hardoim et al. 2008). When vascular tissue is invaded, systemic spreading to the vegetative plant parts and colonization of flowers, fruits and seeds can occur (Compant et al. 2010). Seed endophytic bacteria can be selected by the plant for their beneficial characteristics, providing the next generation with a set of bacteria that could aid during germination and seedling establishment (Truyens et al. 2015). Fungal endophytes reside completely inside the root, leaf or stem tissues and the relationship with the plant can range from mutualistic to neutral or even antagonistic (Chadha et al. 2014). They can be subdivided into two main groups: (i) the clavicipitaceous or class 1 endophytes that reside in the shoots and rhizomes of grasses and (ii) the non-clavicipitaceous endophytes that colonize non-vascular plants, ferns, conifers and angiosperms. This last group is further subdivided into 3 classes: (i) the class 2 endophytes that colonize shoots, roots and rhizomes; (ii) the class 3 endophytes that colonize shoots and (iii) the class 4 endophytes that only colonize roots (reviewed in Rodriguez et al. 2009). Class 3 endophytes colonize the plant tissue locally, while the other classes colonize the plant tissue extensively (Rodriguez et al. 2009). Class 4 endophytes are also known as dark septate endophytes (DSE). Transmission of fungal endophytes mainly occurs horizontally through airborne spores, however, like with bacterial endophytes, fungal endophytes can also be transmitted vertically by hyphae growing into the seeds (Saikkonen et al. 1998). A preference to specific organs and tissues inside the plant may exist resulting from an adaptation to particular physiological conditions that can be found in different plant tissues (Aly et al. 2011).

Another group of microorganisms that occupy both intercellular as well as intracellular spaces inside the plant are the mycorrhizal fungi. They provide the plants with nutrients, water and protection against pathogens, and receive in exchange a fraction of the plant photosynthates (Smith & Read 2008). For such interaction to take place, close physical contact is crucial, and therefore all mycorrhiza develop within the root specialized mycelial structure to increase the surface exchange with the root cells. Two main groups of mycorrhizae are recognized: the ectomycorrhizae and the endomycorrhizae. The ectomycorrhizae form a thick mantle and a Hartig net of intercellular hyphae on the roots. They occur in 3% of all vascular plants, mainly associated with trees and they belong to the phyla Ascomycota, Basidiomycota and some Zygomycota (Barman et al. 2016). Endomycorrhizae invade the root cells intracellularly and are associated with tree species and herbaceous species. They are further subdivided into the arbuscular, ericoid, arbutoid, and monotropoid mycorrhizae, ectendomycorrhizae and orchid mycorrhizae (reviewed in Peterson et al. 2003). The arbuscular mycorrhizae are the most prevalent group belonging to the phylum Glomeromycota and forming associations with about 80% of the vascular plants. All arbuscular mycorrhizae can be recognized by their intracellular formation of finely branched hyphae, called the arbuscules (Barman et al. 2016). They are often found to form associations with crops and are therefore of special interest in applied techniques for improving crop production and protection (Smith & Read 2008).

A group of plant-associated microorganisms that only reside intracellularly are the rhizobia (Hardoim et al. 2008). Legumes harbor these nitrogen-fixing bacteria in special plant organs, the root nodules (Zgadzaj et al. 2016). The nodule is formed after rhizobial infection, that is established by trapping of bacterial cells by a root hair and the following formation of an infection thread. Through this infection thread the bacteria penetrate the root cortex cells, which differentiate into a root nodule, internalizing the rhizobia (Wang et al. 2012a).

### 2.1.2. Interactions between plant-associated bacteria and fungi

A plant does not undergo only one of the above-mentioned interactions with bacteria or fungi, but forms associations with several microorganisms (Mendes et al. 2013). These microorganisms do not form single entities, but undergo interactions with each other as well. Several physical interactions can exist between bacteria and fungi, including plant-associated bacteria and fungi.

*Fungal hyphae as bacterial highways.* Bacteria can use fungal hyphae as a highway to transport themselves to sites that are otherwise unreachable by the bacterial cells on their own (van Overbeek & Saikkonen 2016). They can move along the surface of the fungal hyphae by flagellar motility, for which they need a continuous liquid film, such as the one that is present on fungal hyphae (Kohlmeier et al. 2005). Unlike bacteria, fungi can spread easily in water-unsaturated matrices, facilitating accessibility of pollutant-degrading bacteria to pollutants (Furuno et al. 2010). In addition, fungal hyphae can mobilize bacteria towards plant roots, facilitating their entry into the rhizosphere or plant tissues (Minerdi et al. 2002).

*Bacterial intrahyphal colonization.* Bacteria do not only use the surface of fungal hyphae to move themselves towards plants, they also colonize the hyphae intracellularly, using them as a vector for transmission towards plants (van Overbeek & Saikkonen 2016). Endosymbiotic associations between bacteria and fungi are common in the Basidiomycota, Glomeromycota and Zygomycota and are also occasionally found in the Ascomycota (Grube & Berg 2010). The Basidiomycota and Zygomycota undergo endosymbiotic associations with bacteria that are characterized by a low bacterial abundance in the fungal hyphae, while the Glomeromycota can harbor very high numbers of bacteria inside their spores (Grube & Berg 2010). The bacteria reside in the cytoplasm of the fungal cells (Minerdi et al. 2002). Some are even obligatory endosymbionts, like *Candidatus* Glomeribacter gigasporarum, that lives inside the arbuscular mycorrhizal fungus *Gigaspora margarita* (Vannini et al. 2016). Others are not obligate endosymbionts, like members of the genus *Burkholderia* that are found in several Gigasporaceae species (Minerdi et al. 2002).

*Mixed fungal-bacterial biofilms.* Bacteria and fungi can form mixed species biofilm on the surface of plants which provides them protection to unfavorable environments (Nozhevnikova et al. 2015). A biofilm is defined as a surface assemblage of microorganisms and their associated extracellular products that is typically attached to an abiotic or biotic interface (Davey & Toole 2000). Microorganisms in a biofilm interact physically by co-aggregation, a process in which the members of the biofilm become attached to one another by a protein adhesin on one cell and a complementary receptor on the other cell (Rickard et al. 2003). Adhesins and receptors are found in both bacteria and fungi mediating bacteria-fungi interactions, like the bacterial *Streptococcus oralis* adhesin that connects with a receptor protein on the cell wall of the fungal yeast *Candida albicans* (Yang et al. 2011). Like the preceding example, most cases of mixed biofilms in literature handle clinically relevant interactions, however, like Elias & Banin (2012) mention, similar processes should be expected within biofilms in natural environments. Recently, Velmourougane et al. (2017) reviewed the importance of microbial biofilms in agriculture.

## 2.2. Signalling between plants, bacteria and fungi

In the above section, we described the physical interactions between plants, bacteria and fungi. Apart from cell-to-cell contacts, members of an association communicate with each other via chemical interactions in a process called signalling. Signalling entails the detection and response to low molecular weight compounds originating from plants or the microbiome resulting in a cellular response that is not only restricted to the catabolism, transformation or resistance of the compound being detected (Venturi & Keel 2016). It involves a regulatory response which leads to the transcription of specific genes in response to the detected compound (Venturi & Keel 2016). It is not our aim to provide an exhaustive list of all signalling mechanisms between plants, bacteria and fungi (this has been recently reviewed in Quiza et al. (2015) and Venturi & Keel (2016), however, in what follows, we will discuss several important examples.

### 2.2.1. Quorum sensing

Quorum sensing is a mechanism of microbial communication and regulation of gene expression mediated by small diffusible molecules, called auto-inducers or quorum sensing molecules (QSM) (Barriuso 2015). The concentration of these molecules accumulates throughout microbial growth and after reaching a threshold concentration, a response is initiated regulating gene expression of several cell-density related processes in the whole population (Albuquerque & Casadevall 2012). Quorum sensing ensures that energetically costly activities are only undertaken when the population size is high enough to successfully accomplish them (Clinton & Rumbaugh 2016). This strategy, for example, is used by many pathogenic bacteria to overcome host defences, by synchronizing the expression of virulence factors in function of their population size (Miller & Bassler 2001). Quorum sensing is well studied in bacteria and is known to regulate various processes like motility, biofilm formation, sporulation, antibiotic production and, as mentioned above, the secretion of virulence factors (Albuquerque & Casadevall 2012). In Gram-negative bacteria homoserine lactones (HSLs) are widely present as QSM, while in Gram-positive bacteria, other compounds, like peptides function as QSM (Hartmann & Schikora 2012). Extensive research has led to the discovery of several other QSM in both Gram-positive and Gram-negative bacteria (Barriuso 2015). Quorum sensing is not restricted to bacteria. QSM identified from fungi include farnesol, tyrosol, dodecanol, γ-butyrolactone and γ-heptalactone (Albuquerque & Casadevall 2012; Barriuso 2015). Quorum sensing is not confined within species or even within the same kingdom. Bacteria and fungi interfere with each other using QSM and even plants have evolved means of perceiving and responding to microbial QSM (Hartmann & Schikora 2012). Interference of fungi and bacteria with each other's QSM may be an evolutionary strategy to out-compete neighboring microorganisms for space or the ability to infect hosts (Clinton & Rumbaugh 2016). Plants can both inhibit microbial quorum sensing by degradation of QSM, a mechanism called quorum quenching, but can also induce quorum sensing by producing QSM resembling compounds (Mahmoudi et al. 2016). Plant responses to microbial QSM depend on the QSM structure and concentration and can be defensive or can stimulate developmental changes (Clinton & Rumbaugh 2016).

### 2.2.2. Volatile organic compounds

Bacteria and fungi produce a wide range of volatile organic compounds (VOCs); small molecules with low molecular weight that can vaporize at normal atmospheric temperatures and pressure (Hung et al. 2015; Kanchiswamy et al. 2015). They are characteristically alkenes, alcohols, benzenoids, aldehydes, ketones or terpenes (Venturi & Keel 2016). VOCs play an important role in long distance interactions between microbes and even between microbes and plants (Bitas et al. 2013) and regulate symbiotic associations and the distribution of saprophytic, mycorrhizal and pathogenic organisms (Hung et al. 2015). VOCs-mediated microbe-microbe interactions include antimicrobial activity, interference with quorum sensing systems, coordinating gene expression, biofilm formation, virulence and stress tolerance (Audrain et al. 2015). Microbial VOCs are also known to impact plant health in several ways (Bitas et al. 2013), for example some bacterial and fungal VOCs can act as a biocide, inhibiting growth of plant-pathogenic bacteria and fungi (Bennett et al. 2012). Furthermore, bacterial VOCs can promote plant growth by producing plant growth-promoting volatiles like acetoin, by increasing photosynthetic capacity, stimulating synthesis of plant hormone-like compounds, inducing plant systemic resistance and interfering with plant gene expression (Bennett et al. 2012). Plants also produce VOCs themselves, shaping the plant-associated microbial community by either their antimicrobial effects or, on the contrary, their potential as a microbial carbon source (Junker & Tholl 2013; Farré-Armengol et al. 2016).

#### 2.2.3. Phytohormones

Phytohormones, comprising auxins, like indole-3-acetic acid, gibberellins, ethylene, abscisic acid, brassinosteroids and cytokinins, regulate plant development by affecting many physiological and biochemical processes in plants (Fahad et al. 2015). Beneficial bacteria and fungi can produce phytohormones promoting plant growth and development and inducing tolerance against environmental stresses (Fahad et al. 2015; Priyadharsini & Muthukumar 2017). However, also pathogenic bacteria and fungi can produce phytohormones, thus interfering with plant growth, organ development, immune responses and hormonal signalling (Boivin et al. 2016; Venturi & Keel 2016). Phytohormones have an important role in the formation of symbiotic associations of plants with arbuscular mycorrhizae and rhizobia. Strigolactones are carotenoid-derived plant hormones that are exudated from roots under phosphate or nitrogen limiting conditions, activating growth of arbuscular mycorrhizae and attracting them towards the roots (Gutjahr 2014). Additionally, auxins promote formation of arbuscules, while gibberellins inhibit the formation of arbuscular mycorrhizae (Gutjahr 2014). Root nodule formation in the interaction between plants and rhizobia is controlled by phytohormones (Ferguson & Mathesius 2014). Rhizobia interfere with phytohormone regulation by producing phytohormones themselves and by inducing changes in host phytohormone levels as a response to rhizobial nodulation factors (Ferguson & Mathesius 2014).

#### 2.2.4. Nod and Myc factors

The last group of signalling molecules that will be shortly discussed here is that of the lipo-chitooligosaccharides (LCOs), also known as nodulation (Nod) factors of rhizobia and mycorrhizal (Myc) factors of arbuscular mycorrhizae. They are produced as a response to the release of respectively flavonoids and strigolactones from plant roots and are recognized by the host plant that then initiates a symbiosis signalling pathway (Venturi & Keel 2016). Nod factors produced by different rhizobia vary widely, being important for the specificity of rhizobial interactions with their host plant (Oldroyd 2013). In contrast, Myc factors produced by a specific arbuscular mycorrhizal fungus are recognized by a wider array of host plants, relating to their broader host range (Oldroyd 2013).

### 2.3. New insights into plant-microbe and microbe-microbe interactions

In recent years, advances in different ‘omics’ techniques provided us a better understanding of the underlying mechanisms in plant-microbe and microbe-microbe interactions. Kumar et al. (2016) reviewed the use of metabolic engineering and systems biology tools in understanding plant-microbe interactions and to improve plant traits. Wintermans et al. (2016) used a genome-wide association study on *A. thaliana* to reveal 10 genetic loci highly associated to the responsiveness of *A. thaliana* to the plant growth-promoting activity of a rhizobacterium. Their results can be used in designing plants carrying the correct genes to profit from plant growth-promoting rhizobacteria. Siebers et al. (2016) described that lipids play a major role in plant-microbe interactions, being involved in pathogen recognition, signalling, acquired systemic resistance and in establishing a membrane interface between the two organisms. These lipidomic studies can help us to reveal lipid patterns that are common or different among interactions between plants and pathogenic, symbiotic or beneficial microbes (Siebers et al. 2016). Recently also the importance of noncoding RNAs in the regulation of plant-microbe interactions became apparent (Lelandais-Brière et al. 2016). In a recent review, the role of multi-omics approaches in understanding abiotic stress responses in plants and microbe-mediated stress mitigation was described (Meena et al. 2017).

### 2.4. Plant-associated microbial networks

The examples above illustrate the wide range of interactions plants undergo with their microbiome. Additionally, the members of the microbiome itself don’t live as single entities, but interact extensively, forming complex microbial networks (Agler et al. 2016). These microbial networks can be studied by generating co-occurrence networks, in which keystone species or hub taxa can be identified. These keystone species co-occur frequently with other species and potentially play a major role in the regulation of the microbiome composition (van der |Heijden & Hartmann 2016). Interactions within the microbiome and between the microbiome and the plants can range from mutualistic to commensalistic to parasitic and every interaction between two members can have its effect on a third party. In the next section, the effects of these tripartite interactions between plants, bacteria and fungi on the members of the association will be discussed.

## 3. Effect of plant–bacteria–fungi interactions on members of the association

### 3.1. Effect on the microbiome

#### 3.1.1. Microbial growth and development

In the rhizosphere, microorganisms interact with each other, not only yielding positive effects on the plant, but also on each other (Nadeem et al. 2014). Rhizospheric bacteria can promote mycorrhization of plants, a concept first described by Garbaye (1994) who proposed the term ‘mycorrhiza helper bacteria’ (MHB). MHB can induce mycorrhization by stimulating mycelial growth, by increasing root-fungus recognition and colonization and by reducing the effects of hostile environmental factors (Frey-Klett et al. 2007). It can do so by producing growth factors, by neutralizing antagonistic substances and by inhibiting growth of competing microorganisms (Frey-Klett et al. 2007). For example, co-inoculation of *Boletus edulis* with *Pseudomonas fluorescens* doubled within-plant mycorrhization levels in *Cistus ladanifer* shrubs (Mediavilla et al. 2016). Zhao et al. (2014) isolated a poplar rhizobacterial *Bacillus* sp. strain that promoted ectomycorrhizal colonization of *Pisolithus tinctorius* and *Lactarius insulsus* on *Populus deltoids* trees. Another example is that of Navarro-Ródenas et al. (2016) who isolated a *Pseudomonas mandelii* strain that increased mycorrhizal colonization of *Terfezia claveryi* on *Helianthemum almeriense*. In addition, they also found that bacterial isolates that produced auxins, significantly increased the root-shoot ratio and mycorrhizal colonization (Navarro-Ródenas et al. 2016). Also, endobiotic bacteria residing inside fungal hyphae can have positive effects on mycorrhizal growth. The endobacterium *Candidatus* Glomeribacter gigasporarum influenced growth, calcium signalling and metabolism of the arbuscular mycorrhizal fungus *G. margarita* (Vannini et al. 2016). Fungal primary metabolism and respiration were 50% higher in the strains colonized by the endobacterium, compared to the non-colonized fungi. Furthermore, the non-colonized fungi showed higher oxidative stress levels, which, interestingly, were also observed in their host plants (Vannini et al. 2016). Mycorrhizal fungi can also improve root nodulation in legumes (Lesueur & Duponnois 2005; Sakamoto et al. 2013).

However, the interactions between bacteria and fungi in the rhizosphere can also have negative effects on members of the association. Bacteria with antifungal characteristics, like production of siderophores, cyanides and lytic enzymes, were enriched in the rhizosphere of *Carex arenaria* that had increased densities of saprotrophic fungi (de Boer et al. 2008). Root-associated fungi of forest plants showed the capacity to degrade HSLs and thus interfere with bacterial quorum sensing (Uroz & Heinonsalo 2008).

#### 3.1.2. Microbiome composition

From the diverse microbial community of the bulk soil, plant roots select for specific microorganisms that form the rhizospheric microbiome (Berendsen et al. 2012). Plants thus shape the community composition of the rhizosphere with different plant species growing on the same soil recruiting different microbial communities (Garbeva et al. 2008). The plant also shapes the microbiome associated with plant parts other than the roots. Agler et al. (2016) studied the phyllospheric microbiome of *A. thaliana* and suggest that the plant genotype acts on keystone microbial species, which then transmits information to the rest of the microbial network, ultimately leading to an altered host fitness. The presence of the keystone species *Albugo*, an obligate plant pathogen, depended on the resistance of the plant genotype and had a major contribution in shaping the plant microbiome. Liu et al. (2016) indicated the pathogenic fungus *Fusarium oxysporum*, as a microbial keystone species, that has a negative effect on root nodulation of *Ormosia glaberrima* seedlings. Furthermore, the presence of pathogenic fungi around adult trees promoted accumulation of antagonistic *Burkholderia* strains in the rhizosphere of the seedlings. Next to pathogenic species, also non-pathogenic species can influence the plant microbiome. Ectomycorrhizal fungi for example, select for specific bacterial communities (Deveau 2016). Results from a study of Marupakula et al. (2016) showed that several ectomycorrhizal species colonize a single root system of *Pinus sylvestris*, but each species selects for specific associated bacterial communities. Moreira et al. (2016) observed an increase in rhizospheric microbial diversity when maize was inoculated with both an arbuscular mycorrhizal fungus and plant growth-promoting rhizobacteria. They proposed that fungal exudates form a source of nutrients to the bacteria and can, therefore, attract specific rhizobacterial groups.

### 3.2. Effect on plants

#### 3.2.1. Plant productivity

Synergistic interactions between different microbial groups can also lead to positive effects on plant growth (van der Heijden & Hartmann 2016). Many legume plants form associations with arbuscular mycorrhizal fungi that can stimulate root nodulation and bacterial nitrogen fixation (Nadeem et al. 2014). An enhanced productivity and a strongly enhanced seedling establishment in legumes were observed upon co-inoculation with both rhizobia and arbuscular mycorrhizal fungi, that was not observed when inoculated separately (van der Heijden et al. 2016). Bacterial–fungal interactions can also improve phosphorus solubilization like reported by Moreira et al. (2016), who found an increased phosphorus accumulation in roots of maize upon co-inoculation with plant growth-promoting rhizobacteria and arbuscular mycorrhizal fungi.

#### 3.2.2. Plant health

As discussed earlier, plants associate with complex microbial networks containing some keystone species that have a higher impact on the microbiome composition and functioning than any other member of the association. These keystone species might recruit beneficial organisms or prevent invasion of pathogens for their own benefit hereby benefiting the whole plant–bacterial–fungal network (van der Heijden & Hartmann 2016). Additionally, plants can recruit specific microbes that can aid in their protection against pathogens (Berendsen et al. 2012). Several plant-associated bacteria are shown to be antagonistic towards plant-pathogenic fungi. Potato tubers treated with *Bacillus thuringiensis* proved to suppress rhizoctonia potato disease (Bakhvalov et al. 2015).

Bacteria can induce systemic resistance in plants against fungal pathogens by production of HSLs. Inoculation of tomato plants with the HSL-producing bacteria *Serratia liquefaciens* increased systemic resistance against the fungal leaf pathogen *Alternaria alternata*, by induction of plant genes involved in systemic pathogen response by the HSL molecules (Schuhegger et al. 2006). Also Pang et al. (2009) reported an increased systemic resistance in cucumber plants against the fungal pathogen *Pythium aphanidermatum*, the causal agent of damping-off disease, and in tomato and bean plants against the gray mold fungus *Botrytis cinerea* upon colonization with the HSL-producing rhizobacterium *Serratia plymuthica*.

Another mode of action for bacterial control over fungal plant pathogens is by production of VOCs. Several VOCs isolated from plant-associated bacteria showed antifungal properties (Kai et al. 2009). Also fungi can inhibit the growth of plant pathogens by emitting VOCs (Bennett et al. 2012; Hung et al. 2015). The endophytic fungus *Muscodor albus* produces a blend of VOCs with antimicrobial properties against a wide range of bacterial and fungal plant pathogens (Hung et al. 2015).

Bacteria can, however, also induce pathogenicity of fungi. *Rhizopus* spp. cause rice seedling blight in rice plants via the phytotoxin rhizoxin. This toxin is not produced by the fungus itself, but by its endosymbiotic bacteria belonging to the genus *Burkholderia* (Partida-Martinez & Hertweck 2005).

Plants signal information to each other about possible threats. For this, they make use of the underground network of mycorrhizal mycelia (Babikova et al. 2013). Via this underground messaging system healthy plants can get early warnings from their neighboring infected plants and prepare themselves against the oncoming attack (Babikova et al. 2013).

#### 3.2.3. Plant diversity

Soil microorganisms play an important role in plant diversity, especially the ones that live in symbiosis with plants (van der |Heijden et al. 2016). The soil microbiota can thus be defined as belowground drivers of plant diversity (van der Putten 2017). Teste et al. (2017) provided evidence that feedback between plant and soil microbiota is an important driver of plant diversity, mediated by interactions between plants with different nutrient-acquisition strategies and their associated microbiomes. Additionally, tripartite interactions between plants, bacteria and fungi can increase plant diversity. Van der |Heijden et al. (2016) observed an increased plant diversity in model grassland communities in presence of both arbuscular mycorrhizal fungi and nitrogen-fixing rhizobia.

#### 3.2.4. Plant survival in hostile environments

As discussed earlier, interactions between mycorrhizal fungi and rhizobacteria can be beneficial for plant productivity under normal conditions. Also in hostile environments, the tripartite interactions between bacteria, fungi and plants can assist plants by reducing the negative impact(s) of the stress factor(s) on plant growth and development (Nadeem et al. 2014). Moreira et al. (2016) observed a decreased accumulation of zinc in shoots and roots of maize grown on mine land soil upon co-inoculation with the arbuscular mycorrhizal fungus *Rhizophagus irregularis* and the plant growth-promoting rhizobacterium *Chryseobacterium humi*. Furthermore Lee et al. (2015) reported that co-inoculation of the arbuscular mycorrhizal fungus *Glomus etunicatum* and the plant growth-promoting bacterium *Methylobacterium oryzae* could alleviate salt stress in maize and induce plant growth. Co-occurrence of arbuscular mycorrhizal fungi with endophytic bacteria also is reported to alleviate salt stress in plants. Hashem et al. (2016) described increased shoot and root dry weights, nodule numbers and leghemoglobin contents in *Acacia gerrardii* under salt stress because of the synergistic associations between arbuscular mycorrhizal fungi and plant-associated bacteria.

## 4. Application of bacterial–fungal interactions for bio- and phytoremediation of organic pollutants

Like described above, there are several beneficial effects mediated by microorganisms that can help plants to survive in contaminated environments. These tripartite interactions can, therefore, be exploited for improving phytoremediation of organic pollutants. We describe here several research strategies and successful applications for a selection of organic pollutants.

### 4.1. Enhanced insights in total plant-associated bacterial and fungal communities

Exposure to organic pollutants can influence the composition of microbial communities, since, on the one hand, they can cause toxicity, suppressing certain soil microorganisms, meanwhile favoring the more tolerant community members and on the other hand, the pollutants can serve as an energy or nutrient source, favoring community members which possess the appropriate catabolic pathways to metabolize the present pollutant (Harms et al. 2017). Additionally, the presence of pollutants can influence the degree to which plants interact with their microorganisms. For instance, pollution can select for tolerant microbial community members over sensitive plant-specific microbial taxa that may be lost or significantly reduced (Siciliano et al. 2001; Bell et al. 2014). Pollution can also have a differential effect on bacterial or fungal members of the community.

With the emergence of high-throughput sequencing, we can gain a better understanding in the effects of pollution on plant-associated bacterial and fungal communities which allows us to make more elaborate and adequate decisions when selecting for specific phytoremediation strategies. Bell et al. (2014) used 454 pyrosequencing to define a higher fungal sensitivity to hydrocarbon pollution in comparison to bacteria in rhizosphere soils of different willow cultivars. They described a decline in fungal species in response to hydrocarbon pollutants and a stronger influence of willow on the fungal communities. Lladó et al. (2014) observed a high prevalence of *Fusarium* and *Scedosporium* populations in a PAH-polluted industrial soil and *Cupriavidus*, *Mycobacterium* and *Chithinophagaceae* as potential high molecular weight PAH degraders, based on 454 pyrosequencing data and Denaturing Gradient Gel Electrophoresis (DGGE).

### 4.2. Bio-augmentation with mixed bacterial–fungal consortia

Synergistic interactions between bacteria and fungi cannot only promote plant growth and development, additionally, they can stimulate the biodegradation of organic pollutants. Fungal–bacterial consortia might even perform better than single strains separately (Mikesková et al. 2012). Bacterial–fungal interactions can promote phytoremediation of organics by facilitating the access of degrading microorganisms to the pollutant. As mentioned earlier, fungal mycelia can after all serve as a highway for pollutant-degrading bacteria in water-unsaturated environments, leading to their dispersal in polluted soil (Kohlmeier et al. 2005; Furuno et al. 2010). Moreover, bacteria and fungi can complement each other in the degradation pathway of the pollutant. This co-metabolic degradation can lead to a full degradation of the pollutant, where one can further degrade the intermediates formed by the other. Several studies already investigated co-metabolic degradation of organic pollutants by bacteria and fungi and reported an improved degradation compared to the separate strains (Table 1).

Co-cultures of bacteria and fungi are often explored for the bioremediation of polycyclic aromatic hydrocarbons (PAHs) (Boonchan et al. 2000; Chávez-Gómez et al. 2003; Kim & Lee 2007; Machín-Ramírez et al. 2010; Wang et al. 2012a; Zafra et al. 2014; Ma et al. 2016; Bhattacharya et al. 2017).

**Table 1.** Bacterial-fungal co-inoculations with the potential to enhance biodegradation of organic pollutants.

| Pollutant | Bacteria | | Fungi | Reference |
|---|---|---|---|---|
| PAHs:<br>Pyrene<br>Chrysene<br>Benz[*a*]anthracene<br>Benzo[*a*]pyrene<br>Dibenz[*a,h*]anthracene | *Stenotrophomonas maltophilia* VUN 10,010 | + | *Penicillium janthinellum* VUO 10,201 | Boonchan et al. (2000) |
| | Bacterial consortium VUN 10,009 | + | *Penicillium janthinellum* VUO 10,201 | |
| PAHs:<br>Anthracene<br>Chrysene<br>Fluoranthene<br>Phenanthrene<br>Pyrene | *Rhodococcus* sp. IC10 | + | *A. terreus* | Kim and Lee (2007) |
| | *Rhodococcus* sp. IC10 | + | *Penicillium* sp. | |
| PAHs:<br>Phenanthrene<br>Fluoranthene<br>Pyrene | *Pseudomonos* sp.,<br>*Labrys portucalensis*,<br>*Ralstonia eutropha*,<br>*Rhodococcus globerulus* | + | *Debaryomyces vanrijiae*,<br>*Paecilomyces lilacinus*,<br>*Fusarium* spp.,<br>*Penicillium simplicissimum*,<br>*Trichoderma* sp. | Wang et al. (2012b) |
| PAH:<br>Benzo[a]pyrene | *Pseudomonas aeruginosa* MTCC 1688 | + | *Pleurotus ostreatus* PO-3 | Bhattacharya et al. (2017) |
| PAH:<br>Fluoranthene | *Bacillus subtilis* | + | *Acremonium* sp. | Ma et al. (2016) |
| PAHs:<br>Phenanthrene<br>Pyrene<br>Benzo[a]pyrene | *Klebsiella pneumoniae* B1,<br>*Enterobacter* sp. B3,<br>*Bacillus cereus* B4,<br>*Pseudomas aeruginosa* B6,<br>*Streptomyces* sp. B8,<br>*Klebsiella* sp. B10,<br>*Stenotrophomonas maltophilia* B14 | + | *Aspergillus flavus* H6,<br>*Aspergillus nomius* H7,<br>*Rhizomucor variabilis* H9,<br>*Trichoderma asperellum* H15,<br>*Aspergillus fumigatus* H19 | Zafra et al. (2014) |
| PAH:<br>Phenanthrene | *Burkholderia cepacea* | + | *Penicillium* sp. | Chávez-Gómez et al. (2003) |
| | *Ralstonia picketti* | + | *Penicillium* sp. | |
| | *Pseudomas aeruginosa* | + | *Penicillium* sp. | |
| PAHs:<br>Benzo[a]pyrene | *Serratia marcescens* | + | *Penicillium* sp. | Machín-Ramírez et al. (2010) |
| Petroleum hydrocarbons | *V. rumoiensis* | + | *C. echinulate* | Li and Li (2011) |
| Petroleum hydrocarbons | *Bacillus subtilis*,<br>*P. fluorescens*,<br>*Streptococcus faecalis* | + | *Candida tropicalis* | Qiao et al. (2014) |
| Petroleum hydrocarbons | *Bacillus subtilis*,<br>*Bacillus megaterium*,<br>*Achromobacter xylosoxidans*,<br>*P. fluorescens* | + | *Candida tropicalis*,<br>*Rhodotorula dairenensis*, | He et al. (2014) |
| Crude oil | *Bacillus subtilis* | + | *Acremonium* sp. | Ma et al. (2015) |
| Diesel | *Chryseobacterium* sp.,<br>*Acinetobacter* sp.,<br>*Pseudomonas* sp.,<br>*Stenotrophomonas* sp.,<br>*Alcaligenes* sp., *Gordonia* sp. | + | *T. gibbosa* | Zanaroli et al. (2010) |
| PCBs | *Pseudomonas* sp. MO2A | + | *Debaryomyces maramus* CW36 | Chen et al. (2015) |
| Chlorpyrifos | *Serratia* sp. | + | *Trichosporon* sp. | Xu et al. (2007) |
| β-cypermethrin | *B. licheniformis* B-1 | + | *A. oryzae* M-4 | Zhao et al. (2016) |
| Textile dyes:<br>Reactive navy blue HE2R | *Pseudomonas* sp. SUK1 | + | *Aspergillus ochraceus* NCIM-1146 | Kadam et al. (2011) |
| Textile dyes:<br>Reactive red X-3B | Proteobacteria spp.,<br>Sphingobacteriia spp.,<br>Flavobacteriia spp.,<br>Bacteroidia spp.,<br>Nitrospirales spp.,<br>Phycisphaerae spp. | + | *Geotrichum candidum*,<br>*Candida pseudolambica* | Zhou et al. (2014) |
| Textile dyes:<br>Reactive red X-3B | *Exiguobacterium* sp. TL | + | *Penicillium* sp. QQ | Shi et al. (2014) |
| Textile dyes:<br>Reactive dark blue K-R | *Exiguobacterium* sp. TL | + | *Penicillium* sp. QQ | Qu et al. (2010) |

Boonchan et al. (2000) not only observed an increased PAH degradation in soil inoculated with a bacterial–fungal co-culture, they also observed a reduction of the mutagenicity of organic soil extracts, compared with the native microbes and soil inoculated with only axenic cultures. Similarly, Kim & Lee (2007) reported a reduced ecotoxicity of soil after bioremediation with co-cultures of *Rhodococcus* sp. and *Aspergillus terreus* or *Penicillium* sp., on top of a total biodegradation of anthracene, phenanthrene and pyrene.

Bacterial–fungal co-cultures can also enhance bioremediation of petroleum hydrocarbons (Zanaroli et al. 2010; Li & Li 2011; He et al. 2014; Qiao et al. 2014; Ma et al. 2015). Li & Li (2011) revealed that co-inoculation of hydrocarbon polluted mangrove sediment with *Cunninghamella echinulate* and

*Vibrio rumoiensis* led to a more efficient petroleum hydrocarbons bioremediation than the sum of the individual degradations obtained in axenic cultures of the fungus or bacterium. Bio-augmentation of highly contaminated oilfield soils with a yeast-bacterium consortium had a minor effect on the removal of total petroleum hydrocarbons, however, it did significantly enhance the removal of PAHs, hereby detoxifying the soil (Qiao et al. 2014). A consortium consisting of the fungus *Trametes gibbosa* and bacteria belonging to the genera *Chryseobacterium*, *Acinetobacter*, *Pseudomonas*, *Stenotrophomonas*, *Alcaligenes* and *Gordonia* removed 90% of diesel fuel after 10 days in batch culture, a percentage that could not be reached by either bacteria or fungi alone (Zanaroli et al. 2010).

Chen et al. (2015) studied the potential of a yeast–bacteria co-culture in cleaning up polychlorinated biphenyl (PCB) polluted environments. They observed an enhanced PCB degradation of 69.9% in 14 days in a liquid medium by the yeast–bacteria co-culture, compared to only 27.8% degradation by the yeast or 57.0% by the bacteria alone.

Promising results were also found in biodegradation of pesticides with bacterial–fungal co-cultures (Xu et al. 2007; Zhao et al. 2016). Xu et al. (2007) isolated a chlorpyrifos-degrading bacterial strain belonging to the genus *Serratia* and a chlorpyrifos- and intermediate 3,5,6-trichloro-2-pyridinol-degrading fungal strain belonging to the genus *Trichosporon* from activated sludge by enrichment culture technique. Together they could completely mineralize chlorpyrifos. Likewise, Zhao et al. (2016) observed that the toxic intermediate of β-cypermethrin, 3-phenoxybenzoic acid, formed by degradation with *Bacillus licheniformis* was degraded by *Aspergillus oryzae*, thus co-inoculation of both microbes led to an improved β-cypermethrin degradation.

Lastly, co-metabolism by bacteria and fungi has also been extensively investigated in the bioremediation of textile dyes (Qu et al. 2010; Kadam et al. 2011; Shi et al. 2014; Zhou et al. 2014). Zhou et al. (2014) reported that bacterial contamination during fungal degradation of textile effluents should not be prevented, since they can stimulate reactive red dye decolorization. Also Shi et al. (2014) and Qu et al. (2010) pointed at the positive effects of bacterial-fungal co-culture in decolorization of textile dyes in wastewater treatment.

### 4.3. Biostimulation/biocontrol of specific microbial taxa

An alternative strategy to bio-augmentation is biostimulation of indigenous microorganisms, by supplementing growth limiting nutrients like nitrogen, phosphorous or potassium and the application of additives to improve soil pH and soil structure. In addition, biostimulation of specific microbial taxa can be reached by biocontrol of antagonistic taxa, since many fungi and bacteria engage in antagonistic interactions, combating each other by producing antimicrobial compounds (De Boer et al. 2005; Mille-Lindblom et al. 2006; Hibbing et al. 2010; Lecomte et al. 2011). A wide range of microbial taxa can be active in contaminated soil, but the most effective pollutant degrader(s) might not naturally dominate in the soil. Bell et al. (2013) used gentamicin and vancomycin to inhibit distinct portions of the microbial community in a hydrocarbon contaminated soil and observed an increase of the hydrocarbon biodegradation, despite a reduced bacterial and fungal abundance. Stimulating growth of specific microbial taxa can thus be an effective strategy to improve bioremediation of organic pollutants.

### 4.4. Changing the rhizosphere microbiome by selection of specific plant species and genetic engineering

Plant roots select for specific microorganisms from the broad variety of soil microbes that form the rhizosphere microbiome (Berendsen et al. 2012). Plants thus shape the community composition of the rhizosphere, with different plant species growing on the same soil recruiting different microbial communities (Garbeva et al. 2008). Some plant species can even create similar microbial communities in different soils (Miethling et al. 2000). The selected plant species used for phytoremediation thus affect the plant-associated microbiomes and their degradative capacities. Bell et al. (2014) showed that a specific Pezizomycete-dominated community was promoted by phylogenetically similar willow cultivars in a hydrocarbon contaminated soil, whereas more distantly related varieties formed non-specific associations with the fungi. The authors, therefore, suggested that also the evolutionary relationship between plants and microbes should be taken into consideration for plant selection during phytoremediation. Siciliano et al. (2001) found that plants had the ability to selectively enhance the prevalence of endophytes containing pollutant-degrading catabolic genes.

Rhizodeposits play an important role in selecting the rhizosphere microbiome (Bulgarelli et al. 2013; Jha et al. 2014). Therefore, there has been a major interest in changing the quality and/or quantity of root exudates via plant breeding or genetic engineering to selectively enhance specific microbial colonization (van Aken et al. 2010; Bakker et al. 2012). Furthermore, Wintermans et al. (2016) showed that different plant genotypes can respond differently to the plant growth-promoting effects of rhizobacteria. They used a genome-wide association study on *A. thaliana* to reveal 10 genetic loci highly associated with the responsiveness to the plant growth-promoting activity of a rhizobacterium. Their results demonstrate that plants possess natural genetic variation for the capacity to profit from plant growth-promoting rhizobacteria and that this knowledge can be used in future sustainable breeding strategies (Wintermans et al. 2016).

## 5. Conclusions

Both bacteria and fungi can be important degraders of organic pollutants in contaminated environments and both can have beneficial effects on plant growth. Therefore, a profound knowledge of both, plant–bacteria as well as plant–fungi interactions, is essential for the development of novel phytoremediation strategies. Plants, however, do not only interact with their microbiome but members of the microbiome also interact with each other. This extensive microbial network receives information from the plant and its environment, that is spread throughout the microbial network and responses are perceived again by the plant. These tripartite interactions thus have an impact on every single member of the association and should be taken into account when developing novel phytoremediation strategies. The possibilities of a combined inoculation with both beneficial bacteria and fungi during phytoremediation processes have not been often explored. However, synergistic interactions between bacteria and fungi were shown to improve biodegradation of a broad range of organic pollutants. Moreover, a combined inoculation of both bacteria and fungi can strengthen plant health and survival. On the one hand, the presence of certain bacterial strains can prevent infection of the plant with pathogenic fungi, and the other way around, the presence of certain beneficial fungi can avoid infection with pathogenic bacteria. On the other hand, certain bacterial or fungal strains can benefit colonization of the plant by other beneficial bacteria or fungi. Enrichment with both, bacteria and fungi, during phytoremediation of organic pollutants, therefore, is promising to enhance phytoremediation efficiency.

In future research concerning phytoremediation of organic pollutants, these tripartite interactions between plants, bacteria and fungi should be investigated more in detail. In a next step, the obtained knowledge should be implemented in new experimental set-ups in which these tripartite interactions are taken into account, selecting for the best plant–bacterial–fungal associations, leading to the most optimal phytoremediation of the organic pollutant of concern.

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