Elisabet Nadeu, Robin van Dijk, Nora Hiller

December 2023

RESEARCH BRIEF

THE SOIL MICROBIOME: ITS CONTRIBUTION TO SOIL HEALTH AND ONE HEALTH

Contact:

enadeu@ieep.eu

Suggested citation:

Nadeu, E., van Dijk, R., Hiller, N. 2023. The Soil Microbiome: its contribution to soil health and One Health. Institute for European Environmental Policy, Brussels.

European Sustainable Agriculture Dialogue

DISCLAIMER

THE REPORT SHOULD BE CITED AS FOLLOWS

Nadeu, E., van Dijk, R., Hiller, N. 2023. The Soil Microbiome: its contribution to soil health and One Health. Institute for European Environmental Policy, Brussels.

CORRESPONDING AUTHOR

Elisabet Nadeu (enadeu@ieep.eu

ACKNOWLEDGEMENTS

We gratefully acknowledge helpful reviews and comments from Melanie Muro and Harriet Bradley (IEEP) and the members of the ESAD platform.

Photo by Gabriel Jimenez on Unsplash

This work has been produced with the financial support of the LIFE Programme of the European Union. The paper reflects only the views of its authors and not the donors.

The European Sustainable Agriculture Dialogue (ESAD) is a multi-stakeholder platform created in 2019 that brings together key actors from across society – including industry, civil society, universities, and research centres – to discuss key topics, exchange our views and standpoints, and ultimately shape decisions towards sustainable agriculture. The brief was developed in consultation with ESAD members and the authors took their inputs into account in the drafting process. The paper does not reflect the views and opinions of single ESAD members. As such, their contribution is not to be interpreted as an endorsement of the final paper.

CONTENTS

EXECUTIVE SUMMARY

Soils provide vital ecosystem services such as biomass production, biodiversity conservation, filtering drinking water and pest suppression. Although not widely recognised by the wider public, societies benefit from these ecosystem services performed by soils, and, in particular, the agricultural sector.

Over the past few years, research has emerged on the relevance of the soil microbiome in terms of healthy functioning soils and ecosystems but also linked to the health of humans and animals. The microbiome (community of microbes and the structures and substances they generate) is affected by several biotic and abiotic factors that operate both spatially and temporally. More than fifty thousand species of microbes can be found in one gram of soil, although less than 1% of the microbiome has been studied so far.

The microbiome plays a crucial role in enabling soil functions in agricultural production. The main soil functions with microbial intervention which support agricultural production are carbon dynamics (decomposition and synthesis of organic matter), nutrient cycling (decomposition, transformation, nitrogen fixation and plant nutrient uptake), soil structure and maintenance (particle aggregation and transport) and biological population regulation (pest and disease control).

Agricultural management practices alter the soil and impact its microbial communities. While some practices can negatively affect the soil microbiome, others can increase the beneficial microbes' diversity, composition, and abundance. This brief provides an overview of practices grouped under six headings: physical soil disturbance, crop diversification, synthetic inputs, biocontrol, organic fertilisers and direct microbial inoculation. It concludes that many of the benefits remain context-dependent, and research and field implementation is needed to elucidate the links between the soil microbiome, soil functions and plant and soil health.

Understanding the most effective strategies and tailoring these to each context could contribute towards achieving the European Union’s Green Deal’s objectives, inform soil and agricultural policies and help to enhance the agricultural sector’s capacity to mitigate and adapt to climate change.

Four main areas for further research are identified to increase our knowledge of the soil microbiome and support a transition towards a more sustainable and resilient agriculture:

- Characterisation of the soil microbiome and development of standardised metrics,
- Improved capacity to map, model and predict the soil microbiome,
- Research into farming practices that can enhance the soil microbiome and its benefits (plant diversity, organic fertilisers, biocontrol)
- Elucidating the role of the soil microbiome in the One Health approach

1. INTRODUCTION

Soils provide vital ecosystem services ranging from the production of biomass, biodiversity conservation, filtering drinking water and pest suppression. While the larger public does not widely recognise these ecosystem services performed by soils (Brevik et al, 2019), benefits are drawn for human activities, particularly in the agricultural sector. Over the past years, research has emerged on the relevance of microbes for healthy functioning soils and ecosystems but also linked to the health of humans and animals. While much remains unknown, the microbiome (community of microbes and the structures and substances they generate) seems to play a crucial role in enabling soil functions in agricultural production and contributing to plant, animal and human health, as well as contributing to meeting the European Green Deal’s targets in relation to nutrient losses and pesticide use.

This brief explores current knowledge on the soil microbiome, its links to soil functions and the beneficial or harmful effect of agricultural practices on its health. It also provides recommendations for future research and innovation to enhance the current understanding of the microbiome and its contribution to the environment, animal, and human health.

2. THE SOIL MICROBIOME

A microbiome is a community of microorganisms living in a specific environment with the microbial structures and substances they generate. Such microbiomes are found in humans, animals, plants, soils, oceans, and other environments.

The combination of microorganisms in each environment is unique, but soils are considered to host the most complex and diverse microbiome on our planet (Xiang et al. 2021). More than 50.000 species are present in 1 gram of soil (Bardgett and van der Putten, 2014; Fierer, 2017), making the soil microbiome the most genetically diverse community on the planet (Kendzior, Warren Raffa and Bogdanski, 2022). While the soil microbiome remains largely unstudied, less than 1% has been studied so far (Kendzior, Warren Raffa and Bogdanski, 2022), its diversity is suspected to be a key support to the vast array of functions and services that sustain life (see section 3.1).

The soil microbiome's complexity and diversity result from the variety of environments that soils offer microbial communities (Fierer, 2017). The plural ‘soil microbiomes’ rather than the singular ‘soil microbiome’ is used by researchers to make the diversity in habitats more explicit (e.g. Singh et al, 2023). Globally, soils are characterised by a high heterogeneity, and their properties vary from one site to the next, resulting from a combination of climate, parent material, organisms, and time. Also, in a single soil profile, the environmental conditions can vary largely between and within the soil horizons (the layers), creating a wide variety of habitats for microorganisms.

The soil microbiome comprises soil microbiota as well as microbial structures, genetic elements, and relic DNA. Microbes are generally divided into four main groups. From more to less abundant, these are bacteria, fungi, archaea, and protists (Fierer, 2017). Some classifications also include viruses as microbes, while others consider viruses as part of the “floating genetic material”. Most soil taxa (i.e. microbes grouped by similar characteristics) have not yet been described and cannot be found in reference databases. This is the case for over 80% of the bacteria and archaea taxa found in soil (Ramirez et al, 2014). In addition, the large majority (>95%) of soil microbes are inactive at certain times (Blagodatskaya and Kuzyakov, 2013). Microbial studies have traditionally been biased towards the study of bacteria and fungi, and much remains unknown about microbes in different systems (Fierer, 2017).

Some researchers have pointed out that classifying soil microorganisms based on genetic characterisation rather than their involvement in soil functions makes it difficult to understand the links between the different groups (Kendzior, Warren

Raffa and Bogdanski, 2022). In this sense, the research community is still working to find a way to classify the soil microbiome that allows establishing relationships between taxa, processes, and functions. Fierer (2017) suggested adopting a framework that groups microbes sharing similar functional capacities and ecological strategies to understand better the role of microbes in soil processes and functions.

2.1 Factors affecting the soil microbiome

The composition of a particular soil microbiome is affected by several biotic and abiotic factors which operate both spatially and temporally. These include biotic factors (plant species, microbial predators and competitors), and abiotic factors (soil structure and type, soil moisture, soil pH, soil nutrients and geographical factors) (Blum, Zechmeister-Boltenstern and Keiblinger, 2019; Islam et al, 2020).

While no single factor is consistently determinant for the microbiome composition (Fierer, 2017), the soil environment has been reported to substantially influence microbial community structure and diversity. Soil moisture, soil pH (acidity) and soil texture, for instance, have been singled out as predictors of microbial community composition and diversity globally (Brockett, Prescott and Grayston, 2012; Rousk et al, 2010). Some of the factors affect some microbial groups more than others. For instance, soil moisture has been observed to influence protist composition and is also considered a good predictor of microbial biomass (Mishra, Singh and Singh, 2023).

The communities created by microbes are complex, dynamic (Neher et al, 2022), and sensitive to their surrounding conditions. Most soil microorganisms are found in the rhizosphere, topsoil, where nutrient availability is high and adjacent to plant roots with whom they may establish symbiotic relationships. However, other microorganisms can be found in deeper soil layers, although microbial activity decreases with depth (van Leeuwen et al, 2017). Only a few microbes are found in all soils, and richer soils have rarer species. The impact of the aboveground plant community on the structure of the microbiome is context-dependent and may take years to become evident because other factors are involved (Crowther et al, 2014; Fierer, 2017).

The soil microbiome is also sensitive to soil contamination, such as the presence of heavy metals (e.g. from fertiliser application, industrial emissions), microplastics or pesticides. Heavy metals do not undergo microbial decomposition and can persist in soils for long periods of time, disrupting biochemical processes and the balance of the soil microbiome (Boros-Lajszner et al, 2021). The accumulation of microplastics in soils can also negatively impact the microbiome's structure and functionality (Guo et al, 2020). In terms of pesticide residues, their impact on the soil microbiome has been largely overlooked by the research community, even though between 30-50% of pesticides applied in agriculture can end up in soils (Rodríguez-Eugenio, McLaughlin and Pennock, 2018).

2.2 Approaches and limitations to the measurement of the microbiome

There are several approaches to studying the soil microbiome, which can be classified into two main groups: ecological approaches and molecular approaches. Ecological approaches aim to provide a holistic understanding of the soil microbiome and its interactions with the broader environment. These include using indirect methods to assess and understand the microbial community and its functions. Examples of this are soil respiration, plant bioassays, using soil chemical or physical properties as proxies, or biological indicators such as the presence of mycorrhizal fungi. Microbial isolation techniques, where microbes are grown out of their natural environment, are also ecological approaches.

The reduction of sequencing costs and advances in technologies have facilitated the uptake of molecular approaches. These involve using molecular biology tools to analyse the genetic material of the soil microbiome and determine its composition. It is important to note that molecular approaches based on DNA sequencing provide information on the relative abundance of microbes or genes but not on absolute values (Fierer, 2017).

There are limitations to what molecular approaches can do. For instance, they can overestimate microbial presence. This can happen with DNA sequencing if relic DNA is found in soils, which may increase bacterial and archaea diversity estimates by more than 40% (Carini et al, 2016). Sequencing errors in PCR analyses to characterise soil microbial diversity may overestimate the number of species. But they can also underestimate them if the databases they rely on are incomplete (Choi et al, 2017).

In addition, some of the limitations to the study of the soil microbiome are practical and apply to both approaches. For example, given the vast diversity of environments in a single soil profile, the analysis of a soil core will include several microhabitats, making it challenging to associate microorganisms with particular soil characteristics (Fierer, 2017). Most studies have also focused on the spatial variability of soil microbes rather than the temporal one. One of the reasons is that there are measurement constraints to it. Assessing the temporal variability requires sampling the exact location over time, which is physically impossible since the sample is destroyed each time (Fierer, 2017).

3. THE SOIL MICROBIOME AND SOIL FUNCTIONS

The role of the soil microbiome in healthy soils has been increasingly acknowledged over the past decades. Microbes support many soil processes and functions essential to agroecosystems' sustainability. The main soil functions with microbial intervention which support agricultural production are carbon dynamics (decomposition and synthesis of organic matter), nutrient cycling (decomposition, transformation, nitrogen fixation and plant nutrient uptake), soil structure and maintenance (particle aggregation and transport) and biological population regulation (pest and disease control) (Kibblewhite and Ritz, 2008). Through these functions, microbes also contribute to vital ecosystem services such as climate regulation and the water cycle (Kendzior, Warren Raffa and Bogdanski, 2022).

Soil microbes are mainly considered ‘chemical engineers’ because they intervene in these soil functions by decomposing organic matter, transforming carbon and nutrients and degrading and immobilising contaminants (Turbé et al, 2010). By doing so, they consume and emit trace gases (methane, nitrous oxide, carbon dioxide), regulate soil acidity (pH), nutrient cycling and availability (nitrogen, phosphorus, iron, sulphur) and regulate organic matter dynamics (Fierer, 2017). However, microbes can also act as ‘biological regulators’ by providing protection against pathogens, predating on each other and controlling pests and disease (Sergaki et al, 2018), as well as ‘ecosystem engineers’ contributing (though in a limited way) to soil structure and formation (Turbé et al, 2010).

The specific contribution of microbial taxa to a particular soil function is still poorly understood. There is a general agreement on the microbial groups involved in these processes. For instance, chemical engineers generally comprise archaea, bacteria and fungi, while biological regulators include protists and larger soil organisms (El Mujtar et al, 2019). The role of microbes in soil structure and formation is primarily indirect, as it’s generally performed by larger organisms, including small mammals, but bacteria and fungi can promote soil aggregate formation and thus improve soil structure (da Silva, Southam and Gagen, 2023). Soil microbial communities are strongly influenced by soil aggregates of different sizes that provide habitat for them (Hartmann and Six, 2023).

Despite not having a complete understanding of the mechanisms of intervention of microbes in these processes, there is evidence that many of them can be performed by a broad range of taxa while others are limited to only a few. Two key concepts in describing the role of the soil microbiome in soil functions are functional diversity and redundancy, both of which are needed for a healthy soil. Functional diversity allows soils to perform many biological activities. At the same time, redundancy implies that functions can be developed by more than one species, which increases the resilience of the soil in the face of a shock (Kendzior, Warren Raffa and Bogdanski, 2022).

Several studies have shown that the higher the soil microbial diversity, the higher its multifunctionality across different biomes (e.g. Bastida et al, 2016; Delgado-Baquerizo et al, 2016; Wagg et al, 2014). Understanding this multifunctionality and the participation of microbes in the different functions allows to consider synergies and trade-offs when changes in the microbiome take place (e.g. Wagg et al. 2014). However, establishing links between taxa and soil functions is challenging, and having information on microbial taxa is not enough to identify or predict how soil processes and functions will respond to particular perturbations (Fierer, 2017). In addition, most studies to date have focused on bacterial communities, while other microbial groups remain under-researched (Zheng et al, 2019).

4. AGRICULTURAL MANAGEMENT PRACTICES, SOIL MICROBIOME AND SOIL HEALTH

The FAO recently defined the soil microbiome as “a game changer for food and agriculture” (Kendzior, Warren Raffa and Bogdanski, 2022). Among the main goals of soil microbiome research is understanding how it can improve soil health. Agricultural management practices alter the soil and impact its microbial communities. While some practices can negatively affect the soil microbiome or some of the taxa, others can increase the diversity, composition, and abundance of taxa that are beneficial for soil health. Generally, these practices create favourable living conditions for these microbes or directly add specific microbes into soils.

The sub-sections below provide an overview of the impacts of soil management practices on the microbiome and soil functions. The review aims to raise some of the issues and gaps in our current understanding of their impacts. The practices have been grouped under six headings: i) physical soil disturbance, ii) crop diversification, iii) synthetic inputs, iv) biocontrol, v) organic fertilisers and vi) direct inoculation. In addition, information is also provided for other practices or systems that did not fit into these categories. A summary overview of the impacts of the reviewed practices on the soil microbiome is provided at the end of the section (**Table 1**).

4.1 Physical soil disturbance

Tillage is a widespread agricultural practice that has been in use for centuries. It implies the mechanical disturbance of the soil to prepare the seedbed for crop production, namely incorporating crop residues, alleviating compaction and decreasing the presence of weeds, pests and soilborne pathogen loads (Tilman et al, 2002). However, tillage also homogenises the soil environment (reducing microbial habitats), destroys soil aggregates and buries residues, accelerating microbial activity and in turn changing the diversity, structure and composition of microbial communities present in the soil (Delitte et al, 2021; Sengupta and Dick, 2015; Young and Ritz, 2000). Tillage can impact the microbiome directly, and has been observed to change soil bacteria and particularly fungi communities (Hartman et al, 2018), but also indirectly by reducing soil organic matters in tilled soils, and, therefore, habitat for the microbes (Gao, Li and Li, 2022).

Contrary to tillage, no-till practices where seeds are sown directly, and crop residues decompose on the surface are associated with benefits for soil structure, biodiversity, and conserving carbon. By minimising disturbance, it improves soil aggregation and, in turn, enhances microbial processes (Hartmann and Six, 2023).

Studies indicate that the microbiome's structure differs between soils that are not tilled and those under conventional tillage. For instance, no-till can significantly increase bacterial diversity and richness, depending on the soil type (Khmelevtsova et al, 2022). The absence of tillage has been associated with increased microbial biomass and enzyme activities (Zuber and Villamil, 2016). Nonetheless, no tillage can also bring about inevitable negative consequences, such as increased usage of pesticides and herbicides in the absence of ploughing. Such effects may be detrimental to soil microbes (see section 4.3).

Research studies have shown that reducing the tillage intensity can benefit the soil microbial community and favour those that produce biomolecules that contribute to aggregate formation and stability (Cania et al, 2020), increasing soil health. However, some studies have observed mixed effects (Degrune et al, 2016).

4.2 Crop diversification

Crop diversification refers to the cultivation of several crops in a specific area. Diversification can occur temporally (rotations, cover crops) and spatially (intercropping, companion cropping). The effect of these practices on soil microbial communities is evaluated overall as positive or promising, however, research studies are not always able to single out the effect of the practices among other factors (soil type, sampling strategy, duration of the field experiments) and causal relationships cannot be established. A limitation to current knowledge is that most existing research has focused only on the soil bacteria community.

Crop diversity and microbial communities are closely interlinked and influence each other (Tedersoo, Bahram and Zobel, 2020). Cover crops[1] help the microbiome by reducing topsoil erosion and nutrient leaching (particularly during winter), controlling weeds and enhancing carbon sequestration (Khmelevtsova et al, 2022). They can positively contribute to microbial abundance, activity and diversity (Kim et al, 2020). Specific cover crop roots also maintain soil aggregation and porosity, enhancing microbial habitats and activity (Hartmann and Six, 2023). The effects of using cover crops on the microbiome vary, depending on the type of cover crop (i.e. leguminous vs non-leguminous crops) and the decomposition time of its residues, as well as the structure and microbial diversity of the soil microbiome (Khmelevtsova et al, 2022).

---

[1] the practice of growing vegetation between (cash) crop plantings, diversifying agrobiodiversity and crops (Kendzior et al. 2022)

Crop rotations[2] have been associated with higher yields, a reduced need for nutrient inputs and a lowered concentration of pathogens (Khmelevtsova et al, 2022). Diversified crop rotations enhance the network complexity of the belowground microbiome and provide root exudates, altering the growth and interactions of microorganisms. Findings indicate that diversified crop rotations tend to have a stronger impact on fungal populations than on bacteria, but this may be due to site conditions or other factors (Yang et al, 2023). In contrast to rotations, monocropping has been found to reduce soil biodiversity (Li et al, 2019).

4.3 Synthetic inputs

The application of fertilisers serves to provide nutrients and increase crop yields. However, overusing inorganic fertilisers may result in soil erosion, changes in carbon organic content and soil pH. Especially in the long term, the overapplication of inorganic fertilisers can lead to reduced biodiversity and bacterial abundance. While a balanced application of nitrogen, phosphorus and potassium may prove to increase microbial diversity, most findings indicate that using inorganic fertilisers in substantial quantities harms soil functions (Khmelevtsova et al, 2022). While most studies have been focused on bacteria, in the case of arbuscular mycorrhizal fungi, there are contradictory results, and both increases and decreases in diversity have been reported (Hermans et al, 2023). The indirect effects of fertilisers on nutrient-induced vegetation and soil property changes could also explain differences observed in microbial communities in response to fertiliser applications (Hermans et al, 2023). Note that the combined application of inorganic and organic fertiliser has been proven to positively affect crop productivity and soil microorganisms. Mixing fertilisers can help increase species abundance and the diversity of bacterial communities (Khmelevtsova et al, 2022).

Despite its toxic effects on biodiversity, the impacts of pesticide use on the microbiome have been less researched than fertilisers (Hermans et al, 2023). More than 90% of the herbicides and insecticides used in agriculture reach non-targeted organisms, impacting the microbiome (Mishra, Singh and Singh, 2023). Pesticide residues, present in conventional and organically managed soils[3] (Geissen et al, 2021), have been associated with variable impacts on soil

---

[2] ‘growing different crops in succession, thereby increasing plant diversity over space and time’ (Kendzior et al. 2022)

[3] While organic production does not allow the use of synthetic inputs, their widespread use by the large majority of farmers creates an omnipresent risk of contamination in the whole food supply chain

microbiome traits, ranging from firmly negative to relatively positive. Pesticide residues can negatively affect bacterial diversity, which can be attributed to toxic effects endangering susceptible bacteria. However, pesticide residues have also been positively associated with the metabolising of pesticides by bacteria and fungi (Walder et al, 2022). The resources provided by pesticides may be beneficial for certain microorganisms but could have adverse effects on the microbial growth of others. Pesticide residues in soils also influence the soil microbiome and the presence and abundance of microbes. In a study under field conditions, Walder et al. (2022) showed that pesticide residues favoured fungal diversity to the detriment of bacterial diversity, one of the genes responsible for biological nitrogen fixation (Walder et al. 2022). The positive and negative effects on different soil microbial taxa inevitably result in changes in the soil microbiome, favouring some microbes over others. However, there is a lack of understanding of this disrupting effect on the microbiome and soil health. In addition, because pesticides can remain in soils long after their application ceases, as seen in soils under organic management after two decades (Riedo et al, 2021), further research is needed.

4.4 Biocontrol

Biocontrol practices use living organisms and/or natural substances to prevent and reduce damage and diseases caused by harmful organisms such as animal pests, weeds, and pathogens (Busson, 2022; Hulot and Hiller, 2021; Prajapati et al, 2020). Biocontrol is embedded in a holistic manner interacting between plants, agents, and agricultural methods.

Through different interactions with the soil and biodiversity, the use of biocontrol can create a favourable state for soil microbes and reduce the amount of harmful chemicals in the ground. The long-term vision and long-lasting effects of these practices have a positive effect on biodiversity and soil health. The use of biocontrol can encourage the soil microflora, as well as the ‘volatilisation and sequestration of certain inorganic nutrients’ (Prajapati et al, 2020). The interaction of invertebrates etc. and biological fertilisers with microbial communities, Bajsa et al (2013) indicates that their introduction may have ‘an impact on different groups of soil microbes and at different distances from the root’ (Bajsa et al, 2013; Hulot and Hiller, 2021). Widely used components of biocontrol, such as the fungi Trichoderma spp, has received attention in studies and besides its plant protection properties has also received positive recognition for enhancing the soil’s resistance against abiotic stresses (meaning drought or lack of nutrients) as well as working against soil-borne diseases (Prajapati et al, 2020; Woo and Pepe, 2018). Beyond microbiomes specifically, the use of biocontrol reduced the risk of contamination, reducing the risk of soils being exposed to chemical residues (Geissen et al, 2021).

4.5 Organic fertilisers

Organic fertilisers, such as manure or compost, have been shown to favourably impact microbial diversity and soil biomass (Hartmann and Six, 2023). They tend to activate taxa and introduce exogenous microorganisms in the soil. Another advantage of organic fertilisers, compared to inorganic ones, is that nutrients are released over a more extended period. It should, however, be noted that the concentration and period of fertilisation, vegetation types and soil characteristics can alter the response of the soil microbiome. Overapplying organic fertilisers can reduce bacterial diversity (Khmelevtsova et al, 2022). Organic fertilisers can create microbial habitats in soils by promoting the biological activity of organisms that enhance soil aggregation and porosity (Hartmann and Six, 2023). However, different organic fertilisers vary in their impacts on the soil microbiome.

4.6 Direct microbial inoculation

In agriculture, microbial inoculants, generally bacteria or fungi, are introduced into soils as biostimulants or for biocontrol purposes. Biostimulants promote plant growth by stimulating root growth, enhancing plant water uptake from deeper soil layers or stimulating microbial activity (Kaminsky et al, 2019). Microbial inoculation generally focuses on nitrogen-fixing microbes, phosphate solubilising microbes, protection against soil-borne plant diseases, management of pests, improved abiotic stress tolerance of crops or overall soil health improvement, for instance by stimulating soil aggregate formation (Parnell et al, 2016). Other objectives of microbial inoculation can include greenhouse gas mitigation through carbon sequestration with CO2-fixing microorganisms and bioremediation for contaminated soils.

Microbial inoculants can modify the soil community but the underlying mechanisms of these changes are not well known (Mawarda et al, 2020). One of the significant limitations of microbial inoculation lies in achieving successful field implementation. Some inoculants have been shown to be successfully implemented and persist in soils, while field application fails for others (O'Callaghan, Ballard and Wright, 2022). Inoculations including several microbial groups at the same time (co-inoculation) have shown better results than single microbial inoculations, although the outcomes are context-dependent (e.g. (Iturralde et al, 2020; Trabelsi and Mhamdi, 2013). Testing the efficacy of inoculations at the field level remains, therefore, challenging. Robust experimental designs are needed, which require multi-annual observations and tests across several sites to allow testing of the treatment effect between other confounding factors (O'Callaghan, Ballard and Wright, 2022). Moreover, because knowledge of the interactions between microbial inoculants and native microbial communities remains limited, as well as its impact on soil functions, careful weighing of the risks and benefits posed by the introduction of microbes into is needed.

4.7 Other practices

Grazing alters the growth of plants and nutrient cycles in the soil. Heavy grazing has been found to reduce the diversity of bacteria and fungi. This is primarily attributable to the removal of vegetation and litter mass. Fungi populations tend to thrive in soils where no grazing occurs, whereas bacterial communities favour light grazing conditions. Overgrazing has been linked to repressing overall microbial diversity and activity (Xun et al, 2018).

In the case of liming acidic soils, changes in pH occur, altering microbial composition and abundance. An increase in pH leads to a higher bacteria to fungi ratio, but does not affect protists (Mishra, Singh and Singh, 2023).

4.8 Summary

There seems to be a consensus among scientific literature that soil management practices can profoundly affect soil microorganisms and functions (Kendzior, Warren Raffa and Bogdanski, 2022). Most research over the past decade has referred to the impact of practices on soil biology in general terms, and explicit connections between practices, microbial groups, and soil health are just starting to emerge.

The consulted literature reveals that sustainable soil management practices can substantially benefit microbial diversity, nutrient turnover, soil organic carbon, root exudates, water retention capacity and other soil functions. However, considerable uncertainties remain attributable to the interpretation of data on the impacts of soil management practices. The temporal and spatial variability of the examined soil management practices can profoundly alter the findings of such experiments. Also, when a management practice is examined in isolation, the results may not necessarily account for potential interactions between different practices (Kendzior, Warren Raffa and Bogdanski, 2022). The specific circumstances, time spans, and context under which data are gathered must be accounted for when assessing soil management practices.

Table 1: Summary of the impacts of revised practices on the microbiome, soil processes and functions (P: positive, N: negative, NC: non-conclusive)

Practice	Impact	Description of the impact (based on the above sections)
Tillage	N	Buries residues and destroys soil aggregates. Alters microbial diversity, structure and composition.
No tillage	NC	Decreases soil erosion and enhances water retention. Potentially increases the use of pesticides and herbicides.
Cover crops	P/NC	Provide root exudates, reduce topsoil erosion and control weeds. Increase carbon sequestration and mitigate nitrogen leaching.
Crop rotations	P	Higher yields, disrupt pathogens and reduce need for external inputs.
Crop rotation diversification	P	Higher yields. Enhanced network complexity of belowground microbiome and provides root exudates.
Microbial inoculants	NC	Stimulate root growth and increase plant water uptake. Increase carbon sequestration and reduce CH4 emissions. Knowledge of interactions between microbial inoculants and native microbial communities remains limited, and a lab field gap exists.
Overgrazing	N	Removes vegetation and litter mass. Reduces overall microbial diversity and activity.
Inorganic fertilisers	N	May result in soil degradation, changes in carbon organic content and soil pH. Overapplication affects nutrient balance and leads to lower bacterial abundance.
Pesticides	NC	Toxicity effects threaten microorganisms. Pesticides can change microbial communities due to mixed effects on taxa (favour ones in detriment of others)
Organic fertilisers	NC	Activate taxa and introduce exogenous microorganisms. Provide nutrients over a longer timeframe. Overapplication leads to lower bacterial abundance.
Mixed fertilisers	P	Positive impact on crop productivity and soil microorganism abundance.

5. THE SOIL MICROBIOME AND ONE HEALTH

The concept of One Health connects environmental and human health through the interactions with ecosystems, plants, and animals. It sees multidisciplinary solutions to human, animal, and environmental health as integral to improving life quality. The One Health approach has its origin in the human and veterinary medicine fields (linked to antimicrobial resistance and infectious diseases). Applied to agrifood systems, as promoted by the FAO, One Health sees improvements of soil health as benefits that extend to human health (Kemper and Lal, 2017).

Microbes are thought to play a crucial role in One Health. As mentioned at the start of this brief, microbiomes are present in many different environments. The soil microbiome influences environmental health which in turn affects human health and wellbeing, directly and indirectly. Direct impacts relate to plant growth and promotion, plant pathogens, soil health and mitigating climate change, while it has indirect impacts on soil-borne pathogens, animal social behaviour, geophagia, dust and exposure or antibiotic-resistance bacteria (Banerjee and van der Heijden, 2023). As seen in the previous sections, healthy microbiomes can reduce the need for plant protection products and nutrient inputs in agricultural areas, with environmental benefits as well as for human health.

Over the past decade, research into the human gut microbiome and that of other environments has shown that microbiomes are the most genetically diverse communities on the planet (Kendzior, Warren Raffa and Bogdanski, 2022). Microbes circulate from one environment to the other, and the human gut and the soil microbiome are similar. It is thought that the soil microbiome was essential in the development of the human gut, because of the functional similarities between them (Blum, Zechmeister-Boltenstern and Keiblinger, 2019). The microbial diversity in the human gut is only 10% of that in soils, and it has decreased over time (Blum, Zechmeister-Boltenstern and Keiblinger, 2019).

The links between the soil microbiome and human health are increasingly being studied. While theoretically the links between the two microbiomes seem quite clear, in practice research is just starting to show that the soil microbiome could play a key role in processes that do have an impact on human health (Kendzior, Warren Raffa and Bogdanski, 2022). Soil microbes regulate soil functions, which enable crucial ecosystem services and terrestrial life. Direct exposure to soil microorganisms could impact our immune system from early childhood (Mills, Kelly and O'Neill, 2017). This has been corroborated by animal studies where it is shown that ingestion of soil microbiota can be beneficial for the functioning of the gut microbiome (Liddicoat et al, 2020).

Moreover, soil microbes regulate the cycling of essential elements and facilitate their uptake by plants, such as zinc and selenium, which are delivered by mycorrhizal fungi (Smith and Read, 2008). Certain microbes can enhance the production of vitamins and amino acids that humans cannot synthesise, as well as antibiotics, immunosuppressants, and anti-cancer and anti-inflammatory drugs (Hirt, 2020). Manzeke-Kangara et al (2023) reviewed the impact of regenerative[4] agriculture practices on improving the nutritional quality of crops. While they showed that the results are very context-specific, a few of their observations were generalisable across several studies. Examples they cite are increases in Vitamin C of tomatoes or higher grain zinc concentrations in rice. Similarly, Carrara et al (2023) showed that maintaining healthy populations of beneficial soil fungi (in their case, arbuscular mycorrhizal fungi) could increase the levels of an antioxidant and anti-inflammatory amino acid in a range of plants.

The presence of beneficial microbes, therefore, can enhance human health, yet, negative impacts related to the microbiome are equally possible. Loss in microbial diversity can increase the risk of disease that emerges with increased pests and pathogens (Wall, Nielsen and Six, 2015). In addition, soil is also a reservoir of pathogens for humans, animals, and plants, and exposure to several soil-borne pathogens causes hundreds of millions of infections annually (Singh et al, 2023).

In conclusion, the evidence reviewed suggests that whilst the relationships between agricultural practices and the soil microbiome and subsequent impacts on soil and human health are receiving increasing attention by the research community, substantial knowledge gaps still exist.

---

[4] Regenerative agriculture can be defined as a system of farming principles and practices that increases biodiversity, enriches soils, improves watersheds and enhances ecosystem services (EIT Food)

6. RESEARCH AND INNOVATION ON THE MICROBIOME

In this section, we provide an overview of current research directions and gaps in the study of the soil microbiome and its links to soil and human health. We also review current and past projects focusing on soil biodiversity and the microbiome and draw some conclusions on how increased knowledge on the soil microbiome could contribute to meeting European Green Deal targets.

6.1 Knowledge gaps and future research

The past decades have seen a surge in the interest in the study of the microbiome, in general, and the soil microbiome has not been exempted from this. Methodological approaches to its study have multiplied, genomic techniques that allow taxa identification have become cheaper and faster, and elucidation of the role of microbes in soil processes and functions is progressing (Fierer, 2017).

Despite these advances, challenges remain. Linking microbial taxa to functions is, in most cases, still not possible. Holistic conceptual frameworks that explain patterns in the soil microbiome are lacking, and our predictive capacity to translate observed changes in microbial communities to environmental responses, and vice versa, is far from optimal. In agriculture, the links between agronomic practices, the soil microbiome and impacts on soil functions are poorly understood, limiting the capacity of translating laboratory knowledge to the field. Little is known about the specific microbial groups affected by soil and crop management practices (see Sections 2 and 3 for references). And attention has been placed on a narrow group of taxa, underestimating the role that other microbes may play in soil functions.

Several methodological tools are being explored which could expand current knowledge and analytical capacities. Genomic techniques are allowing better descriptions of microbial diversity and identifying taxa, and the genes responsible for the processes that are of interest for particular goals. This opens the door for bacterial treatments to increase plant tolerance and resistance to stress factors, such as drought, or soil applications of fungi to enhance plant drought resistance (Duc, Csintalan and Posta, 2018). Microbial genetic engineering has also been proposed to use microbial properties to increase soil and plant health. This line of research investigates boosting interesting functions of microorganisms in the lab to increase our capacity to respond to ecosystem challenges by addressing issues such as ecosystem restoration, crop yields or pest control.

Soil health could also benefit from further development of biofertilisers and biopesticides, as well as research looking into ‘feeding’ beneficial microbes with specific compounds to stimulate their growth and overall microbiome health (e.g. sugars, metabolites) (Wei and Jousset, 2017). A better understanding of the associations between plant varieties, rhizosphere microbes and their surrounding environment could increase plant resistance against stresses and reduce the need for external inputs, increasing the sustainability of agricultural systems (Kendzior, Warren Raffa and Bogdanski, 2022). Finally, microbes also have a potential role in soil health assessments. They are starting to be used as biomarkers or bioindicators to obtain information from soils that are difficult to measure directly and which can benefit agricultural management (Fierer, 2017; Wilhelm et al, 2023).

The identified research directions and gaps among the reviewed literature can be grouped around the following topics:

Box 1: Four identified areas for future research

- **Characterisation of the soil microbiome and development of standardised metrics**

Research is needed to improve current definitions of microbial species. A narrow focus on bacteria, as has been the case until recently, can lead to misleading conclusions about the role of the microbiome in ecosystems (Geisen, 2021). Advances in the use of soil markers as a proxy (DNA and RNA) have allowed for faster and more precise identification of soil microbial communities Harkes 2020[5]). Although genomic data is being produced at a very fast pace, it is still not very useful for predicting microbial processes. Approaching the study of the microbiome by focusing on the particular process or function that needs to be addressed and selecting the tests according to it could provide a set forward in the development of methodological tools for monitoring (Fierer, 2017; Fierer, Wood and Bueno de Mesquita, 2021), including the development of digital tools. Moreover, it would allow the creation of frameworks classifying microbial communities in relation to the functions and soil health parameters of interest.

---

[5] https://research.wur.nl/en/publications/a-leap-towards-unravelling-the-soil-microbiome

- **Improving the capacity to map, model and predict the soil microbiome**

Some soil microbes can help predicting how the microbial communities will respond to a particular driver and, therefore, how this will impact biogeochemical processes in soils (e.g. temperature increase as studied by (Oliverio, Bradford and Fierer, 2017). They can be used as bioindicators. Improving our capacity to predict these changes requires further research into the spatial, but also temporal variability of microbial communities, as well as developing models that can take into account not only microbial diversity but also interactions within microbial communities. Current knowledge is also limited regarding the differences between microbial communities in the topsoil and subsoil. Collection of harmonised data across the EU remains a challenge, although since 2018 the LUCAS Soil database has included information on soil biodiversity.

- **Farming practices to enhance the soil microbiome and its benefits**

Increased knowledge on the role played by the soil microbiome in soil functions and plant nutrition and protection can increase the sustainability of agricultural systems. However, current capacity to translate knowledge advances into farming practices to improve soil and plant health is still limited because many of the experiments performed do not capture the complexity of the interactions that take place in agricultural soils (Sergaki et al, 2018). Integrated ecological approaches can help bridge the gap between theoretical knowledge and practical agricultural implementation. Such studies could look into how different farming systems, some of which already promote many of the microbiome enhancing practices (e.g. organic agriculture, agroecology) compare in terms of plant and soil health.

Additional work is needed to develop knowledge on the effects of pesticide cocktails on soil microbial communities (Geissen et al, 2021). Research into the interactions between crop diversity, application of organic fertilisers and biocontrol on the soil microbiome and soil health is also needed not only in relation to the specific taxa but microbial community dynamics as well. Field research on the impact of biocontrol on harmful and beneficial microbes could be particularly useful given the objective set out in the Farm to Fork Strategy of reducing use and risk of chemical pesticides. In addition, the connection between crop traits (e.g. tolerances, resistance, nutrient use efficiency) and the microbiome could be further explored since the genomics that lead to recruitment of beneficial microbes can support plant breeding.

- **Elucidating the role of the soil microbiome in the One Health approach**

Research directed at increasing our understanding of how the soil microbiome impacts crop nutritional quality and human health is showing promising results but has just started

6.2 EU funded projects on the microbiome

The review of existing knowledge demonstrates that most of the research and thinking around the microbiome has taken place over the last couple of decades. A recent study by the JRC on the focus of the topics funded under EU Framework Programmes shows that there has been a shift from 'soil contamination' and 'soil and water' to 'climate change' and 'soil conservation' between Framework Programme 1 (1980s) and H2020 (Arias-Navarro et al, 2023). Under H2020, concepts like sustainable intensification and soil health become more recurrent. The study does not mention whether there has been an increase in research on soil microbes. However, a network map representing the main terms found in titles and objectives of projects does mention under climate change: 'soil microbial communities', 'soil microbes' and 'soil functions', and contaminated soil 'soil bioremediation'. There is also a mention of 'arbuscular mycorrhizal fungi'.

An analysis of the CORDIS database for EU-funded projects shows that a small number of ongoing projects focus directly on the microbiome (see **Table 2**). Given their start dates in 2022 and 2023 respectively, it will take some time before results can be expected.

More projects on soil and soil biodiversity are expected to be funded over the coming years. The study of the microbiome has been identified as one of the ten selected pathways of the Food2030 research and innovation latest report (EC 2020). This means that funding is made available for its study under Horizon Europe. In addition, one of the four key strategic orientations of the Horizon

Europe Work Programme (2021-2024)[6] is "restoring Europe's ecosystems and biodiversity and managing sustainably natural resources to ensure food security and a clean and healthy environment" (Cluster 6). Under this orientation, one of the three impact areas includes helping to develop biodiversity-friendly practices in agriculture, likely contributing to research into the microbiome. In addition, Horizon Europe introduced the EU Missions concept to address the most significant global challenges. There are five missions, and one of them, the Soil Mission, focuses on developing 100 living labs and lighthouses to lead the transition towards healthy soils by 2030. Specifically, one of the eight objectives of the soil mission is to improve soil structure to enhance soil biodiversity.

Table 2: EU-funded projects with mention of the microbiome or including soil biodiversity organised by topic

Topic	Projects
Tools and indicators for soil quality and/or soil management in agriculture	SERENA (doesn't directly mention the microbiome), iSQAPER, SIREN, LANDMARK
Modelling and mapping of soil biodiversity	MINOTAUR
Characterisation of the microbiome	MicCropHealth, MIBIREM, TRIBIOME
Agricultural applications of microbes	WISH-ROOTS (focus on wheat and rhizosphere tuning), EXCALIBUR (horticulture)
Microbial functional diversity, resistance and resilience	SoilResist, MicroRescue
Agricultural management and policies	SOILCARE

Search covered concluded and ongoing projects with titles mentioning soil biodiversity, microbes or microbiome. Because of their relevance, we also included those under EJP-Soil.

To conclude, there have been several EC-funded projects looking into soil biodiversity, some of them precisely on the microbiome and the overall impact of

---

[6] https://research-and-innovation.ec.europa.eu/document/download/26755d13-3e91-4e86-a05c-771cd89f1b07_en

agricultural practices on human health, but the funds to address the many remaining gaps are just starting to be mobilised and over the coming five years many new insights, as well as research avenues in relation to the microbiome, and are expected to develop[7]. Some of the topics to be funded under Horizon Europe's Cluster 6 (*Food, Bioeconomy, Natural Resources, Agriculture and Environment*) which specifically mention some form of research into the microbiome of agricultural soils, are:

- Biodiversity-friendly practices in agriculture – breeding for Integrated Pest Management (IPM)
- Valorisation of ecosystem services provided by legume crops
- Interlinkages between biodiversity loss and degradation of ecosystems and the emergence of zoonotic diseases

In addition to the mentioned calls, Horizon Europe is also devoting funding to the study of the gut microbiome, which could, in relation to research into the soil microbiome, expand knowledge and practical applications to the One Health approach.

---

[7] The 2023 call for projects under "A Soil Deal for Europe" closed with almost 130 proposals submitted for a budget of 126 million EUR. Two projects are expected to be funded under the "Discovering the subsoil" call. There are also calls focusing on developing decision-support tools, modelling for soil pollution processes and onsite digital tools to monitor soil and plant stressors.

7. CONCLUSIONS AND RECOMMENDATIONS

The past decades have seen a surge in the interest in the study of the microbiome, in general, and the soil microbiome has not been exempted from this. Agricultural soil management could benefit from increased microbiome knowledge, particularly studies that investigate practical applications to enhance plant and soil health. A review of agricultural practices showed that reduced tillage, crop diversification and replacement of synthetic inputs with organic ones can promote the abundance, diversity, and activity of soil microbes. However, many of these benefits remain context-dependent and research and field implementation are needed to elucidate the links between the soil microbiome, soil functions and plant and soil health.

Understanding the most effective strategies and tailoring these to each context could guide the transition towards a more sustainable and resilient agriculture, inform soil and agricultural policies and help to meet the European Union's Green Deal's objectives, such as reductions in fertiliser and plant protection product use. The target of 25% organic farming on EU agricultural land should promote the application of practices that enhance the soil microbiome and help meet the reduction in chemical pesticide use and risk.

There are several instruments in place to help farmers implement such practices, but knowledge and financial barriers often keep farmers from engaging. Improving advisory services and rewarding farmers during the initial years of the transition towards sustainable soil management practices could increase its uptake. In addition, the living labs set up in the framework of the European Commission's Soil Mission should also contribute to increasing awareness and accelerating the application of these practices.

Box 1: Four main areas for further research identified in this brief:

- Better characterisation of the soil microbiome and development of standardised metrics
- Improving the capacity to map, model and predict the soil microbiome
- Farming practices to enhance the soil microbiome and its benefits
- Elucidating the role of the soil microbiome in the One Health approach

8. REFERENCES

Arias-Navarro, C, Panagos, P, Jones, A, Amaral, M J, Schneegans, A, Van Liedekerke, M, Wojda, P and Montanarella, L (2023) Forty years of soil research funded by the European Commission: Trends and future. A systematic review of research projects. *European Journal of Soil Science* No 74 (5), e13423.

Bajsa, N, Morel, M A, Bra˜na, V and Castro-Sowinski, S (2013) The Effect of Agricultural Practices on Resident Soil Microbial Communities: Focus on Biocontrol and Biofertilization, *Molecular Microbial Ecology of the Rhizosphere*, pp687-700.

Banerjee, S and van der Heijden, M G A (2023) Soil microbiomes and one health. *Nature Reviews Microbiology* No 21 (1), 6-20.

Bardgett, R D and van der Putten, W H (2014) Belowground biodiversity and ecosystem functioning. *Nature* No 515 (7528), 505-511.

Bastida, F, Torres, I F, Moreno, J L, Baldrian, P, Ondoño, S, Ruiz-Navarro, A, Hernández, T, Richnow, H H, Starke, R, García, C and Jehmlich, N (2016) The active microbial diversity drives ecosystem multifunctionality and is physiologically related to carbon availability in Mediterranean semi-arid soils. *Molecular Ecology* No 25 (18), 4660-4673.

Blagodatskaya, E and Kuzyakov, Y (2013) Active microorganisms in soil: Critical review of estimation criteria and approaches. *Soil Biology and Biochemistry* No 67, 192-211.

Blum, W E H, Zechmeister-Boltenstern, S and Keiblinger, K M (2019) *Does Soil Contribute to the Human Gut Microbiome? , Microorganisms*.

Boros-Lajszner, E, Wyszkowska, J, Borowik, A and Kucharski, J (2021) *The Response of the Soil Microbiome to Contamination with Cadmium, Cobalt and Nickel in Soil Sown with Brassica napus, Minerals*.

Brevik, E C, Steffan, J J, Rodrigo-Comino, J, Neubert, D, Burgess, L C and Cerdà, A (2019) Connecting the public with soil to improve human health. *European Journal of Soil Science* No 70 (4), 898-910.

Brockett, B F T, Prescott, C E and Grayston, S J (2012) Soil moisture is the major factor influencing microbial community structure and enzyme activities across seven biogeoclimatic zones in western Canada. *Soil Biology and Biochemistry* No 44 (1), 9-20.

Busson, M (2022) Biocontrol : Definition. Dictionnaire d'agroécologie. No.

Cania, B, Vestergaard, G, Suhadolc, M, Mihelič, R, Krauss, M, Fliessbach, A, Mäder, P, Szumełda, A, Schloter, M and Schulz, S (2020) Site-Specific Conditions Change the Response of Bacterial Producers of Soil Structure-Stabilizing Agents Such as Exopolysaccharides and Lipopolysaccharides to Tillage Intensity. *Frontiers in Microbiology* No 11.

Carini, P, Marsden, P J, Leff, J W, Morgan, E E, Strickland, M S and Fierer, N (2016) Relic DNA is abundant in soil and obscures estimates of soil microbial diversity. *Nature Microbiology* No 2 (3), 16242.

Carrara, J E, Lehotay, S J, Lightfield, A R, Sun, D, Richie Jr, J P, Smith, A H and Heller, W P (2023) Linking soil health to human health: Arbuscular mycorrhizae play a key role in plant uptake of the antioxidant ergothioneine from soils. *PLANTS, PEOPLE, PLANET* No 5 (3), 449-458.

Choi, J, Yang, F, Stepanauskas, R, Cardenas, E, Garoutte, A, Williams, R, Flater, J, Tiedje, J M, Hofmockel, K S, Gelder, B and Howe, A (2017) Strategies to improve reference databases for soil microbiomes. *The ISME Journal* No 11 (4), 829-834.

Crowther, T W, Maynard, D S, Leff, J W, Oldfield, E E, McCulley, R L, Fierer, N and Bradford, M A (2014) Predicting the responsiveness of soil biodiversity to deforestation: a cross-biome study. *Global Change Biology* No 20 (9), 2983-2994.

da Silva, G O A, Southam, G and Gagen, E J (2023) Accelerating soil aggregate formation: a review on microbial processes as the critical step in a post-mining rehabilitation context. *Soil Research* No 61 (3), 209-223.

Degrune, F, Theodorakopoulos, N, Dufrêne, M, Colinet, G, Bodson, B, Hiel, M-P, Taminiau, B, Nezer, C, Daube, G and Vandenbol, M (2016) No favorable effect of reduced tillage on microbial community diversity in a silty loam soil (Belgium). *Agriculture, Ecosystems & Environment* No 224, 12-21.

Delgado-Baquerizo, M, Maestre, F T, Reich, P B, Jeffries, T C, Gaitan, J J, Encinar, D, Berdugo, M, Campbell, C D and Singh, B K (2016) Microbial diversity drives multifunctionality in terrestrial ecosystems. *Nature Communications* No 7 (1), 10541.

Delitte, M, Caulier, S, Bragard, C and Desoignies, N (2021) Plant Microbiota Beyond Farming Practices: A Review. *Frontiers in Sustainable Food Systems* No 5.

Duc, N H, Csintalan, Z and Posta, K (2018) Arbuscular mycorrhizal fungi mitigate negative effects of combined drought and heat stress on tomato plants. *Plant Physiology and Biochemistry* No 132, 297-307.

EC, Directorate-General for, R and Innovation (2020) Food 2030 pathways for action – The microbiome world – A life science opportunity for our society and our planet. Publications Office of the European Union.

El Mujtar, V, Muñoz, N, Prack Mc Cormick, B, Pulleman, M and Tittonell, P (2019) Role and management of soil biodiversity for food security and nutrition; where do we stand? *Global Food Security* No 20, 132-144.

Fierer, N (2017) Embracing the unknown: disentangling the complexities of the soil microbiome. *Nature Reviews Microbiology* No 15 (10), 579-590.

Fierer, N, Wood, S A and Bueno de Mesquita, C P (2021) How microbes can, and cannot, be used to assess soil health. *Soil Biology and Biochemistry* No 153, 108111.

Gao, M, Li, H and Li, M (2022) Effect of No Tillage System on Soil Fungal Community Structure of Cropland in Mollisol: A Case Study. *Frontiers in Microbiology* No 13.

Geisen, S (2021) The Future of (Soil) Microbiome Studies: Current Limitations, Integration, and Perspectives. *mSystems* No 6 (4), 10.1128/msystems.00613-00621.

Geissen, V, Silva, V, Lwanga, E H, Beriot, N, Oostindie, K, Bin, Z, Pyne, E, Busink, S, Zomer, P, Mol, H and Ritsema, C J (2021) Cocktails of pesticide residues in conventional and organic farming systems in Europe – Legacy of the past and turning point for the future. *Environmental Pollution* No 278, 116827.

Guo, J-J, Huang, X-P, Xiang, L, Wang, Y-Z, Li, Y-W, Li, H, Cai, Q-Y, Mo, C-H and Wong, M-H (2020) Source, migration and toxicology of microplastics in soil. *Environment International* No 137, 105263.

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* No 6 (1), 14.

Hartmann, M and Six, J (2023) Soil structure and microbiome functions in agroecosystems. *Nature Reviews Earth & Environment* No 4 (1), 4-18.

Hermans, S M, Lear, G, Case, B S and Buckley, H L (2023) The soil microbiome: An essential, but neglected, component of regenerative agroecosystems. *iScience* No 26 (2), 106028.

Hirt, H (2020) Healthy soils for healthy plants for healthy humans. *EMBO Reports* No 21 (8), e51069.

Hulot, J F and Hiller, N (2021) *Exploring the benefits of biocontrol for sustainable agriculture - A literature review on biocontrol in light of the European Green Deal*. Institute for European Environmental Policy, Brussels.

Islam, W, Noman, A, Naveed, H, Huang, Z and Chen, H Y H (2020) Role of environmental factors in shaping the soil microbiome. *Environmental Science and Pollution Research* No 27 (33), 41225-41247.

Iturralde, E T, Stocco, M C, Faura, A, Mónaco, C I, Cordo, C, Pérez-Giménez, J and Lodeiro, A R (2020) Coinoculation of soybean plants with Bradyrhizobium japonicum and Trichoderma harzianum: Coexistence of both microbes and relief of nitrate inhibition of nodulation. *Biotechnology Reports* No 26, e00461.

Kaminsky, L M, Trexler, R V, Malik, R J, Hockett, K L and Bell, T H (2019) The Inherent Conflicts in Developing Soil Microbial Inoculants. *Trends in Biotechnology* No 37 (2), 140-151.

Kemper, K J and Lal, R (2017) Pay dirt! human health depends on soil health. *Complementary Therapies in Medicine* No 32, A1-A2.

Kendzior, J, Warren Raffa, D and Bogdanski, A (2022) *A review of the impacts of crop production on the soil microbiome*. FAO, Rome.

Khmelevtsova, L E, Sazykin, I S, Azhogina, T N and Sazykina, M A (2022) *Influence of Agricultural Practices on Bacterial Community of Cultivated Soils*, *Agriculture*.

Kibblewhite, M and Ritz, K (2008) Soil health in agricultural systems. *Philosophical Transactions of the Royal Society B: Biological Sciences* No 363, 685-701.

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 Biology and Biochemistry* No 142, 107701.

Li, X, Jousset, A, de Boer, W, Carrión, V J, Zhang, T, Wang, X and Kuramae, E E (2019) Legacy of land use history determines reprogramming of plant physiology by soil microbiome. *The ISME Journal* No 13 (3), 738-751.

Liddicoat, C, Sydnor, H, Cando-Dumancela, C, Dresken, R, Liu, J, Gellie, N J C, Mills, J G, Young, J M, Weyrich, L S, Hutchinson, M R, Weinstein, P and Breed, M F (2020) Naturally-diverse airborne environmental microbial exposures modulate the gut microbiome and may provide anxiolytic benefits in mice. *Science of The Total Environment* No 20 (1879-1026 (Electronic)).

Manzeke-Kangara, M G, Joy, E J M, Lark, R M, Redfern, S, Eilander, A and Broadley, M R (2023) Do agronomic approaches aligned to regenerative agriculture improve the micronutrient concentrations of edible portions of crops? A scoping review of evidence. *Frontiers in Nutrition* No 10.

Mawarda, P C, Le Roux, X, Dirk van Elsas, J and Salles, J F (2020) Deliberate introduction of invisible invaders: A critical appraisal of the impact of microbial inoculants on soil microbial communities. *Soil Biology and Biochemistry* No 148, 107874.

Mills, E L, Kelly, B and O'Neill, L A J (2017) Mitochondria are the powerhouses of immunity. *Nature Immunology* No 18 (5), 488-498.

Mishra, A, Singh, L and Singh, D (2023) Unboxing the black box—one step forward to understand the soil microbiome: A systematic review. *Microbial Ecology* No 85 (2), 669-683.

Neher, D A, Harris, J M, Horner, C E, Scarborough, M J, Badireddy, A R, Faulkner, J W, White, A C, Darby, H M, Farley, J C and Bishop-von Wettberg, E J (2022) Resilient Soils for Resilient Farms: An Integrative Approach to Assess, Promote, and Value Soil Health for Small- and Medium-Size Farms. *Phytobiomes Journal* No 6 (3), 201-206.

O'Callaghan, M, Ballard, R A and Wright, D (2022) Soil microbial inoculants for sustainable agriculture: Limitations and opportunities. *Soil Use and Management* No 38 (3), 1340-1369.

Oliverio, A A-O, Bradford, M A and Fierer, N (2017) Identifying the microbial taxa that consistently respond to soil warming across time and space. *Global Change Biology* No 23 (1365-2486 (Electronic)), 2117-2129.

Parnell, J J, Berka, R, Young, H A, Sturino, J M, Kang, Y, Barnhart, D M and DiLeo, M V (2016) From the Lab to the Farm: An Industrial Perspective of Plant Beneficial Microorganisms. *Frontiers in Plant Science* No 7.

Prajapati, S, Kumar, N, Kumar, S, Scholar, Lakhran, L and Maurya, S (2020) Biological control a sustainable approach for plant diseases management: A review. No 9, 1514-1523.

Ramirez, K S, Leff, J W, Barberán, A, Bates, S T, Betley, J, Crowther, T W, Kelly, E F, Oldfield, E E, Shaw, E A, Steenbock, C, Bradford, M A, Wall, D H and Fierer, N (2014) Biogeographic patterns in below-ground diversity in New York City's Central Park are similar to those observed globally. LID - 10.1098/rspb.2014.1988 [doi] LID - 20141988. *Proc. R. Soc. B Biol. Sci* No 281 (1471-2954 (Electronic)).

Rodríguez-Eugenio, N, McLaughlin, M and Pennock, D (2018) *Soil pollution: a hidden reality*. FAOpp.

Rousk, J, Bååth, E, Brookes, P C, Lauber, C L, Lozupone, C, Caporaso, J G, Knight, R and Fierer, N (2010) Soil bacterial and fungal communities across a pH gradient in an arable soil. *The ISME Journal* No 4 (10), 1340-1351.

Sengupta, A and Dick, W A (2015) Bacterial Community Diversity in Soil Under two Tillage Practices as Determined by Pyrosequencing. *Microbial Ecology* No 70 (3), 853-859.

Sergaki, C, Lagunas, B, Lidbury, I, Gifford, M L and Schäfer, P (2018) Challenges and Approaches in Microbiome Research: From Fundamental to Applied. *Frontiers in Plant Science* No 9.

Singh, B K, Yan, Z-Z, Whittaker, M, Vargas, R and Abdelfattah, A (2023) Soil microbiomes must be explicitly included in One Health policy. *Nature Microbiology* No 8 (8), 1367-1372.

Smith, S E and Read, D (2008) *Mycorrhizal Symbiosis*. ElSevier Academic Presspp.

Tedersoo, L, Bahram, M and Zobel, M (2020) How mycorrhizal associations drive plant population and community biology. *Science* No 367 (6480), eaba1223.

Tilman, D, Cassman, K G, Matson, P A, Naylor, R and Polasky, S (2002) Agricultural sustainability and intensive production practices. *Nature* No 418 (6898), 671-677.

Trabelsi, D and Mhamdi, R (2013) Microbial inoculants and their impact on soil microbial communities: a review. No (2314-6141 (Electronic)).

Turbé, A, de Toni, A, Benito, P, Lavelle, P, Lavelle, P, Ruiz Camacho, N, van Der Putten, W H, Labouze, E and Mudgal, S (2010) *Soil biodiversity: functions, threats and tools for policy makers*.   unpublished work.

van Leeuwen, J P, Djukic, I, Bloem, J, Lehtinen, T, Hemerik, L, de Ruiter, P C and Lair, G J (2017) Effects of land use on soil microbial biomass, activity and community structure at different soil depths in the Danube floodplain. *European Journal of Soil Biology* No 79, 14-20.

Wagg, C, Bender, S F, Widmer, F and van der Heijden, M G A (2014) Soil biodiversity and soil community composition determine ecosystem multifunctionality. *Proceedings of the National Academy of Sciences* No 111 (14), 5266-5270.

Walder, F, Schmid, M W, Riedo, J, Valzano-Held, A Y, Banerjee, S, Büchi, L, Bucheli, T D and van der Heijden, M G A (2022) Soil microbiome signatures are associated with pesticide residues in arable landscapes. *Soil Biology and Biochemistry* No 174, 108830.

Wall, D H, Nielsen, U N and Six, J (2015) Soil biodiversity and human health. *Nature* No (1476-4687 (Electronic)).

Wei, Z and Jousset, A (2017) Plant Breeding Goes Microbial. *Trends in Plant Science* No 22 (7), 555-558.

Wilhelm, R C, Amsili, J P, Kurtz, K S M, van Es, H M and Buckley, D H (2023) Ecological insights into soil health according to the genomic traits and environment-wide associations of bacteria in agricultural soils. *ISME Communications* No 3 (1), 1.

Woo, S L and Pepe, O (2018) Microbial Consortia: Promising Probiotics as Plant Biostimulants for Sustainable Agriculture. *Frontiers in Plant Science* No 9.

Xun, W, Yan, R, Ren, Y, Jin, D, Xiong, W, Zhang, G, Cui, Z, Xin, X and Zhang, R (2018) Grazing-induced microbiome alterations drive soil organic carbon turnover and productivity in meadow steppe. *Microbiome* No 6, 170.

Yang, X, Hu, H-W, Yang, G-W, Cui, Z-L and Chen, Y-L (2023) Crop rotational diversity enhances soil microbiome network complexity and multifunctionality. *Geoderma* No 436, 116562.

Young, I M and Ritz, K (2000) Tillage, habitat space and function of soil microbes. *Soil and Tillage Research* No 53 (3), 201-213.

Zheng, Q, Hu, Y, Zhang, S, Noll, L, Böckle, T, Dietrich, M, Herbold, C W, Eichorst, S A, Woebken, D, Richter, A and Wanek, W (2019) Soil multifunctionality is affected by the soil environment and by microbial community composition and diversity. *Soil Biology and Biochemistry* No 136, 107521.

Zuber, S M and Villamil, M B (2016) Meta-analysis approach to assess effect of tillage on microbial biomass and enzyme activities. *Soil Biology and Biochemistry* No 97, 176-187.

European
Sustainable
Agriculture
Dialogue