



# Plant Microbiota Beyond Farming Practices: A Review

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Plants have always grown and evolved surrounded by numerous microorganisms that inhabit their environment, later termed microbiota. To enhance food production, humankind has relied on various farming practices such as irrigation, tilling, fertilization, and pest and disease management. Over the past few years, studies have highlighted the impacts of such practices, not only in terms of plant health or yields but also on the microbial communities associated with plants, which have been investigated through microbiome studies. Because some microorganisms exert beneficial traits that improve plant growth and health, understanding how to modulate microbial communities will help in developing smart farming and favor plant growth-promoting (PGP) microorganisms. With tremendous cost cuts in NGS technologies, metagenomic approaches are now affordable and have been widely used to investigate crop-associated microbiomes. Being able to engineer microbial communities in ways that benefit crop health and growth will help decrease the number of chemical inputs required. Against this background, this review explores the impacts of agricultural practices on soil- and plant-associated microbiomes, focusing on plant growth-promoting microorganisms from a metagenomic perspective.

**Keywords:** farming practices, PGPR, metagenomics, microbiome engineering, microbiota, soil microbial ecology

## INTRODUCTION

For 10 millennia, humankind has continuously reshaped its environment for the purpose of food production. With the green revolution, farmers began to intentionally reshape their microbial niches through the massive use of chemical inputs such as pesticides. The intensification of farming practices dramatically unbalanced crop-associated microbial communities. The emergence in the 1980s of plant growth-promoting rhizobacteria (PGPR) was designed to take account of microbial communities and their beneficial traits for crops as a whole (Kloepper et al., 1980). Since then, numerous beneficial microorganisms have been identified and broadly characterized.

Most PGPR or biocontrol agents are associated with rhizosphere and root endosphere microbiota that may be considered derivatives of surrounding bulk soil microbiota. Understanding the fate of such microbiota is fundamental to developing smart farming practices, although a tremendous amount of work is required to determine how to achieve this. Rhizosphere microbial communities are modulated by various abiotic and biotic factors. There are numerous underlying mechanisms explaining the composition, structure, and fate of belowground microbiota, such as the rhizosphere effect mediated by bipartite interactions (Hartmann et al., 2008; Mendes et al., 2013). Some bacteria can be vertically transmitted from the seed to the next generation and thrive

in the early stages of root development (Hardoim et al., 2012; Liu et al., 2012). Aboveground microbial community assembly is also strongly host- and compartment-dependent, suggesting an important relationship between a plant and its epiphytic microbiota, which can originate from seed, soil, and air (Vorholt, 2012; Hardoim et al., 2015). Despite the tremendous progress that has been made in the study of crop-beneficial microbes, there has been no successful development of field-effective bio-based plant protection products. This highlights the need to consider the fate of such microorganisms in the agroecosystems to which they have been introduced and the biological functionalities effectively provided by a crop-associated microbiome.

A microbiome was initially defined as the genome of microbial communities inhabiting specific ecological niches and interacting through distinctive and specific functions (Whipps et al., 1988). Recently, Berg G. et al. (2020) expanded this definition, enlarging the concept of the microbiome to include all microbiota, including prokaryote and eukaryote microorganisms, their habitats, and their “theater of activity” mediated by microbial structures, metabolites, and nucleic elements.

Addressing the diversity, composition, and structure of a microbiome will provide deeper insights in the numerous microbial functionalities supporting plant health and growth (Lemanceau et al., 2017; Compant et al., 2019). Such metagenomic studies have only been achievable following the emergence of next-generation sequencing (NGS) technologies. NGS also contributes to the development of other omics technologies (transcriptomic and proteomic), enabling the description of biological functions carried out by microbiota. In the coming years, considerable progress in the understanding of microbiomes will be achieved through a combination of NGS technologies and descriptive approaches that equate more closely to biological facts.

One can expect to decrease the need for chemical inputs by modulating microbial communities in a way that benefits crop health and growth. Against this background, the present work reviews, from a metagenomic perspective, the impacts of cropping practices on soil and plant microbiomes with a focus on microorganisms promoting plant growth.

## IMPACT OF TILLAGE PRACTICES ON SOIL MICROBIOTA

For centuries, tilling has been helping farmers to prepare land for crops. Plowing assists in incorporating crop residues, preparing the seedbed, alleviating soil compaction in topsoil layers, and decreasing weed, pest, and soilborne plant pathogen load (Tilman et al., 2002; Hobbs et al., 2008). Although plowing is known to increase soil fertility and yield in the short term, it leads to a major soil structure disturbance. The destruction of soil macroaggregates and networks of pores results in severe soil erosion and ecological niche homogenization. Conservation or reduced tilling as well as no-till practices emerged in the 1930s to address the detrimental effects of conventional tillage. With massive improvements in NGS technologies, tilling practices are now increasingly investigated from a microbial perspective.

Indeed, most studies describe plowing as one of the major drivers of soil microbiome diversity along with pedological context and farming practices such as organic management or cover crops (Hartmann et al., 2015; Wang et al., 2017; Alahmad et al., 2019; Babin et al., 2019; Degruene et al., 2019). Tilling regimes impact soil and plant microbial communities in terms of their diversity, structure, and composition.

From a metagenomic perspective, the impact of tilling on soil microbial diversity is usually investigated through  $\alpha$ - or  $\beta$ -diversity indexes describing respective differences within and between communities. Conventional tillage has a low impact on fungal  $\alpha$ -diversity, while increasing prokaryotic  $\alpha$ -diversity has a significant impact on prokaryotic  $\beta$ -diversity favoring opportunistic commensal and copiotroph microbes (Degruene et al., 2017; Hartman et al., 2018; Sommermann et al., 2018; Babin et al., 2019; Banerjee et al., 2019; Piazza et al., 2019; Srour et al., 2020). Tilling facilitates fast organic matter decomposition resulting in a sudden nutrient release that is homogeneously distributed in tilled soil columns, thus increasing the abundance of r-strategists or fast-growing microorganisms (Degruene et al., 2017; Schmidt et al., 2018). A fall in  $\alpha$ -diversity under conservation tillage practices is common and attributable to a reduction in evenness as much as in richness (Degruene et al., 2016; Piazza et al., 2019; Tyler, 2019). Nevertheless, conservation tillage and no-till practices favor slower organic matter degradation and the establishment of less diverse but more oligotrophic, complex, and stable microbial communities (Degruene et al., 2017; Song et al., 2017; Wang et al., 2017; Tyler, 2019; Srour et al., 2020). Babin et al. (2019) consistently observed a higher abundance of predicted genes involved in oligotrophic lifestyles under low tillage conditions. On a long-term basis, decreasing tilling intensity promotes a higher abundance of microbes degrading more complex organic compounds, which enhances soil fertility (Karlen et al., 1994; Souza et al., 2013). Wang et al. (2017) reported concordant results indicating higher soil organic carbon and nitrogen leading to higher nitrogen and carbon plant accumulation under reduced tillage regimes. Low soil disturbance farming systems appear to increase soil nutrient content and stability as well as the number of oligotrophic and structured soil microbiota (Srour et al., 2020; Wang et al., 2020).

The impact of tilling on the structure of microbial communities is often evidenced through  $\beta$ -diversity analyses; however, network analyses are required to investigate its complexity in greater depth. The exploration of such networks requires specific metrics describing their size (nodes and edges), the degree of co-occurrence/exclusion of interacting operational taxonomic units (OTUs), network cohesion (density), centrality, and modularity (Schmidt et al., 2019). Hartman et al. (2018) found that plowing to structure soil bacterial communities by increasing network density also diminishes their size, modularity, and stability. Higher density indicates a larger proportion of interacting prokaryotic OTUs, whether through co-occurrence or co-exclusion relationships. This is consistent with the increases in prokaryotic  $\alpha$ -diversity discussed above. A lower modularity index suggests conventional tilling practices break down the structure of soil prokaryotic communities (Newman, 2006). The effects of tilling on networks of fungal communities

remain unclear but negatively impact the structure of fungal microbiota. Banerjee et al. (2019) identified a significant negative correlation between plowing intensity and fungal network connectivity. They demonstrated that fungal networks were larger and are more densely connected under no till while tilling disrupted hyphal networks.

In addition to the impacts of soil inversion on the complexity and stability of soil microbial networks, tilling has been shown to noticeably affect the composition of microbial communities (Wang et al., 2017; Hartman et al., 2018; Nelkner et al., 2019). Historically, one of the reasons farmers used to plow land was to decrease soilborne pathogen load (Tilman et al., 2002). In fact, by burying crop residues, moldboard plowing helps to control residue-borne or moist-dependent plant pathogens. Reduced tilling or no tilling keeps crop residues in upper soil horizons which favors plant pathogens belonging to *Fusarium* species (Hartman et al., 2018; Sommermann et al., 2018). However, the absence of soil disturbance promotes other fungi forming hyphal networks such as plant-beneficial arbuscular mycorrhizal fungi (AMF) (Degruene et al., 2017; Srour et al., 2020). Consistent with this, Lienhard et al. (2014) suggest that Actinobacteria exhibiting a mycelia-like growth habit are more sensitive to soil work.

Thus, taxonomical data generated through metagenomic approaches should be considered cautiously depending on the taxonomical level and specific biological and/or ecological functions. While both conventional and conservation tillage increase the abundance of Actinobacteria (Hartman et al., 2018; Babin et al., 2019), Cania et al. (2020) demonstrated that low tilling intensity favors those harboring a higher potential to produce exo- and lipopolysaccharides. These biomolecules are crucial in soil macroaggregate formation and stability and, therefore, play crucial roles in preventing severe erosion events and ecological niche homogenization. Favoring heterogeneous soil microbial niches with overlapping phylogenetic groups and redundant ecological functions contributes to the creation of more resilient and sustainable agroecosystems (Schmidt et al., 2019; Srour et al., 2020). The sustainability of such agroecosystems also relies on disease-suppressive traits favored under no till conditions as described by Srour et al. (2020). However, among  $\alpha$ -Proteobacteria, Sphingomonads associated with disease-suppressive traits are favored in till soils, while the abundance of Rhizobiales, encompassing symbiotic nitrogen-fixing bacteria, increases under conservation tilling (Souza et al., 2013; Wang Z. et al., 2016; Degruene et al., 2017; Babin et al., 2019). These findings illustrate the need to consider lower taxonomical levels when investigating soil microbiomes. Ultimately, these studies are paving the way for informed soil work decision-making that will help in recruiting specific microbial guilds and building healthier soils.

## IMPACT OF SOIL COVER ON SOIL MICROBIOTA

In addition to adaptation of the tilling regime, growing cover crops, also known as catch crops, is another efficient way to

prevent soil erosion and increase long-term soil fertility. Abdalla et al. (2019) recently reviewed the impacts of cover crops on the leaching of soil nutrients and crop productivity. They concluded that seeding catch crops significantly decreases nitrogen leaching and increases soil organic carbon sequestration and grain yields when favoring mixed legume–non-legume cover crops.

Indeed, mixing cover crops seems to favor more abundant and specialized microbiomes (Finney et al., 2017). Overall, although the  $\alpha$ -diversity of soil microbial communities is not impacted, specific microbial guilds seem to be recruited when catch crops are implemented in crop rotation (Cloutier et al., 2020; Kim et al., 2020). Cloutier et al. (2020) identified significant changes in soil fungal microbiome with more abundant and distinct arbuscular mycorrhizal fungal communities under cover crop mixtures. Their findings corroborate previous work that shows cover crop mixture and some specific cover crop species (oat and cereal rye) increase AMF abundance in bulk soils (Finney et al., 2017). By contrast, Detheridge et al. (2016) observed lower levels of root endophytic fungi such as AMF under clover cover crops. Because clovers are leguminous crops, the authors argued that this finding might be due to the release of bacterially fixed nitrogen as they identified a negative correlation between high soil nitrate levels and root-associated fungal populations such as AMF. The importance of considering the identity and diversity of cover crops when attempting to benefit from fungal microbiome management has been pointed out by Cloutier et al. (2020). A recent study highlights a positive effect of cover crop diversity on bacterial microbiota evenness. However, Garland et al. (2021) showed this effect to be negligible when considering environmental factors. The low impact of cover crop diversity on microbial biodiversity might be attributed to the occurrence of sampling when one crop is implemented in the field. The authors suggest that diversifying crop systems in a space by intercropping might have a significant impact on overall microbial diversity. By contrast, this study evidences the proportion of time spent using cover crops to be a determinant of taxa-specific and soil microbial diversity.

Soil as much as plant bacterial microbiomes are impacted by cover crops when implemented and destroyed (Fernandez et al., 2016; Finney et al., 2017). As expected, cover crop burial brings fresh organic matter into the soil and increases bacterial diversity and abundance. Some oligotrophic microbes among Acidobacteria and Verrucomicrobia phyla are promoted along with fast-growing bacteria involved in rapid organic matter decomposition among Actinobacteria and Firmicutes (Ramirez et al., 2012; Pascault et al., 2013). Cover crops also contribute to an increased functional redundancy and complementarity in soil prokaryotic communities. The increased functional redundancy derives from the larger soil heterogeneity and niche partitioning provided by the implementation and burial of catch crops (Alahmad et al., 2019). Remarkably, Nivelle et al. (2016) observed that conventional tilling by disrupting macroaggregates diminishes the beneficial impact of cover crops and impairs microbial functional diversity. Alahmad et al. (2019) demonstrated that bacterial communities favored under cover crop regimes are specifically involved in the metabolism of numerous carboxylic acids. Accordingly,

Nivelle et al. (2016) report faster catabolism of carbohydrate and phenolic compounds within microbial communities associated with cover crops. Both studies support the hypothesis advocated by Alahmad et al. (2019) of a functional complementarity within cover crop-associated bacterial microbiomes.

Beyond the beneficial traits harbored by cover crop-recruited soil microbiota, Romdhane et al. (2019) considered how to select an appropriate way to terminate cover crops. According to Alahmad et al. (2019), Cloutier et al. (2020), and Garland et al. (2021), farmers could eventually resort to cover crop diversity and duration to induce shifts in both bacterial and fungal microbiomes in order to reduce fertilization needs while maintaining yields. There is still much work to be done with regard to the low number of studies investigating the impact of cover crops from a metagenomic perspective.

## FERTILIZATION AND AMENDMENTS

Traditionally employed in agriculture, fertilization and amendments have an important impact on soil and plant microbiomes. By modulating the availability of nitrogen or other minerals, carbon, or through modification of the soil structure, these inputs affect the soil and plant life. On the other hand, microbiome can increase the bioavailability of soilborne nutrients. Most nutrients (N, P, S) are results from organic matter degradation and have to be mineralized by telluric bacteria or fungi in order to be available for plants (Van Der Heijden et al., 2008). In natural conditions, microbial mineralization is the key driver of plant growth (Schimel and Bennett, 2004). Plant exudates are known to shape the microbiome and enhance nutrient microbial conversion and bioavailability for plants (Jacoby et al., 2017). Through this molecular dialog, plants established a “microbial nutrient supply chain”. This relation can be unbalanced by fertilization, especially chemical inputs.

### Fertilization

It has been established that nitrogen supply can impact disease development. Indeed, high concentrations of nitrogen, usually in crops, are often positively correlated with an increase in the susceptibility of plants to diseases (Agrios, 2005).

One notable study led by Fierer et al. (2012) investigated soil communities across nitrogen gradients using genomic as well as physiological tools. In terms of diversity, both sites receiving the highest levels of nitrogen differed from others (intermediate and low levels). The authors evidenced a shift to copiotrophic bacterial communities. This shift was confirmed by metagenomic analyses, with high-rate reproducing copiotrophic bacteria exhibiting an increase in DNA, RNA, and protein metabolism and a decrease in urea decomposition, suggesting a diminishing reliance on organic forms of nitrogen. These observations may have an impact on specific organisms such as plant pathogens. Wei et al. (2015) suggested that the invasion of plant roots by pathogens decreases when there is an overlap between the resident communities and invading pathogens due to intensified competition for resources. However, when the results of Wei et al. (2015) and Fierer et al. (2012) are compared, it can be inferred that N fertilization, by limiting resource

competition, enhances phytopathological disorders. Berg and Koskella (2018) confirmed that N also decreases the protective ability of phyllosphere microbiota. After evidencing that a phyllosphere microbiome could prevent leaf colonization by *Pseudomonas syringae*, the authors demonstrated that the use of a fertilizer significantly decreased this protective effect.

Another study found that N fertilization drastically reduced phagotrophic protists in different soil types. These protists are microbial predators and could play a role in the modulation of soil microbial communities (Zhao et al., 2020).

Nitrogen fertilization can also have an impact on the phosphorus cycle. Dai et al. (2020) demonstrated that the long-term use of N fertilization decreased microbial P-solubilizing and mineralizing capacity by modulating microbial communities while P fertilization favored immobilization by microorganisms by altering the functional profiles of soil microbiota. Another study focusing on phosphorus inputs alone also found that acid phosphatase activity was reduced along with the solubility of mineral P (Pantigoso et al., 2018). Similar to the findings of Dai et al. (2020) for N inputs, the authors suggested that P fertilization decreases the P-solubilizing abilities of soil microbiomes.

Few studies have been conducted on K fertilization alone. Although Pan et al. (2014) showed that K fertilization shapes the soil communities but not the functions in grasslands, no other study was found to be relevant in this context. Studies on NPK fertilization in combination revealed the same trends in soil microbiomes (Pan et al., 2014; Chen et al., 2020). Based on such findings, Zhang et al. (2017) suggested that the affected pH rather than the nutrients was responsible for these shifts in microbial communities.

### Organic Amendments

Bonanomi et al. (2018) reported that the suppressive effects of organic amendments have been exhibited in 78 plant pathogens since the 1940s. Although the authors recognized that the results were often inconsistent and difficult to adapt in prediction tools, the comprehension of chemical actions such as glucosinolates in suppressiveness (Larkin and Griffin, 2007) or the link between amendment, suppressiveness, and bacterial communities (He et al., 2012) paves the way to a better management of beneficial microbes through amendments. Nevertheless, numerous studies concerning amendments and microbiomes focus on a single pathology or a single crop (Cesarano et al., 2017; Inderbitzin et al., 2018) or describe microbiomes in different conditions (Bonanomi et al., 2016), without successfully identifying guidelines for microbiome management. A notable point of view on this issue was presented by Bonanomi et al. (2010) in a meta-analysis of 252 papers. The authors primarily explored the characteristics of organic soil amendments linked to a suppressive effect in soilborne diseases. They found that multiple characteristics can apparently be discarded and that six parameters are particularly useful for predicting suppressiveness prediction. These parameters, both enzymatic and microbial, are the FDA (fluorescein diacetate), enzymatic activity, substrate respiration, microbial biomass, total culturable bacteria, and populations of *Pseudomonads* and *Trichoderma* spp.



Another potentially notable mechanism is the determination of the feeding preferences of microbes. Bonanomi et al. (2018) compiled an analysis of recent studies based on  $^{13}\text{C}$  cross-polarized magic angle spinning nuclear magnetic resonance (C-NMR) and evidenced several differences in substrate preferences. Although these data provide valuable insights, the authors insist on the need for an in-depth study in collaboration with laboratories worldwide. Although studies demonstrate the positive effect of a combination of organic amendment and beneficial microorganisms (Latha et al., 2011; Shen et al., 2015), these current solutions cannot be generalized.

Fertilization and organic amendments shape the soil microbiome, principally through nutrient availabilities, but also through pH or modulation of other soil parameters. Although chemical fertilization seems to make the soil microbiome “dependent” of these nutrients, favoring copiotrophic bacteria, and decreases the solubilizing and mineralizing abilities of bacteria of N and P cycles, organic amendments offer more possibilities. In this respect, Ling et al. (2016) found that long-term organic amendments support stronger functional potential and more interactions within soil communities than chemical fertilization, most likely due to better soil stabilities and a good buffering capacity.

## PLANT GENOTYPE AND MICROBIOME

Several factors can influence the composition of plant microbiomes, including genotypes, plant developmental stage, and plant health (Berg et al., 2015). Characteristic root exudates are usually considered the causative factor underlying the recruitment of specific microbial communities and are influenced by plant genotype. The recruitment of the plant-associated microbiome can vary in terms of structure and functionality and depends to a great extent on the physical properties of soil and nutrient availability (Berg and Smalla, 2009).

Numerous studies have linked microbial diversity with a reduction in the incidence of disease (Keesing et al., 2010; Kopecky et al., 2019). A low potato common scab is observed, even in favorable conditions, when high bacterial diversity is present in the soil (Latz et al., 2012; van Elsas et al., 2012). Higher soil microbiome diversity offers better odds of finding a higher abundance of rare species able to bring specific protective functions against pathogens (Latz et al., 2012). As reported by Mendes et al. (2018), the exclusive and abundant presence of a bacterial taxon is a poorer indicator of disease suppression than the relative abundance of bacterial taxa.

The breeding of cultivars resistant to pathogens is a well-known practice in the control of diseases. In some cases, the genetic background of the plant may not be the only driver of such resistance. Wei et al. (2019) demonstrated that the apparent resistance of cotton cultivar to *Verticillium* wilt is partially due to the plant microbiome. An abundance of beneficial microbes in the cotton rhizosphere offers a complementary protection against this soilborne pathogen. Similar findings were reported for cucumber resistance to *Fusarium* wilt (Yao and Wu, 2010) and tomato resistance to *Ralstonia solanacearum* (Kwak et al., 2018).

The relative abundance of well-known beneficial rhizospheric and root endospheric microbial groups can vary significantly between resistant and susceptible cultivars (Wei et al., 2019).

However, plant genotype is not the major driver of the early establishment of a rhizospheric microbiome. Several studies indicate that soil type rather than cultivar determines the composition of the rhizospheric microbiome (Van Overbeek and Van Elsas, 2008; Xu et al., 2009; Chen et al., 2019). This feature has been specifically evidenced for fungi (Nallanchakravarthula et al., 2014), bacteria (Schlemper et al., 2017), and arbuscular mycorrhizal fungi (Santos-González et al., 2011).

Plant genotype becomes an obvious determinant of root-associated microbiomes as plants mature (Inceoglu et al., 2010; Schlemper et al., 2017). For a particular growth stage, different cultivars can have different dynamics in their exudate release dynamics (Micallef et al., 2009; Mönchgesang et al., 2016; Sasse et al., 2018), thereby affecting rhizosphere microbial communities in a particular way.

The effect of the host genotype on microbial populations is much more important in the endosphere (Urbina et al., 2018). This is not surprising as co-evolution processes have selected populations that are well-adapted to this niche. In the very early stages of a plant's life, i.e., around germination, the microbial community of the spermosphere is composed of microbes originating from inside and outside the seed as well as microbes recruited from the soil during imbibition (Lemanceau et al., 2017). At this point, the main factor affecting the colonizer communities of the spermosphere is the seed genotype (Adam et al., 2018; Sahadevan et al., 2019). Microbial communities associated with germinating seeds can have a direct impact on the promotion of plant growth, nitrogen fixation, and disease control (Walitang et al., 2017; Rahman et al., 2018; Sabu et al., 2019). With the transformation of rootlets in the spermosphere into roots creating the rhizosphere, the plant genotype becomes of minor importance in community shaping compared with soil type.

A recent study on tomato root endospheric fungi evidenced a clear difference in the phytohormone profiles between two cultivars harboring different endophytic communities (Manzotti et al., 2020). More work is needed to determine whether the hormonal profile determines the composition of endophytic communities (as with root exudates) or whether it is a consequence of mycobiont composition. For bacteria, it has been shown that most endophytic bacteria can interfere with plant hormonal systems (Jasim et al., 2015, 2016).

Plant genotype can also play a critical role under mixed cropping conditions. It has been shown that two varieties of pea can influence each other in terms of root-associated bacterial and fungal populations (Horner et al., 2019). In this particular study, the root bacterial community of one cultivar remains stable (similar to single-crop community) in response to mixed cropping, whereas the bacterial community of the second cultivar shifts toward the first. Conversely, the root fungal community of the second cultivar remains stable when mixed-cropped, whereas the fungal community of the first cultivar shifts toward the second.

Polyculture has been identified as a way to enhance rhizospheric fungal diversity (LeBlanc et al., 2015), which can be

modulated by the identity of plant species (LeBlanc et al., 2017) and by environmental parameters that can also have a significant influence (Schlatter et al., 2015).

Differential shifts in bacterial and fungal communities can be attributed to microbial interactions, a change in soil attributes or a change in root exudates resulting from competition between intervarieties, plant communication, or a better mineralization of organic matter enhancing nutrient availability (Hinsinger et al., 2011; Reiss and Drinkwater, 2018).

## BIOSTIMULANTS AND MICROBIOMES

Biostimulants can be defined as substances or microorganisms that stimulate natural processes to enhance tolerance to abiotic stress, crop quality, and nutrient uptake and efficiency (du Jardin, 2015). The effect of biostimulants can be attributable to the direct effects of carbon or nitrogen metabolism (Calvo et al., 2014) but also indirectly through the modulation of plant microbiomes through the enhancement of microbial activity (Colla et al., 2015).

Biostimulants are relatively new products and their effects on microbiomes are not well-known, partly due to the great diversity of biostimulant origins. In this paper, we focus on biostimulants obtained from protein hydrolysates from seaweed and on microbial biostimulants.

### Biostimulants Based on Protein Hydrolysates

Tejada et al. (2011) tested four biostimulants on degraded soils. They identified an alteration in microbial community structure and higher microbial activity, which facilitates better plant development on degraded soils. The biostimulant with the best effect in terms of microbial activity and plant development was the one derived from rice bran extract. The authors hypothesized that the effect of this biostimulant was due to its richness in little peptides (<3 kDa), easily assimilable by microorganisms. Other studies focused on the phyllosphere microbiome. Luziatelli et al. (2016) found that a biostimulant from protein hydrolysates modulated the leaf microbiome on lettuce. Notably, microbes isolated from lettuce leaves treated with biostimulant indicated the presence of bacteria enabling phosphorous solubilization or producing phytohormones (IAA). Moreover, the biostimulant favored the presence of *Bacillus* species exhibiting an inhibitory activity against leaf lettuce pathogens *Erwinia amylovora* and *Fusarium oxysporum*. The biostimulant could thus shape the phyllosphere, promoting plant growth.

Regarding protein hydrolysate (PH) biostimulants, Colla et al. (2017) concluded that this kind of biostimulant can help provide better resilience to biotic and abiotic stresses by modulating the microbiome. Given that PH biostimulants can only select beneficial microorganisms present in the rhizo- or phyllosphere, the authors proposed their use in synergy with beneficial microbes.

### Biostimulants Derived From Seaweed

Most investigations of seaweed-derived biostimulants have been conducted under the scope of the functional diversity of the

microbiome, through enzyme activity research rather than an analysis of the microbial community diversity. Ji et al. (2017) reported that the P solubility was higher after a seaweed biostimulant application but without affecting the microbial communities. The positive action of seaweed biostimulants indicated greater activity of hydrogenase (Onet et al., 2019), invertase, urease, proteinase, and phosphatase (Wang Y. et al., 2016). These enzymes, involved in the carbon, nitrogen, and phosphorus cycles, explain the better nutrition status of the plants.

### Microbial Biostimulants

Despite the fact that microbial biostimulants are relatively common in agriculture, usually through PGPR products or vermicomposts, their effect on microbiomes is poorly documented. Berg S. et al. (2020) studied the effect of microbial biostimulants on soil and root microbial communities. Although no significant differences were found in the diversity of these communities, except for the fungi, the tested biostimulants did not increase the yield.

Mahnert et al. (2018) studied the impact of vermicompost on leaf and environment microbiomes under controlled conditions. It appeared that the biostimulant reshaped the microbiomes of the leaves, with an increase in Bacteroidetes and other phyla such as Verrucomicrobia, Acidobacteria, and Thaumarchaeota. Other groups containing beneficial microorganisms also increased. The authors demonstrated that the effect of the biostimulant on microbiome composition could be predicted with an accuracy of 87%. To the best of our knowledge, no other significant research has been conducted on this theme. The two research papers yield different results, maybe lightening the impact of field conditions on plant biostimulation, and that a stronger impact of plant biostimulant products are observed under controlled conditions or synthetic substrates.

## IMPACT OF IRRIGATION/WATER ON MICROBIOME

Irrigation can have an impact on microbial communities and plant microbiomes through the frequency of irrigation or the quality of irrigation water. Due to climatic changes, the irrigated area is predicted to increase to 62% from 2020 to 2070, with an impact on soil and, therefore, microbial communities (Döll, 2002). Without irrigation, soils will alternate between drying and rewetting periods. In these conditions, more active microbes are known to be affected more by these drying–rewetting stresses (Van Gestel et al., 1993). For an active microbial rhizosphere, drying and rewetting periods could be damaging. Fierer et al. (2003) focused on the impact of this alternation on soil bacterial community structure. They found that microbial communities in annual grasslands were less affected in terms of biodiversity by these events than forest (oak) soils. Nonetheless, Wu and Brookes (2005) reported a 44% decrease in microbial biomass in a single dry–rewet cycle in grassland. It is unclear whether these impacts on microbial structure are direct effects of the dry–rewet cycle or indirect effects through the perturbation of physical or biochemical soil processes, such as the C cycle (Schimel, 2018).

Long-term monoculture irrigation has been relatively poorly studied. Nevertheless, Mavrodi et al. (2018) studied the effect of long-term irrigation on wheat. They reported that beneficial phenazine producing (Phz+) *Pseudomonas* spp. were less abundant or detectable in irrigated fields or in higher rainfall areas. Irrigation should alter rhizodeposition and soil properties, disturbing microbiomes. Mavrodi et al. (2018) found that irrigation had a slight effect on the diversity of the wheat rhizosphere microbiome. However, some taxa displayed strong positive and negative responses to irrigation such as Bacteroidetes and Proteobacteria. Some genera, previously identified as phytopathogen antagonists such as *Chryseobacter* spp., *Pedobacter* spp., or *Brevundimonas* spp., were among the bacteria with the highest relative increase in abundance under irrigation.

The quality of irrigation water also seems to have an important impact on plant microbiomes. Cui et al. (2019), from the perspective of water management, tested different water qualities. They found that reclaimed water and piggery wastewater use increased the abundance of Bacteroidetes while decreasing Acidobacteria abundance. Although PGPR were logically more abundant in the rhizosphere microbiome, their response to the different water qualities (distilled, reclaimed, piggery wastewater) was quite variable. Finally, no increase in (phyto)pathogenic bacteria was evidenced after irrigation with reclaimed water or piggery wastewater.

Gu et al. (2019) also evidenced a modulation of the spinach microbiome according to the quality of irrigation water. Although they did not find any increase in foodborne pathogens, they evidenced an increase in potential opportunistic (phyto)pathogens. These two publications highlight the importance of a quality of irrigation water survey for plant and consumer health.

Some authors have studied the resilience of soil microbial communities after irrigation with water of different quality. It appears that a soil microbiome—and to the same extent plant microbiome—is not resistant to irrigation with treated wastewater. Differences have been observed between irrigation with freshwater and treated wastewater. Nevertheless, during the rainy season, the baseline state of microbiomes is recovered, evidencing the resilience of soil and plant microbiomes in the long term (Frenk et al., 2014). Frenk et al. (2018) showed that under conditions of high mineral and organic carbon activities, bacterial communities can change drastically, exhibiting proteobacterial dominance. These changing communities displayed less resistance to environmental stress such as heat disturbance as they have less diversity than soils with low resource availability. However, the authors evidenced a functional resilience after the end of the stress, probably due to the high growth rates of certain groups such as Bacteroidetes or Proteobacteria.

In conclusion, if irrigation and quality of irrigation have a relative impact on diversity, the impact on biomass of different groups can be important. If populations are resilient in the long term, thanks to microbial seed banks (bacteria in dormancy) (Lennon and Jones, 2011), the impact of irrigation and the quality of irrigation have to be considered in the short term,

during one agricultural season. In this respect, observations have been nuanced. Some studies evidenced the positive role of irrigation on PGPR (Mavrodi et al., 2018), while others obtained variable (Cui et al., 2019) or negative results (Phz+ not present in irrigated soils, Mavrodi et al., 2018). Ultimately, even if wastewater did not seem so harmful when applied in the short term, repeated applications of this kind of wastewater have to be studied for a longer period. According to the observations of Frenk et al. (2018), the use of high availability resource irrigation water in the longer term could probably and durably reshape agricultural soil microbial communities. Conversely, plant microbiome management will probably be a future tool employed to better exploit limited water resources (de Vries et al., 2020).

## CROP PROTECTION

The application of pesticides in fields influences microbial populations inside aerial and belowground plant parts, as well as in the soil. The effects can be due to the applied molecule itself, but also the degradation products of the molecule. Degradation can occur through multiple processes: degradation by microorganisms, hydrolysis, photolysis, sorption and binding to organic and soil components, plant uptake, and volatilization (Srivastava et al., 2020). If microorganisms are able to survive in the environment contaminated by the molecule, they can then metabolize and degrade the pesticides (Wołejko et al., 2020). Therefore, microorganisms can play a significant role in plant tolerance to herbicides (Tétard-Jones and Edwards, 2016).

Depending on the chemical, the active ingredient can be a racemic mixture or enantiomer-enriched solution. Sometimes only one of the two enantiomers has a desired effect, with the other having an indirect effect on non-target organisms (Asad et al., 2017). When a pesticide is applied, it usually leads to the eradication of groups of microorganisms sensitive to the active ingredient. Niches are consequently freed and colonized by microbes previously of minor abundance in the community (Chen et al., 2001) or thriving as a result of the release from competition (Roesti et al., 2005; Nettles et al., 2016). It is also possible that treatment has no significant effect on some parts of the community, such as an effect on the fungal rhizosphere community but not on bacterial communities (Nettles et al., 2016). If a microbial population is well-adapted to the pesticide, the treatment can induce a short-term increase in microbial carbon, indicating increasing biodegradation (Astaykina et al., 2020).

In the presence of pollution, microorganisms can enhance their adaptation to the prevailing conditions by altering their metabolism (Sun et al., 2004; Rangasamy et al., 2018). Therefore, groups of microorganisms can take advantage of an active ingredient in the environment (Webber et al., 2015). For example, Newman et al. (2016) showed a shift in a bacterial community toward a tolerant community after long-term glyphosate adaptation. With the destruction of certain groups of microbes involved in the degradation of another molecule, the stability of this second product can increase (White et al., 2010).



A long-lasting product in the environment can be important in ensuing long-term protection for the crop. This can also increase the likelihood of unintended effects on non-target microbiomes (Nettles et al., 2016). Plants are also capable of exuding pesticides absorbed on their aerial parts with their roots, in addition to endogenous exudates (Dinelli et al., 2007). All these mechanisms can influence the microbiota. Regarding the effects of a pesticide application, as reviewed by Wolejko et al. (2020), the effects of fungicide, insecticide, or herbicide on microbial communities varies greatly according to the molecule used and the microbial group studied. Although most studies agree on the lack of impacts on  $\alpha$ -diversity in the rhizosphere (Lupwayi et al., 2004, 2009; Nettles et al., 2016), the effects on microbiome functionality (Fournier et al., 2020), or structure (Nettles et al., 2016) have been reported with shifts in relative abundance and community composition. In the phyllosphere, microbial diversity can even increase after a foliar treatment (Katsoula et al., 2020). Seed treatments can have a more pronounced and dynamic impact on microbial diversity. As shown by Li et al. (2018), the richness of bacteria and fungi species at the seedling stage decreased with a neonicotinoid seed coating. With a decreasing concentration of neonicotinoids when reviving, the growth of microorganisms was stimulated. Overall, general microbiomes recovered at the end of the cultural season.

## DISCUSSION

From this work, a major trend appears to dictate the process followed when investigating microbial communities from a metagenomic perspective. DNA extractions are almost exclusively performed using a FastDNA Soil SPIN Kit (MP Biomedicals, USA) or PowerSoil DNA Kit (MoBio, Qiagen, USA). Consideration of the extraction procedures implemented remains relevant and may induce bias when comparing one study to another (Kennedy et al., 2014).

When studying prokaryotes, most authors target the 16S RNA gene, focusing on the V4 region or a wider region including V4. Overlapping between V2 and V3 regions is also commonly used. The diversity of eukaryotic communities is often investigated *via* the sequencing of an internal transcriber region (ITS) or 28S ribosomal unit. Ideally, several genetic markers should be considered (Sommermann et al., 2018).

Currently, sequencing usually relies on Illumina technology when 454-pyrosequencing tends to become more anecdotal. When Illumina technology is used, a large majority of researchers make use of the MiSeq platform and, more recently, the HiSeq platform. Third-generation technologies such as PacBio or Ion Torrent continue to be marginal when investigating soil and plant microbiomes but are expected to become a gold standard in metagenomic approaches (Lee et al., 2016; van Dijk et al., 2018).

Most of the studies presented in this paper used barcoded rRNA sequences. Although this approach enables researchers to assess the impact on microbial composition and diversity, it is notable that when shotgun or enzymatic analyses are applied, authors gain better insight into the networks, relationships inside the communities, and the functional aspects of the microbiome.

The interpretation of metadata produced by next-generation sequencing technologies depends mostly on the data management methodologies implemented. Several best practices are required, such as choosing an adapted normalization strategy (Schlatter et al., 2017; Knight et al., 2018). The normalization process should be selected to fit the size and organization of the datasets, as suggested by Weiss et al. (2017). Sufficient technical replicates should be performed in order to quantify sequencing error rates within an assay and between assays (Nguyen et al., 2015; Schloss et al., 2016).

In almost every paper reviewed, the composition and diversity of microbial communities are affected by the agronomic parameters investigated. Networks and functionalities are nearly always impacted, although these attributes have been poorly studied. Of 54 papers, only 14 studies describe networks, 14 consider biological functionalities, and only three address both aspects simultaneously.

A deeper understanding of crop-associated microbiomes and their functionalities requires a more holistic approach that combines data not only from omics technologies. Investigating the fate of microbial communities requires a four-dimension perspective that examines microbiomes in terms of their diversity, structure, composition, and biological functions. Functionalizing microbial communities not only through prediction tools but also through quantification technologies such as qPCR or enzymatic assays will provide relevant insights that illustrate how those microbial communities and the services they provide are affected by farming practices.

Before studying the impacts of any agricultural parameter on microbiota, environmental features should be systematically considered with greater concern when interpreting the results of such studies. Organic carbon content, nitrogen content, pH, soil structure, soil classification, and moisture content are several parameters that vary from field to field and significantly impact microbiomes. Moreover, some authors highlight the indirect activity of certain practices through pH change (e.g., Zhang et al., 2017). For instance, in 2006, Fierer and Jackson found that soil pH is the main parameter influencing microbiome structure (Fierer and Jackson, 2006). This has since been confirmed by numerous studies (Lauber et al., 2009; Rousk et al., 2010; Geyer et al., 2014; Qi et al., 2018; O'Brien et al., 2019; Schlatter et al., 2020; Tan et al., 2020).

Soil pH determines the chemical forms of element in the soil, therefore affecting their bioavailability for plants. This would also be an indirect limiting factor for microbial life, as suggested by Zhálnina et al. (2015). In addition to nutrient availability, pH also exerts effects on catabolic activities, soil structure, and biomass activities (Wakelin et al., 2008). Low pH can have direct toxic effects on microbe cells. Some organisms, better adapted to acidophilic conditions, possess a special membrane structure, proton pumps, or special transporters (Lehtovirta-Morley et al., 2016). The relationship between soil pH and microbial diversity can also be explained by the wide range of optimal pH tolerance for a community in contrast with the rather narrow pH optima for individual species (Fernández-Calviño and Bååth, 2010). Therefore, a shift in pH will affect the survival of some but not all microbials (Santoyo et al., 2017). Numerous



studies also link pH with microbial activities, such as phosphate solubilization or ammonia oxidation (Nautiyal et al., 2000; Hu et al., 2013; Sharma et al., 2013). Indeed, pH is thought to drive the community composition of ammonia-oxidizing organisms by modifying the ammonia to ammonium ratio (Gubry-Rangin et al., 2011; Stempfhuber et al., 2015).

A recent study demonstrated the influence of pH and depth on microbiomes in an agricultural soil configuration (Schlatter et al., 2020). The authors showed that pH decreases from the surface to a 10-cm depth and so do bacterial richness and diversity. Notably, they observed that bacterial richness and diversity did not recover with increasing pH at depths below 10 cm. These results suggest that pH is the main factor affecting diversity at near-surface depths, while other factors (dispersal, nutrient availability) become prevalent at greater soil depths. This lower microbial diversity at around 10 cm deep could reduce the functional redundancy and resilience of the communities in the seed zone (Shade et al., 2012).

Land use history is also an important parameter to consider when investigating soil-associated microbiota. Although the underlying mechanisms are not well-understood, it is known that plants can recruit specific root microbiomes through root exudates, enabling them to select beneficial microbial traits. Time after time, the soil microbiome is enriched in certain specific taxa, as suggested by the concept of a soilborne legacy (Bakker et al., 2018). Recruited microbiomes produce bioactive metabolites or useful resources for plants. Once the crops are harvested, molecular signals and other plant-beneficial compounds might remain in the soil and benefit the next generation. This phenomenon was proposed by Lapsansky et al. (2016) and is called the soil memory effect.

Considering the duration of assays is therefore of tremendous importance as is the implementation of cover crops, intercropping, and crop rotation composition, all of which are among the numerous parameters to examine when studying crop-associated microbiomes. The long-term studies reviewed in this work reported a certain resilience or results different from those in the short term (Mavrodi et al., 2018), probably due to microbial seed banks (Lennon and Jones, 2011).

In this review, we investigated the impacts of farming practices on soil and plant microbiomes. Within the heterogeneity of the reviewed studies, as previously noted, supplementary approaches to omics facilitated a strong comprehension of underlying mechanisms. Levy et al. (2018) reviewed the different advantages and limitations of -omics techniques. They conclude that no -omics approaches provide the necessary causality and argue that, more than amplicon-based studies, a functional metagenomic

approach is needed and can be supplemented by synthetic communities or reverse genomics approaches. Vorholt et al. (2017) also advise using synthetic communities for a better understanding of microbiomes. They argue that the factors shaping microbial communities in soil matrices are not well-understood because of the complexity of environmental samples. For a better understanding of plant microbiome interactions, they recommend the use of multispecies synthetic communities.

If the impact of agricultural practices on microbiomes exists, we wonder whether the microbiome could be farmed as “collaborative crops.” “Seeding” practices through microbial or consortia inoculation, or a selection of varieties promoting positive microbiomes, are likely to be the future of microbiome management (Compant et al., 2019). These inoculations of strains or microbiome engineering in plants can be obtained in different ways. They can occur through host-mediated and multigeneration microbiome selection; inoculation into bulk soil, rhizosphere, seeds, or seedlings; atomization into tissues such as stems, leaves, and flowers; and direct injection into tissues or wounds. Some recent relevant studies involving the aforementioned techniques are reviewed below. Given the lability of existing microbiomes and the fact that soil memory is more active in a low nutrient environment and thus less adapted to conventional agricultural soils (Lapsansky et al., 2016), microbiome engineering consisting of community inoculation and host-mediated “microbiome maintenance” in single (Orozco-Mosqueda et al., 2018) or associated crops (Horner et al., 2019) could be a useful tool for future pest integrated management.

## AUTHOR CONTRIBUTIONS

CB reviewed the paper. All authors contributed to the article and approved the submitted version.

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## SUPPLEMENTARY MATERIAL

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## REFERENCES

- Abdalla, M., Hastings, A., Cheng, K., Yue, Q., Chadwick, D., Espenberg, M., et al. (2019). A critical review of the impacts of cover crops on nitrogen leaching, net greenhouse gas balance and crop productivity. *Glob. Chang. Biol.* 25, 2530–2543. doi: 10.1111/gcb.14644
- Adam, E., Bernhart, M., Müller, H., Winkler, J., and Berg, G. (2018). The *Cucurbita pepo* seed microbiome: genotype-specific composition and implications for breeding. *Plant Soil* 422, 35–49. doi: 10.1007/s11104-016-3113-9
- Agrios, G. (2005). *Plant Pathology*. 5th Edn. San Diego, CA: Academic Press.
- Alahmad, A., Decocq, G., Spicher, F., Kheirbeik, L., Kobaissi, A., Tetu, T., et al. (2019). Cover crops in arable lands increase functional complementarity and redundancy of bacterial communities. *J. Appl. Ecol.* 56, 651–664. doi: 10.1111/1365-2664.13307
- Asad, M. A. U., Lavoie, M., Song, H., Jin, Y., Fu, Z., and Qian, H. (2017). Interaction of chiral herbicides with soil microorganisms, algae and vascular plants. *Sci. Tot. Environ.* 580, 1287–1299. doi: 10.1016/j.scitotenv.2016.12.092

- Astaykina, A., Streletskaia, R., Maslov, M., Belov, A., Gorbatov, V., and Stepanov, A. (2020). The impact of pesticides on the microbial community of agrosoddy-podzolic soil. *Euras. Soil Sci.* 53, 696–706. doi: 10.1134/S1064229320050038
- Babin, D., Deubel, A., Jacquiod, S., Sørensen, S. J., Geistlinger, J., Grosch, R., et al. (2019). Impact of long-term agricultural management practices on soil prokaryotic communities. *Soil Biol. Biochem.* 129, 17–28. doi: 10.1016/j.soilbio.2018.11.002
- Bakker, P. A. H. M., Pieterse, C. M. J., de Jonge, R., and Berendsen, R. L. (2018). The soil-borne legacy. *Cell* 172, 1178–1180. doi: 10.1016/j.cell.2018.02.024
- Banerjee, S., Walder, F., Büchi, L., Meyer, M., Held, A. Y., Gättinger, A., et al. (2019). Agricultural intensification reduces microbial network complexity and the abundance of keystone taxa in roots. *ISME J.* 13, 1722–1736. doi: 10.1038/s41396-019-0383-2
- Berg, G., Rybakova, D., Fischer, D., Cernava, T., Vergès, M.-C. C., Charles, T., et al. (2020). Microbiome definition re-visited: old concepts and new challenges. *Microbiome* 8:103. doi: 10.1186/s40168-020-00905-x
- Berg, G., Rybakova, D., Grube, M., and Köberl, M. (2015). The plant microbiome explored: implications for experimental botany. *J. Exp. Bot.* 67, 995–1002. doi: 10.1093/jxb/erv466
- Berg, G., and Smalla, K. (2009). Plant species and soil type cooperatively shape the structure and function of microbial communities in the rhizosphere. *FEMS Microbiol. Ecol.* 68, 1–13. doi: 10.1111/j.1574-6941.2009.00654.x
- Berg, M., and Koskella, B. (2018). Nutrient- and dose-dependent microbiome-mediated protection against a plant pathogen. *Curr. Biol.* 28, 2487–2492. doi: 10.1016/j.cub.2018.05.085
- Berg, S., Dennis, P. G., Paungfoo-Lonhienne, C., Anderson, J., Robinson, N., Brackin, R., et al. (2020). Effects of commercial microbial biostimulants on soil and root microbial communities and sugarcane yield. *Biol. Fertil. Soils* 56, 565–580. doi: 10.1007/s00374-019-01412-4
- Bonanomi, G., Antignani, V., Capodilupo, M., and Scala, F. (2010). Identifying the characteristics of organic soil amendments that suppress soilborne plant diseases. *Soil Biol. Biochem.* 42, 136–144. doi: 10.1016/j.soilbio.2009.10.012
- Bonanomi, G., De Filippis, F., Cesarano, G., La Stora, A., Ercolini, D., and Scala, F. (2016). Organic farming induces changes in soil microbiota that affect agro-ecosystem functions. *Soil Biol. Biochem.* 103, 327–336. doi: 10.1016/j.soilbio.2016.09.005
- Bonanomi, G., Lorito, M., Vinale, F., and Woo, S. L. (2018). Organic amendments, beneficial microbes, and soil microbiota: toward a unified framework for disease suppression. *Annu. Rev. Phytopathol.* 56, 1–20. doi: 10.1146/annurev-phyto-080615-100046
- Calvo, P., Nelson, L., and Kloepper, J. W. (2014). Agricultural uses of plant biostimulants. *Plant Soil* 383, 3–41. doi: 10.1007/s11104-014-2131-8
- Cania, B., Vestergaard, G., Suhadolc, M., Mihelič, R., Krauss, M., Fliessbach, A., et al. (2020). Site-specific conditions change the response of bacterial producers of soil structure-stabilizing agents such as exopolysaccharides and lipopolysaccharides to tillage intensity. *Front. Microbiol.* 11:568. doi: 10.3389/fmicb.2020.00568
- Cesarano, G., De Filippis, F., La Stora, A., Scala, F., and Bonanomi, G. (2017). Organic amendment type and application frequency affect crop yields, soil fertility and microbiome composition. *Appl. Soil Ecol.* 120, 254–264. doi: 10.1016/j.apsoil.2017.08.017
- Chen, L., Xin, X., Zhang, J., Redmile-Gordon, M., Nie, G., and Wang, Q. (2019). Soil characteristics overwhelm cultivar effects on the structure and assembly of root-associated microbiomes of modern maize. *Pedosphere* 29, 360–373. doi: 10.1016/S1002-0160(17)60370-9
- Chen, Q., Xin, Y., and Liu, Z. (2020). Long-term fertilization with potassium modifies soil biological quality in K-rich soils. *Agronomy* 10:771. doi: 10.3390/agronomy10060771
- Chen, S.-K., Edwards, C. A., and Subler, S. (2001). Effects of the fungicides benomyl, captan and chlorothalonil on soil microbial activity and nitrogen dynamics in laboratory incubations. *Soil Biol. Biochem.* 33, 1971–1980. doi: 10.1016/S0038-0717(01)00131-6
- Cloutier, M. L., Murrell, E., Barbercheck, M., Kaye, J., Finney, D., García-González, I., et al. (2020). Fungal community shifts in soils with varied cover crop treatments and edaphic properties. *Sci. Rep.* 10:6198. doi: 10.1038/s41598-020-63173-7
- Colla, G., Hoagland, L., Ruzzi, M., Cardarelli, M., Bonini, P., Canaguier, R., et al. (2017). Biostimulant action of protein hydrolysates: unraveling their effects on plant physiology and microbiome. *Front. Plant Sci.* 8:2202. doi: 10.3389/fpls.2017.02202
- Colla, G., Nardi, S., Cardarelli, M., Ertani, A., Lucini, L., Canaguier, R., et al. (2015). Protein hydrolysates as biostimulants in horticulture. *Sci. Hortic.* 196, 28–38. doi: 10.1016/j.scienta.2015.08.037
- Compant, S., Samad, A., Faist, H., and Sessitsch, A. (2019). A review on the plant microbiome: ecology, functions, and emerging trends in microbial application. *J. Adv. Res.* 19, 29–37. doi: 10.1016/j.jare.2019.03.004
- Cui, E., Fan, X., Li, Z., Liu, Y., Neal, A. L., Hu, C., et al. (2019). Variations in soil and plant-microbiome composition with different quality irrigation waters and biochar supplementation. *Appl. Soil Ecol.* 142, 99–109. doi: 10.1016/j.apsoil.2019.04.026
- Dai, Z., Liu, G., Chen, H., Chen, C., Wang, J., Ai, S., et al. (2020). Long-term nutrient inputs shift soil microbial functional profiles of phosphorus cycling in diverse agroecosystems. *ISME J.* 14, 757–770. doi: 10.1038/s41396-019-0567-9
- Degrune, F., Boeraeve, F., Dufrière, M., Cornélis, J.-T., Frey, B., and Hartmann, M. (2019). The pedological context modulates the response of soil microbial communities to agroecological management. *Front. Ecol. Evol.* 7:261. doi: 10.3389/fevo.2019.00261
- Degrune, F., Theodorakopoulos, N., Colinet, G., Hiel, M.-P., Bodson, B., Taminiau, B., et al. (2017). Temporal dynamics of soil microbial communities below the seedbed under two contrasting tillage regimes. *Front. Microbiol.* 8:1127. doi: 10.3389/fmicb.2017.01127
- Degrune, F., Theodorakopoulos, N., Dufrière, M., Colinet, G., Bodson, B., Hiel, M.-P., et al. (2016). No favorable effect of reduced tillage on microbial community diversity in a silty loam soil (Belgium). *Agric. Ecosyst. Environ.* 224, 12–21. doi: 10.1016/j.agee.2016.03.017
- Detheridge, A. P., Brand, G., Fychan, R., Crotty, F. V., Sanderson, R., Griffith, G. W., et al. (2016). The legacy effect of cover crops on soil fungal populations in a cereal rotation. *Agric. Ecosyst. Environ.* 228, 49–61. doi: 10.1016/j.agee.2016.04.022
- Dinelli, G., Bonetti, A., Marotti, I., Minelli, M., Busi, S., and Catizone, P. (2007). Root exudation of diclofop-methyl and triasulfuron from foliar-treated durum wheat and ryegrass. *Weed Res.* 47, 25–33. doi: 10.1111/j.1365-3180.2007.00549.x
- Döll, P. (2002). Impact of climate change and variability on irrigation requirements: a global perspective. *Clim. Change* 54, 269–293. doi: 10.1023/A:1016124032231
- du Jardin, P. (2015). Plant biostimulants: definition, concept, main categories and regulation. *Sci. Hortic.* 196, 3–14. doi: 10.1016/j.scienta.2015.09.021
- Fernandez, A. L., Sheaffer, C. C., Wyse, D. L., Staley, C., Gould, T. J., and Sadowsky, M. J. (2016). Structure of bacterial communities in soil following cover crop and organic fertilizer incorporation. *Appl. Microbiol. Biotechnol.* 100, 9331–9341. doi: 10.1007/s00253-016-7736-9
- Fernández-Calviño, D., and Bååth, E. (2010). Growth response of the bacterial community to pH in soils differing in pH. *FEMS Microbiol. Ecol.* 73, 149–156. doi: 10.1111/j.1574-6941.2010.00873.x
- Fierer, N., Lauber, C. L., Ramirez, K. S., Zaneveld, J., Bradford, M. A., and Knight, R. (2012). Comparative metagenomic, phylogenetic and physiological analyses of soil microbial communities across nitrogen gradients. *ISME J.* 6, 1007–1017. doi: 10.1038/ismej.2011.159
- Fierer, N., Schimel, J. P., and Holden, P. A. (2003). Influence of drying–rewetting frequency on soil bacterial community structure. *Microb. Ecol.* 45, 63–71. doi: 10.1007/s00248-002-1007-2
- Finney, D. M., Buyer, J. S., and Kaye, J. P. (2017). Living cover crops have immediate impacts on soil microbial community structure and function. *J. Soil Water Conserv.* 72, 361–373. doi: 10.2489/jswc.72.4.361
- Fournier, B., Pereira Dos Santos, S., Gustavsen, J. A., Imfeld, G., Lamy, F., Mitchell, E. A. D., et al. (2020). Impact of a synthetic fungicide (fosetyl-Al and propamocarb-hydrochloride) and a biopesticide (*Clonostachys rosea*) on soil bacterial, fungal, and protist communities. *Sci. Tot. Environ.* 738:139635. doi: 10.1016/j.scitotenv.2020.139635
- Frenk, S., Hadar, Y., and Minz, D. (2014). Resilience of soil bacterial community to irrigation with water of different qualities under Mediterranean climate. *Environ. Microbiol.* 16, 559–569. doi: 10.1111/1462-2920.12183
- Frenk, S., Hadar, Y., and Minz, D. (2018). Quality of irrigation water affects soil functionality and bacterial community stability in response to heat disturbance. *Appl. Environ. Microbiol.* 84, e02087-17. doi: 10.1128/AEM.02087-17

- Garland, G., Edlinger, A., Banerjee, S., Degrune, F., García-Palacios, P., Pescador, D. S., et al. (2021). Crop cover is more important than rotational diversity for soil multifunctionality and cereal yields in European cropping systems. *Nature Food* 2, 28–37. doi: 10.1038/s43016-020-00210-8
- Gubry-Rangin, C., Hai, B., Quince, C., Engel, M., Thomson, B. C., James, P., et al. (2011). Niche specialization of terrestrial archaeal ammonia oxidizers. *Proc. Natl. Acad. Sci. U. S. A.* 108, 21206–21211. doi: 10.1073/pnas.1109000108
- Hardoim, P. R., Hardoim, C. P., van Overbeek, L. S., and van Elsas, J. D. (2012). Dynamics of seed-borne rice endophytes on early plant growth stages. *PLoS ONE* 7:e30438. doi: 10.1371/journal.pone.0030438
- Hardoim, P. R., van Overbeek, L. S., Berg, G., Pirttilä, A. M., Compant, S., Campisano, A., et al. (2015). The hidden world within plants: ecological and evolutionary considerations for defining functioning of microbial endophytes. *Microbiol. Mol. Biol. Rev.* 79:293. doi: 10.1128/MMBR.00050-14
- Hartman, K., van der Heijden, M. G. A., Wittwer, R. A., Banerjee, S., Walser, J.-C., and Schlaeppi, K. (2018). Cropping practices manipulate abundance patterns of root and soil microbiome members paving the way to smart farming. *Microbiome* 6:14. doi: 10.1186/s40168-017-0389-9
- Hartmann, A., Rothballer, M., and Schmid, M. (2008). Lorenz Hiltner, a pioneer in rhizosphere microbial ecology and soil bacteriology research. *Plant Soil* 312, 7–14. doi: 10.1007/s11104-007-9514-z
- Hartmann, M., Frey, B., Mayer, J., Mäder, P., and Widmer, F. (2015). Distinct soil microbial diversity under long-term organic and conventional farming. *ISME J.* 9, 1177–1194. doi: 10.1038/ismej.2014.210
- He, M., Tian, G., Semenov, A. M., and van Bruggen, A. H. C. (2012). Short-term fluctuations of sugar beet damping-off by *Pythium ultimum* in relation to changes in bacterial communities after organic amendments to two soils. *Phytopathology* 102, 413–420. doi: 10.1094/PHYTO-07-11-0189
- Hinsinger, P., Betencourt, E., Bernard, L., Brauman, A., Plassard, C., Shen, J., et al. (2011). P for two, sharing a scarce resource: soil phosphorus acquisition in the rhizosphere of intercropped species. *Plant Physiol.* 156, 1078–1086. doi: 10.1104/pp.111.175331
- Hobbs, P. R., Sayre, K., and Gupta, R. (2008). The role of conservation agriculture in sustainable agriculture. *Philos. Trans. R. Soc. B Biol. Sci.* 363, 543–555. doi: 10.1098/rstb.2007.2169
- Horner, A., Browett, S. S., and Antwis, R. E. (2019). Mixed-cropping between field pea varieties alters root bacterial and fungal communities. *Sci. Rep.* 9:16953. doi: 10.1038/s41598-019-53342-8
- Hu, H.-W., Zhang, L.-M., Dai, Y., Di, H.-J., and He, J.-Z. (2013). pH-dependent distribution of soil ammonia oxidizers across a large geographical scale as revealed by high-throughput pyrosequencing. *J. Soils Sediments* 13, 1439–1449. doi: 10.1007/s11368-013-0726-y
- Inceoglu, Ö., Salles, J. F., van Overbeek, L., and van Elsas, J. D. (2010). Effects of plant genotype and growth stage on the betaproteobacterial communities associated with different potato cultivars in two fields. *Appl. Environ. Microbiol.* 76, 3675–3684. doi: 10.1128/AEM.00040-10
- Inderbitzin, P., Ward, J., Barbella, A., Solares, N., Izyumin, D., Burman, P., et al. (2018). Soil microbiomes associated with *Verticillium* wilt-suppressive broccoli and chitin amendments are enriched with potential biocontrol agents. *Phytopathology* 108, 31–43. doi: 10.1094/PHYTO-07-17-0242-R
- Jacoby, R., Peukert, M., Succurro, A., Koprivova, A., and Kopriva, S. (2017). The role of soil microorganisms in plant mineral nutrition—current knowledge and future directions. *Front. Plant Sci.* 8:1617. doi: 10.3389/fpls.2017.01617
- Jasim, B., Anish, M. C., Shimil, V., Jyothis, M., and Radhakrishnan, E. K. (2015). Studies on plant growth promoting properties of fruit-associated bacteria from *Elettaria cardamomum* and molecular analysis of ACC deaminase gene. *Appl. Biochem. Biotechnol.* 177, 175–189. doi: 10.1007/s12010-015-1736-6
- Jasim, B., Mathew, J., and Radhakrishnan, E. K. (2016). Identification of a novel endophytic *Bacillus* sp. from *Capsicum annuum* with highly efficient and broad spectrum plant probiotic effect. *J. Appl. Microbiol.* 121, 1079–1094. doi: 10.1111/jam.13214
- Ji, R., Dong, G., Shi, W., and Min, J. (2017). Effects of liquid organic fertilizers on plant growth and rhizosphere soil characteristics of chrysanthemum. *Sustainability* 9:841. doi: 10.3390/su9050841
- Karlen, D. L., Wollenhaupt, N. C., Erbach, D. C., Berry, E. C., Swan, J. B., Eash, N. S., et al. (1994). Crop residue effects on soil quality following 10-years of no-till corn. *Soil Till. Res.* 31, 149–167. doi: 10.1016/0167-1987(94)90077-9
- Katsoula, A., Vasileiadis, S., Sapountzi, M., and Karpouzias, D. G. (2020). The response of soil and phyllosphere microbial communities to repeated application of the fungicide iprodione: accelerated biodegradation or toxicity? *FEMS Microbiol. Ecol.* 96:faa056. doi: 10.1093/femsec/faa056
- Keesing, F., Belden, L. K., Daszak, P., Dobson, A., Harvell, C. D., Holt, R. D., et al. (2010). Impacts of biodiversity on the emergence and transmission of infectious diseases. *Nature* 468, 647–652. doi: 10.1038/nature09575
- Kennedy, N. A., Walker, A. W., Berry, S. H., Duncan, S. H., Farquarson, F. M., Louis, P., et al. (2014). The impact of different DNA extraction kits and laboratories upon the assessment of human gut microbiota composition by 16S rRNA gene sequencing. *PLoS ONE* 9:e88982. doi: 10.1371/journal.pone.0088982
- Kim, N., Zabaloy, M. C., Guan, K., and Villamil, M. B. (2020). Do cover crops benefit soil microbiome? A meta-analysis of current research. *Soil Biol. Biochem.* 142:107701. doi: 10.1016/j.soilbio.2019.107701
- Kloepper, J. W., Leong, J., Teintze, M., and Schroth, M. N. (1980). Enhanced plant growth by siderophores produced by plant growth-promoting rhizobacteria. *Nature* 286, 885–886. doi: 10.1038/286885a0
- Knight, R., Vrbanac, A., Taylor, B. C., Aksenov, A., Callewaert, C., Debelius, J., et al. (2018). Best practices for analysing microbiomes. *Nat. Rev. Microbiol.* 16, 410–422. doi: 10.1038/s41579-018-0029-9
- Kopecky, J., Samkova, Z., Sarikhani, E., Kyselková, M., Omelka, M., Kristufek, V., et al. (2019). Bacterial, archaeal and micro-eukaryotic communities characterize a disease-suppressive or conducive soil and a cultivar resistant or susceptible to common scab. *Sci. Rep.* 9:14883. doi: 10.1038/s41598-019-51570-6
- Kwak, M.-J., Kong, H. G., Choi, K., Kwon, S.-K., Song, J. Y., Lee, J., et al. (2018). Rhizosphere microbiome structure alters to enable wilt resistance in tomato. *Nat. Biotechnol.* 36, 1100–1109. doi: 10.1038/nbt.4232
- Lapsansky, E. R., Milroy, A. M., Andales, M. J., and Vivanco, J. M. (2016). Soil memory as a potential mechanism for encouraging sustainable plant health and productivity. *Curr. Opin. Biotechnol.* 38, 137–142. doi: 10.1016/j.copbio.2016.01.014
- Larkin, R. P., and Griffin, T. S. (2007). Control of soilborne potato diseases using Brassica green manures. *Crop Prot.* 26, 1067–1077. doi: 10.1016/j.cropro.2006.10.004
- Latha, P., Anand, T., Prakasam, V., Jonathan, E. I., Paramathma, M., and Samiyappan, R. (2011). Combining *Pseudomonas*, *Bacillus* and *Trichoderma* strains with organic amendments and micronutrient to enhance suppression of collar and root rot disease in physic nut. *Appl. Soil Ecol.* 49, 215–223. doi: 10.1016/j.apsoil.2011.05.003
- Latz, E., Eisenhauer, N., Rall, B. C., Allan, E., Roscher, C., Scheu, S., et al. (2012). Plant diversity improves protection against soil-borne pathogens by fostering antagonistic bacterial communities. *J. Ecol.* 100, 597–604. doi: 10.1111/j.1365-2745.2011.01940.x
- LeBlanc, N., Kinkel, L., and Kistler, H. C. (2017). Plant diversity and plant identity influence Fusarium communities in soil. *Mycologia* 109, 128–139. doi: 10.1080/00275514.2017.1281697
- LeBlanc, N., Kinkel, L. L., and Kistler, H. C. (2015). Soil fungal communities respond to grassland plant community richness and soil edaphics. *Microb. Ecol.* 70, 188–195. doi: 10.1007/s00248-014-0531-1
- Lee, H., Gurtowski, J., Yoo, S., Nattestad, M., Marcus, S., Goodwin, S., et al. (2016). Third-generation sequencing and the future of genomics. *bioRxiv*. p.048603. doi: 10.1101/048603
- Lehtovirta-Morley, L. E., Sayavedra-Soto, L. A., Gallois, N., Schouten, S., Stein, L. Y., Prosser, J. I., et al. (2016). Identifying potential mechanisms enabling acidophily in the ammonia-oxidizing archaeon “*Candidatus Nitrosotalea devanattera*”. *Appl. Environ. Microbiol.* 82, 2608–2619. doi: 10.1128/AEM.04031-15
- Lemanceau, P., Barret, M., Mazurier, S., Mondy, S., Pivato, B., Fort, T., et al. (2017). “Chapter five - plant communication with associated microbiota in the spermosphere, rhizosphere and phyllosphere,” in *Advances in Botanical Research*, ed G. Becard (San Diego, CA: Academic Press), 101–133. doi: 10.1016/bs.abr.2016.10.007
- Lennon, J. T., and Jones, S. E. (2011). Microbial seed banks: the ecological and evolutionary implications of dormancy. *Nat. Rev. Microbiol.* 9, 119–130. doi: 10.1038/nrmicro2504



- Levy, A., Conway, J. M., Dangl, J. L., and Woyke, T. (2018). Elucidating bacterial gene functions in the plant microbiome. *Cell Host Microbe* 24, 475–485. doi: 10.1016/j.chom.2018.09.005
- Li, Y., An, J., Dang, Z., Lv, H., Pan, W., and Gao, Z. (2018). Treating wheat seeds with neonicotinoid insecticides does not harm the rhizosphere microbial community. *PLoS ONE* 13:e0205200. doi: 10.1371/journal.pone.0205200
- Lienhard, P., Terrat, S., Prévost-Bouré, N. C., Nowak, V., Régner, T., Sayphoummie, S., et al. (2014). Pyrosequencing evidences the impact of cropping on soil bacterial and fungal diversity in Laos tropical grassland. *Agron. Sustain. Dev.* 34, 525–533. doi: 10.1007/s13593-013-0162-9
- Ling, N., Zhu, C., Xue, C., Chen, H., Duan, Y., Peng, C., et al. (2016). Insight into how organic amendments can shape the soil microbiome in long-term field experiments as revealed by network analysis. *Soil Biol. Biochem.* 99, 137–149. doi: 10.1016/j.soilbio.2016.05.005
- Liu, Y., Zuo, S., Xu, L., Zou, Y., and Song, W. (2012). Study on diversity of endophytic bacterial communities in seeds of hybrid maize and their parental lines. *Arch. Microbiol.* 194, 1001–1012. doi: 10.1007/s00203-012-0836-8
- Lupwayi, N. Z., Harker, K. N., Clayton, G. W., O'Donovan, J. T., and Blackshaw, R. E. (2009). Soil microbial response to herbicides applied to glyphosate-resistant canola. *Agric. Ecosyst. Environ.* 129, 171–176. doi: 10.1016/j.agee.2008.08.007
- Lupwayi, N. Z., Harker, K. N., Clayton, G. W., Turkington, T. K., Rice, W. A., and O'Donovan, J. T. (2004). Soil microbial biomass and diversity after herbicide application. *Can. J. Plant Sci.* 84, 677–685. doi: 10.4141/P03-121
- Luziatelli, F., Ficca, A. G., Colla, G., Svecova, E., and Ruzzi, M. (2016). Effects of a protein hydrolysate-based biostimulant and two micronutrient based fertilizers on plant growth and epiphytic bacterial population of lettuce. *Int. Soc. Horticult. Sci.* 1148, 43–48. doi: 10.17660/ActaHortic.2016.1148.5
- Mahnert, A., Haratani, M., Schmuck, M., and Berg, G. (2018). Enriching beneficial microbial diversity of indoor plants and their surrounding built environment with biostimulants. *Front. Microbiol.* 9:2985. doi: 10.3389/fmicb.2018.02985
- Manzotti, A., Bergna, A., Burow, M., Jørgensen, H. J. L., Cernava, T., Berg, G., et al. (2020). Insights into the community structure and lifestyle of the fungal root endophytes of tomato by combining amplicon sequencing and isolation approaches with phytohormone profiling. *FEMS Microbiol. Ecol.* 96:fiia052. doi: 10.1093/femsec/fiia052
- Mavrodi, D. V., Mavrodi, O. V., Elbourne, L. D. H., Tetu, S., Bonsall, R. F., Parejko, J., et al. (2018). Long-term irrigation affects the dynamics and activity of the wheat rhizosphere microbiome. *Front. Plant Sci.* 9:345. doi: 10.3389/fpls.2018.00345
- Mendes, L. W., Mendes, R., Raaijmakers, J. M., and Tsai, S. M. (2018). Breeding for soil-borne pathogen resistance impacts active rhizosphere microbiome of common bean. *ISME J.* 12, 3038–3042. doi: 10.1038/s41396-018-0234-6
- Mendes, R., Garbeva, P., and Raaijmakers, J. M. (2013). The rhizosphere microbiome: significance of plant beneficial, plant pathogenic, and human pathogenic microorganisms. *FEMS Microbiol. Rev.* 37, 634–663. doi: 10.1111/1574-6976.12028
- Micallef, S. A., Channer, S., Shiaris, M. P., and Colón-Carmona, A. (2009). Plant age and genotype impact the progression of bacterial community succession in the *Arabidopsis* rhizosphere. *Plant Signal. Behav.* 4, 777–780. doi: 10.4161/psb.4.8.9229
- Mönchgesang, S., Strehmel, N., Schmidt, S., Westphal, L., Taruttis, F., Müller, E., et al. (2016). Natural variation of root exudates in *Arabidopsis thaliana*-linking metabolomic and genomic data. *Sci. Rep.* 6:29033. doi: 10.1038/srep29033
- Nallanchakravarthula, S., Mahmood, S., Alström, S., and Finlay, R. D. (2014). Influence of soil type, cultivar and *Verticillium dahliae* on the structure of the root and rhizosphere soil fungal microbiome of strawberry. *PLoS ONE* 9:e111455. doi: 10.1371/journal.pone.0111455
- Nautiyal, C. S., Bhaduria, S., Kumar, P., Lal, H., Mondal, R., and Verma, D. (2000). Stress induced phosphate solubilization in bacteria isolated from alkaline soils. *FEMS Microbiol. Lett.* 182, 291–296. doi: 10.1111/j.1574-6968.2000.tb08910.x
- Nelkner, J., Henke, C., Lin, T. W., Pätzold, W., Hassa, J., Jaenicke, S., et al. (2019). Effect of long-term farming practices on agricultural soil microbiome members represented by metagenomically assembled genomes (MAGs) and their predicted plant-beneficial genes. *Genes* 10:424. doi: 10.3390/genes10060424
- Nettles, R., Watkins, J., Ricks, K., Boyer, M., Licht, M., Atwood, L. W., et al. (2016). Influence of pesticide seed treatments on rhizosphere fungal and bacterial communities and leaf fungal endophyte communities in maize and soybean. *Appl. Soil Ecol.* 102, 61–69. doi: 10.1016/j.apsoil.2016.02.008
- Newman, M. E. J. (2006). Modularity and community structure in networks. *Proc. Natl. Acad. Sci. U. S. A.* 103, 8577–8582. doi: 10.1073/pnas.0601602103
- Newman, M. M., Lorenz, N., Hoilett, N., Lee, N. R., Dick, R. P., Liles, M. R., et al. (2016). Changes in rhizosphere bacterial gene expression following glyphosate treatment. *Sci. Tot. Environ.* 553, 32–41. doi: 10.1016/j.scitotenv.2016.02.078
- Nguyen, N. H., Smith, D., Peay, K., and Kennedy, P. (2015). Parsing ecological signal from noise in next generation amplicon sequencing. *New Phytol.* 205, 1389–1393. doi: 10.1111/nph.12923
- Nivellet, E., Verzeaux, J., Habbib, H., Kuzyakov, Y., Decocq, G., Roger, D., et al. (2016). Functional response of soil microbial communities to tillage, cover crops and nitrogen fertilization. *Appl. Soil Ecol.* 108, 147–155. doi: 10.1016/j.apsoil.2016.08.004
- Onet, A., Dincă, L. C., Grenni, P., Laslo, V., Teusdea, A. C., Vasile, D. L., et al. (2019). Biological indicators for evaluating soil quality improvement in a soil degraded by erosion processes. *J. Soils Sediments* 19, 2393–2404. doi: 10.1007/s11368-018-02236-9
- Orozco-Mosqueda, M. d. C., Rocha-Granados, M. d. C., Glick, B. R., and Santoyo, G. (2018). Microbiome engineering to improve biocontrol and plant growth-promoting mechanisms. *Microbiol. Res.* 208, 25–31. doi: 10.1016/j.micres.2018.01.005
- Pan, Y., Cassman, N., de Hollander, M., Mendes, L. W., Korevaar, H., Geerts, R. H. E. M., et al. (2014). Impact of long-term N, P, K, and NPK fertilization on the composition and potential functions of the bacterial community in grassland soil. *FEMS Microbiol. Ecol.* 90, 195–205. doi: 10.1111/1574-6941.12384
- Pantigoso, H. A., Manter, D. K., and Vivanco, J. M. (2018). Phosphorus addition shifts the microbial community in the rhizosphere of blueberry (*Vaccinium corymbosum* L.). *Rhizosphere* 7, 1–7. doi: 10.1016/j.rhisph.2018.06.008
- Pascual, N., Ranjard, L., Kaisermann, A., Bachar, D., Christen, R., Terrat, S., et al. (2013). Stimulation of different functional groups of bacteria by various plant residues as a driver of soil priming effect. *Ecosystems* 16, 810–822. doi: 10.1007/s10021-013-9650-7
- Piazza, G., Ercoli, L., Nuti, M., and Pellegrino, E. (2019). Interaction between conservation tillage and nitrogen fertilization shapes prokaryotic and fungal diversity at different soil depths: evidence from a 23-year field experiment in the mediterranean area. *Front. Microbiol.* 10:2047. doi: 10.3389/fmicb.2019.02047
- Rahman, M. D. M., Flory, E., Koyro, H.-W., Abideen, Z., Schikora, A., Suarez, C., et al. (2018). Consistent associations with beneficial bacteria in the seed endosphere of barley (*Hordeum vulgare* L.). *Syst. Appl. Microbiol.* 41, 386–398. doi: 10.1016/j.syapm.2018.02.003
- Ramirez, K. S., Craine, J. M., and Fierer, N. (2012). Consistent effects of nitrogen amendments on soil microbial communities and processes across biomes. *Glob. Chang. Biol.* 18, 1918–1927. doi: 10.1111/j.1365-2486.2012.02639.x
- Rangasamy, K., Athiappan, M., Devarajan, N., Samykanu, G., Parray, J. A., Aruljothi, K. N., et al. (2018). Pesticide degrading natural multidrug resistance bacterial flora. *Microb. Pathog.* 114, 304–310. doi: 10.1016/j.micpath.2017.12.013
- Reiss, E. R., and Drinkwater, L. E. (2018). Cultivar mixtures: a meta-analysis of the effect of intraspecific diversity on crop yield. *Ecol. App.* 28, 62–77. doi: 10.1002/eap.1629
- Roesti, D., Ineichen, K., Braissant, O., Redecker, D., Wiemken, A., and Aragno, M. (2005). Bacteria associated with spores of the arbuscular mycorrhizal fungi *Glomus geosporum* and *Glomus constrictum*. *Appl. Environ. Microbiol.* 71, 6673–6679. doi: 10.1128/AEM.71.11.6673-6679.2005
- Romdhane, S., Spor, A., Busset, H., Falchetto, L., Martin, J., Bizouard, F., et al. (2019). Cover crop management practices rather than composition of cover crop mixtures affect bacterial communities in no-till agroecosystems. *Front. Microbiol.* 10:1618. doi: 10.3389/fmicb.2019.01618
- Sabu, R., Aswani, R., Jishma, P., Jasim, B., Mathew, J., and Radhakrishnan, E. K. (2019). Plant growth promoting endophytic *Serratia* sp. ZoB14 protecting ginger from fungal pathogens. *Proc. Natl. Acad. Sci. B Biol. Sci.* 89, 213–220. doi: 10.1007/s40011-017-0936-y
- Sahadevan, N., Radhakrishnan, E. K., and Mathew, J. (2019). “Mechanism of interaction of endophytic microbes with plants,” in *Seed Endophytes: Biology and Biotechnology*, eds S. K. Verma and J. J. F. White (Cham: Springer International Publishing), 237–257. doi: 10.1007/978-3-030-10504-4\_12
- Santos-González, J. C., Nallanchakravarthula, S., Alström, S., and Finlay, R. D. (2011). Soil, but not cultivar, shapes the structure of arbuscular mycorrhizal



- fungal assemblages associated with strawberry. *Microb. Ecol.* 62, 25–35. doi: 10.1007/s00248-011-9834-7
- Santoyo, G., Hernández-Pacheco, C., Hernández-Salmerón, J., and Hernández-León, R. (2017). The role of abiotic factors modulating the plant-microbe-soil interactions: toward sustainable agriculture. A review. *Spanish J. Agric. Res.* 15:e03R01. doi: 10.5424/sjar/2017151-9990
- Sasse, J., Martinoia, E., and Northen, T. (2018). Feed Your friends: do plant exudates shape the root microbiome? *Trends Plant Sci.* 23, 25–41. doi: 10.1016/j.tplants.2017.09.003
- Schimel, J. P. (2018). Life in dry soils: effects of drought on soil microbial communities and processes. *Annu. Rev. Ecol. Evol. Syst.* 49, 409–432. doi: 10.1146/annurev-ecolsys-110617-062614
- Schimel, J. P., and Bennett, J. (2004). Nitrogen mineralization: challenges of a changing paradigm. *Ecology* 85, 591–602. doi: 10.1890/03-8002
- Schlatter, D., Kinkel, L., Thomashow, L., Weller, D., and Paulitz, T. (2017). Disease suppressive soils: new insights from the soil microbiome. *Phytopathology* 107, 1284–1297. doi: 10.1094/PHYTO-03-17-0111-RVW
- Schlatter, D. C., Bakker, M. G., Bradeen, J. M., and Kinkel, L. L. (2015). Plant community richness and microbial interactions structure bacterial communities in soil. *Ecology* 96, 134–142. doi: 10.1890/13-1648.1
- Schlatter, D. C., Kahl, K., Carlson, B., Huggins, D. R., and Paulitz, T. (2020). Soil acidification modifies soil depth-microbiome relationships in a no-till wheat cropping system. *Soil Biol. Biochem.* 149:107939. doi: 10.1016/j.soilbio.2020.107939
- Schlemper, T. R., Leite, M. F. A., Lucheta, A. R., Shimels, M., Bouwmeester, H. J., van Veen, J. A., et al. (2017). Rhizobacterial community structure differences among sorghum cultivars in different growth stages and soils. *FEMS Microbiol. Ecol.* 93:fix096. doi: 10.1093/femsec/fix096
- Schloss, P. D., Jenior, M. L., Koumpouras, C. C., Westcott, S. L., and Highlander, S. K. (2016). Sequencing 16S rRNA gene fragments using the PacBio SMRT DNA sequencing system. *PeerJ.* 4:e1869. doi: 10.7717/peerj.1869
- Schmidt, J. E., Kent, A. D., Brisson, V. L., and Gaudin, A. C. M. (2019). Agricultural management and plant selection interactively affect rhizosphere microbial community structure and nitrogen cycling. *Microbiome* 7:146. doi: 10.1186/s40168-019-0756-9
- Schmidt, R., Gravuer, K., Bossange, A. V., Mitchell, J., and Scow, K. (2018). Long-term use of cover crops and no-till shift soil microbial community life strategies in agricultural soil. *PLoS ONE* 13:e0192953. doi: 10.1371/journal.pone.0192953
- Shade, A., Peter, H., Allison, S., Baho, D., Berga, M., Buergermann, H., et al. (2012). Fundamentals of microbial community resistance and resilience. *Front. Microbiol.* 3:417. doi: 10.3389/fmicb.2012.00417
- Sharma, S. B., Sayyed, R. Z., Trivedi, M. H., and Gobi, T. A. (2013). Phosphate solubilizing microbes: sustainable approach for managing phosphorus deficiency in agricultural soils. *Springerplus* 2:587. doi: 10.1186/2193-1801-2-587
- Shen, Z., Wang, B., Lv, N., Sun, Y., Jiang, X., Li, R., et al. (2015). Effect of the combination of bio-organic fertiliser with *Bacillus amyloliquefaciens* NJN-6 on the control of banana Fusarium wilt disease, crop production and banana rhizosphere culturable microflora. *Biocontrol Sci. Technol.* 25, 716–731. doi: 10.1080/09583157.2015.1010482
- Sommermann, L., Geistlinger, J., Wibberg, D., Deubel, A., Zwanzig, J., Babin, D., et al. (2018). Fungal community profiles in agricultural soils of a long-term field trial under different tillage, fertilization and crop rotation conditions analyzed by high-throughput ITS-amplicon sequencing. *PLoS ONE* 13:e0195345. doi: 10.1371/journal.pone.0195345
- Song, H.-K., Song, W., Kim, M., Tripathi, B. M., Kim, H., Jablonski, P., et al. (2017). Bacterial strategies along nutrient and time gradients, revealed by metagenomic analysis of laboratory microcosms. *FEMS Microbiol. Ecol.* 93:fix114. doi: 10.1093/femsec/fix114
- Souza, R. C., Cantão, M. E., Vasconcelos, A. T. R., Nogueira, M. A., and Hungria, M. (2013). Soil metagenomics reveals differences under conventional and no-tillage with crop rotation or succession. *Appl. Soil Ecol.* 72, 49–61. doi: 10.1016/j.apsoil.2013.05.021
- Srivastava, P. K., Singh, V. P., Singh, A., and Chauhan, D. K. (2020). *Pesticides in Crop Production*. New York, NY: Wiley Online Library. doi: 10.1002/9781119432241
- Srouf, A. Y., Ammar, H. A., Subedi, A., Pimentel, M., Cook, R. L., Bond, J., et al. (2020). Microbial communities associated with long-term tillage and fertility treatments in a corn-soybean cropping system. *Front. Microbiol.* 11:1363. doi: 10.3389/fmicb.2020.01363
- Stempflhuber, B., Engel, M., Fischer, D., Neskovic-Prit, G., Wubet, T., Schöning, L., et al. (2015). pH as a driver for ammonia-oxidizing archaea in forest soils. *Microb. Ecol.* 69, 879–883. doi: 10.1007/s00248-014-0548-5
- Sun, L., Dong, Y., Zhou, Y., Yang, M., Zhang, C., Rao, Z., et al. (2004). Crystallization and preliminary X-ray studies of methyl parathion hydrolase from *Pseudomonas* sp. WBC-3. *Acta Crystallograph. Sect. D* 60, 954–956. doi: 10.1107/S0907444904005669
- Tejada, M., Benítez, C., Gómez, I., and Parrado, J. (2011). Use of biostimulants on soil restoration: effects on soil biochemical properties and microbial community. *Appl. Soil Ecol.* 49, 11–17. doi: 10.1016/j.apsoil.2011.07.009
- Tétard-Jones, C., and Edwards, R. (2016). Potential roles for microbial endophytes in herbicide tolerance in plants. *Pest Manag. Sci.* 72, 203–209. doi: 10.1002/ps.4147
- Tilman, D., Cassman, K. G., Matson, P. A., Naylor, R., and Polasky, S. (2002). Agricultural sustainability and intensive production practices. *Nature* 418, 671–677. doi: 10.1038/nature01014
- Tyler, H. L. (2019). Bacterial community composition under long-term reduced tillage and no till management. *J. Appl. Microbiol.* 126, 1797–1807. doi: 10.1111/jam.14267
- Urbina, H., Breed, M. F., Zhao, W., Lakshmi Gurrula, K., Andersson, S. G. E., Ågren, J., et al. (2018). Specificity in *Arabidopsis thaliana* recruitment of root fungal communities from soil and rhizosphere. *Fungal Biol.* 122, 231–240. doi: 10.1016/j.funbio.2017.12.013
- Van Der Heijden, M. G. A., Bardgett, R. D., and Van Straalen, N. M. (2008). The unseen majority: soil microbes as drivers of plant diversity and productivity in terrestrial ecosystems. *Ecol. Lett.* 11, 296–310. doi: 10.1111/j.1461-0248.2007.01139.x
- van Dijk, E. L., Jaszczyszyn, Y., Naquin, D., and Thermes, C. (2018). The third revolution in sequencing technology. *Trends Genet.* 34, 666–681. doi: 10.1016/j.tig.2018.05.008
- van Elsas, J. D., Chiurazzi, M., Mallon, C. A., Elhottová, D., Křišťufek, V., and Salles, J. F. (2012). Microbial diversity determines the invasion of soil by a bacterial pathogen. *Proc. Natl. Acad. Sci. U. S. A.* 109, 1159–1164. doi: 10.1073/pnas.1109326109
- Van Gestel, M., Merckx, R., and Vlassak, K. (1993). Microbial biomass responses to soil drying and rewetting: the fate of fast- and slow-growing microorganisms in soils from different climates. *Soil Biol. Biochem.* 25, 109–123. doi: 10.1016/0038-0717(93)90249-B
- Van Overbeek, L., and Van Elsas, J. D. (2008). Effects of plant genotype and growth stage on the structure of bacterial communities associated with potato (*Solanum tuberosum* L.). *FEMS Microbiol. Ecol.* 64, 283–296. doi: 10.1111/j.1574-6941.2008.00469.x
- Vorholt, J. (2012). Microbial life in the phyllosphere. *Nat. Publ. Gr.* 10, 828–840. doi: 10.1038/nrmicro2910
- Vorholt, J. A., Vogel, C., Carlström, C. I., and Müller, D. B. (2017). Establishing causality: opportunities of synthetic communities for plant microbiome research. *Cell Host Microbe* 22, 142–155. doi: 10.1016/j.chom.2017.07.004
- Wakelin, S. A., Macdonald, L. M., Rogers, S. L., Gregg, A. L., Bolger, T. P., and Baldock, J. A. (2008). Habitat selective factors influencing the structural composition and functional capacity of microbial communities in agricultural soils. *Soil Biol. Biochem.* 40, 803–813. doi: 10.1016/j.soilbio.2007.10.015
- Walitang, D. I., Kim, K., Madhaiyan, M., Kim, Y. K., Kang, Y., and Sa, T. (2017). Characterizing endophytic competence and plant growth promotion of bacterial endophytes inhabiting the seed endosphere of Rice. *BMC Microbiol.* 17:209. doi: 10.1186/s12866-017-1117-0
- Wang, Y., Fu, F., Li, J., Wang, G., Wu, M., Zhan, J., et al. (2016). Effects of seaweed fertilizer on the growth of *Malus hupehensis* Rehd. seedlings, soil enzyme activities and fungal communities under replant condition. *Eur. J. Soil Biol.* 75, 1–7. doi: 10.1016/j.ejsobi.2016.04.003
- Wang, Z., Li, T., Li, Y., Zhao, D., Han, J., Liu, Y., et al. (2020). Relationship between the microbial community and catabolic diversity in response to conservation tillage. *Soil Tillage Res.* 196:104431. doi: 10.1016/j.still.2019.104431

- Wang, Z., Liu, L., Chen, Q., Wen, X., and Liao, Y. (2016). Conservation tillage increases soil bacterial diversity in the dryland of northern China. *Agron. Sustain. Dev.* 36:28. doi: 10.1007/s13593-016-0366-x
- Wang, Z., Liu, L., Chen, Q., Wen, X., Liu, Y., Han, J., et al. (2017). Conservation tillage enhances the stability of the rhizosphere bacterial community responding to plant growth. *Agron. Sustain. Dev.* 37:44. doi: 10.1007/s13593-017-0454-6
- Webber, M. A., Whitehead, R. N., Mount, M., Loman, N. J., Pallen, M. J., and Piddock, L. J. V. (2015). Parallel evolutionary pathways to antibiotic resistance selected by biocide exposure. *J. Antimicrob. Chemother.* 70, 2241–2248. doi: 10.1093/jac/dkv109
- Wei, F., Zhao, L., Xu, X., Feng, H., Shi, Y., Deakin, G., et al. (2019). Cultivar-dependent variation of the cotton rhizosphere and endosphere microbiome under field conditions. *Front. Plant Sci.* 10:1659. doi: 10.3389/fpls.2019.01659
- Wei, Z., Yang, T., Friman, V.-P., Xu, Y., Shen, Q., and Jousset, A. (2015). Trophic network architecture of root-associated bacterial communities determines pathogen invasion and plant health. *Nat. Commun.* 6:8413. doi: 10.1038/ncomms9413
- Weiss, S., Xu, Z. Z., Peddada, S., Amir, A., Bittinger, K., Gonzalez, A., et al. (2017). Normalization and microbial differential abundance strategies depend upon data characteristics. *Microbiome* 5:27. doi: 10.1186/s40168-017-0237-y
- Whipps, J., Lewis, K., and Cooke, R. (1988). "Mycoparasitism and plant disease control," in *Fungi in Biological Control Systems*, ed M. N. Burge (Manchester: Manchester University Press), 161–187.
- White, P. M., Potter, T. L., and Culbreath, A. K. (2010). Fungicide dissipation and impact on metolachlor aerobic soil degradation and soil microbial dynamics. *Sci. Total Environ.* 408, 1393–1402. doi: 10.1016/j.scitotenv.2009.11.012
- Wolejko, E., Jabłońska-Trypuć, A., Wydro, U., Butarewicz, A., and Łozowicka, B. (2020). Soil biological activity as an indicator of soil pollution with pesticides – a review. *Appl. Soil Ecol.* 147:103356. doi: 10.1016/j.apsoil.2019.09.006
- Wu, J., and Brookes, P. C. (2005). The proportional mineralisation of microbial biomass and organic matter caused by air-drying and rewetting of a grassland soil. *Soil Biol. Biochem.* 37, 507–515. doi: 10.1016/j.soilbio.2004.07.043
- Xu, Y., Wang, G., Jin, J., Liu, J., Zhang, Q., and Liu, X. (2009). Bacterial communities in soybean rhizosphere in response to soil type, soybean genotype, and their growth stage. *Soil Biol. Biochem.* 41, 919–925. doi: 10.1016/j.soilbio.2008.10.027
- Yao, H., and Wu, F. (2010). Soil microbial community structure in cucumber rhizosphere of different resistance cultivars to fusarium wilt. *FEMS Microbiol. Ecol.* 72, 456–463. doi: 10.1111/j.1574-6941.2010.00859.x
- Zhalnina, K., Dias, R., de Quadros, P. D., Davis-Richardson, A., Camargo, F. A. O., Clark, I. M., et al. (2015). Soil pH determines microbial diversity and composition in the park grass experiment. *Microb. Ecol.* 69, 395–406. doi: 10.1007/s00248-014-0530-2
- Zhang, Y., Shen, H., He, X., Thomas, B. W., Lupwayi, N. Z., Hao, X., et al. (2017). Fertilization shapes bacterial community structure by alteration of soil pH. *Front. Microbiol.* 8:1325. doi: 10.3389/fmicb.2017.01325
- de Vries, F. T., Griffiths, R. I., Knight, C. G., Nicolotch, O., and Williams, A. (2020). Harnessing rhizosphere microbiomes for drought-resilient crop production. *Science* 368, 270–274. doi: 10.1126/science.aaz5192
- Gu, G., Yin, H.-B., Ottesen, A., Bolten, S., Patel, J., Rideout, S., et al. (2019). Microbiomes in ground water and alternative irrigation water, and spinach microbiomes impacted by irrigation with different types of water. *Phytobio. J.* 2, 137–147. doi: 10.1094/PBIOMES-09-18-0037-R
- Zhao, Z., He, J.-Z., Quan, Z., Wu, C.-F., Sheng, R., Zhang, L.-M., and Geisen, S. (2020). Fertilization changes soil microbiome functioning, especially phagotrophic protists. *Soil Biol. Biochem.* 148:107863. doi: 10.1016/j.soilbio.2020.107863
- Fierer, N., and Jackson, R. B. (2006). The diversity and biogeography of soil bacterial communities. *Proc. Natl. Acad. Sci. U.S.A.* 103, 626–631. doi: 10.1073/pnas.0507535103
- Lauber, C. L., Hamady, M., Knight, R., and Fierer, N. (2009). Pyrosequencing-based assessment of soil pH as a predictor of soil bacterial community structure at the continental scale. *Appl. Environ. Microbiol.* 75, 5111–5120. doi: 10.1128/aem.00335-09
- Rousk, J., Bååth, E., Brookes, P. C., Lauber, C. L., Lozupone, C., Caporaso, J. G., et al. (2010). Soil bacterial and fungal communities across a pH gradient in an arable soil. *ISME J.* 4, 1340–1351. doi: 10.1038/ismej.2010.58
- Geyer, K. M., Altrichter, A. E., Takacs-Vesbach, C. D., Van Horn, D. J., Gooseff, M. N. and Barrett, J. E. (2014). Bacterial community composition of divergent soil habitats in a polar desert. *FEMS Microbiol. Ecol.* 89, 490–494. doi: 10.1111/1574-6941.12306
- Qi, D., Wieneke, X., Tao, J., Zhou, X., and Desilva, U. (2018). Soil pH is the primary factor correlating with soil microbiome in karst rocky desertification regions in the Wushan County, Chongqing, China. *Front. Microbiol.* 9:1027. doi: 10.3389/fmicb.2018.01027
- O'Brien, F. J. M., Almaraz, M., Foster, M. A., Hill, A. F., Huber, D. P., King, E. K., et al. (2019). Soil salinity and pH drive soil bacterial community composition and diversity along a lateritic slope in the Avon River Critical Zone Observatory, Western Australia. *Front. Microbiol.* 10:1486. doi: 10.3389/fmicb.2019.01486
- Tan, W., Wang, J., Bai, W., Qi, J., and Chen, W. (2020). Soil bacterial diversity correlates with precipitation and soil pH in long-term maize cropping systems. *Sci. Rep.* 10:6012. doi: 10.1038/s41598-020-62919-7

**Conflict of Interest:** The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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