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Unlocking the Secrets of Soil: Exploring the Microbiome and Its Applications—Part 1

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The term “microbiome” refers to a collective assembly of microorganisms within a specific environment, including fungi, bacteria, and viruses, influencing dynamic functions within the system. Microbes play a pivotal role in the production of various food items, wines, and medicinal compounds. Their significance in agriculture and ecology is monumental, which will be explored in this two-part article. In this first part, we’ll cover microbiome components and applications, the rhizosphere and microbiome interaction, and environmental factors determining the soil-microbe-plant interactions.

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Microbes, the tiny microorganisms ubiquitous in our bodies, food, and environment, wield significant influence over human existence. Throughout human history, we have faced deadly epidemics, such as the bubonic plague in 1500s, which wiped out one-third of the European population (Glatter & Finkelman, 2021); the Irish potato famine, which caused the death of one million in the Irish population (Kinealy, 1995); the Spanish flu, which resulted in around 50 million deaths in 1918–1920 (CDC, 2019); and the most recent COVID-19 pandemic, which rapidly engulfed the entire world and caused the death of seven million people (WHO, 2024). These epidemics, driven by viruses, bacteria, or fungi, directly assail human health or indirectly disrupt vital ecosystems supporting life.

Paradoxically, amidst their potential for devastation, microbes also confer invaluable benefits upon us. The presence of microbes in the human gut helps in food digestion, supplies essential metabolites, and bolsters immunity while contributing to the functioning of the brain and whole body systems. Moreover, microbes play a pivotal role in the production of various food items, wines, and medicinal compounds. Their significance in agriculture and ecology is monumental, a topic we shall explore in depth in this two-part article. Let us commence by delving into the concept of the microbiome and its constituent elements.

The term “microbiome” refers to a collective assembly of microorganisms within a specific environment, including fungi,

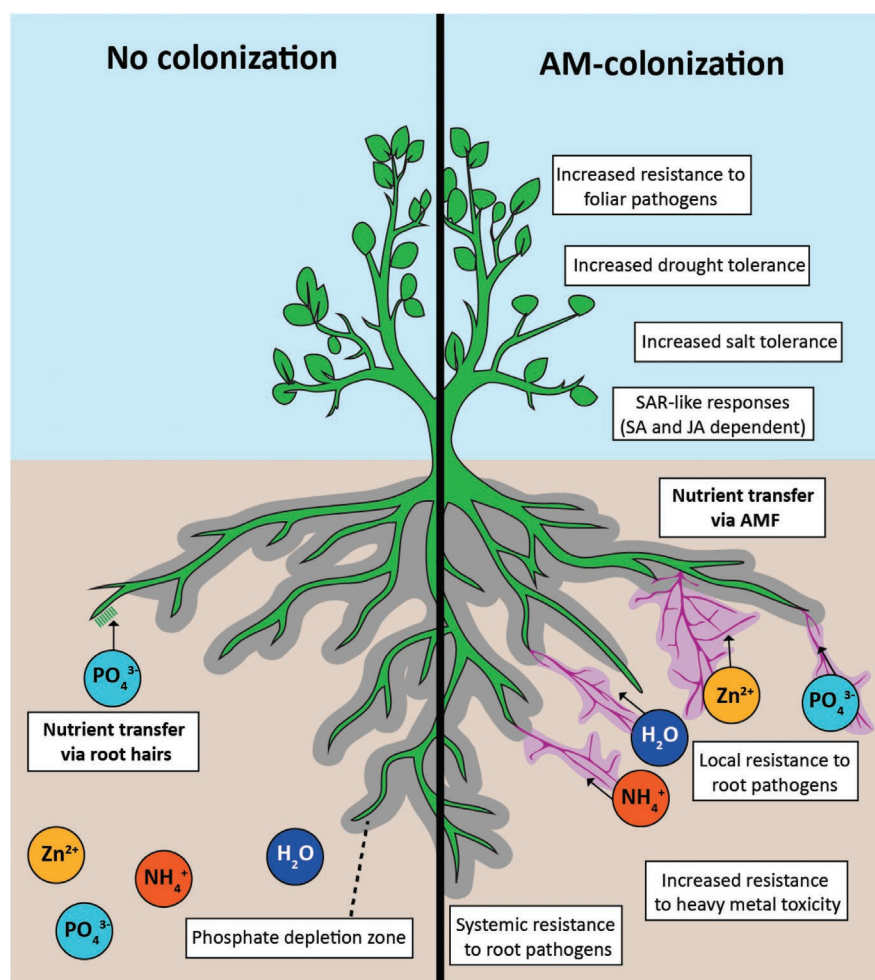
bacteria, and viruses, influencing dynamic functions within the system. This community shows distinct physicochemical properties, establishing specific ecological niches and forming an interactive and dynamic relationship prone to changes in both time and scale. Microbiomes are categorized based on diverse environments and host organisms, such as human microbiomes, gut microbiomes, soil microbiomes, and root microbiomes. The composition and diversity of microbiomes vary across different systems and environments. For example, the soil microbiome comprises bacteria, fungi, archaea, viruses, small protists, and algae while the human microbiome is predominantly composed of bacteria and fungi with its diversity amounting to only 10% of that found in the soil microbiome (Blum et al., 2019). Furthermore, microbiomes can be commensal, symbiotic, or parasitic, depending on their interactions with the host or other environments.

A gram of soil harbors an impressive 100 million to a billion microorganisms, indicating its richness (Raynaud & Nunan, 2014). The rhizosphere, the region around plant roots, hosts millions and billions of coexisting microbes, including endophytes, mycorrhizae, nitrogen-fixing and phosphorus-solubilizing organisms, and saprophytes. These rhizospheric microbes dynamically orchestrate crucial soil processes, including nutrient cycling, soil aggregation, crop nutrient uptake, and plant defense against disease. Furthermore, soil microbes serve a pivotal role in decomposing organic matter,

facilitating the release of carbon and nitrogen while harnessing carbon sources from plants via root and mycorrhizal networks.

Microbiome: Components and Applications

In an agroecological context, the microbiome is crucial in fostering plant growth, boosting crop yield, and ameliorating stress resilience. The symbiotic association between microorganisms and plants is pivotal for sustaining agricultural systems. Higher diversity in microbial communities contribute significantly to combatting plant diseases and enhancing crop productivity. Rhizosphere microbes play a vital role in bolstering disease resistance by repelling or outcompeting plant pathogens, forming physical barriers, enhancing nutrient availability, and diminishing resources accessible to pathogens (Li et al., 2021). Additionally, plants release organic compounds through roots, also known as root exudates, which attract and shape microbial dynamics. Approximately 3–30% of the carbon produced from photosynthesis is released as root exudates, thereby regulating microbial activities and influencing plant–microbe interactions (Huang & Osbourn, 2019; Panchal, 2022). Soil microbes, particularly in rhizosphere zones, encompass both saprophytes and symbionts. Saprophytes, including *Bacillus*, *Fusarium*, *Penicillium*, *Trichoderma*, and *Mortierella*, thrive by decomposing dead organic matter, thereby enriching carbon and essential nutrients vital to plant nutrition. Symbionts, which include



Arbuscular mycorrhizal fungi (AMF) are adept at absorbing phosphate, zinc, nitrate, water, and various other nutrients. This illustration, originally published in Jacott et al. (2017) in the journal *Agronomy*, shows how the AMF hyphal network extends beyond the depletion zone (grey), accessing a greater area of soil for nutrient and water uptake. Benefits from colonization include tolerances to many abiotic and biotic stresses through induction of systemic acquired resistance (SAR). Illustration reprinted under this license: <https://creativecommons.org/licenses/by-sa/4.0/deed.en>.

nitrogen-fixing bacteria, endophytic and epiphytic fungi, and mycorrhizal fungi, form symbiotic relationships with plants, facilitating nutrient acquisition and promoting plant growth (Cahanovitic et al., 2022). All the microbes present in soil are known as soil microbiota.

Let us look at soil microbiota in detail.

Endophytes are endosymbiotic microorganisms that inhabit various plant organs and tissues, serving as significant sources of secondary metabolites, growth-promoting

regulators, and mediators of plant defense signaling. Their presence significantly bolsters plant immunity. They complete their life cycles within plant tissues and provide defense against various pathogens. Notable examples include species like *Neotyphodium* and *Piriformospora*, which confer resistance against *Fusarium*- and *Sclerotinia*-related diseases, respectively. Similarly, *Phomopsis liquidambaris* elicits resistance against *Fusarium oxysporum* in peanuts (Zhang et al., 2020). Other common endophytes

are *Actobacter*, *Proteobacter*, *Enterobacter*, etc.

Mycorrhizae are symbiotic fungi that reside within plant roots and require a host to survive and thrive. They obtain their carbon source from host plants and acquire nutrients from the soil, facilitating the indirect absorption of nutrients and water from distant soil regions to the plant roots. There are two types of mycorrhizae: ectomycorrhizae and endomycorrhizae. Ectomycorrhizae, belonging to the Basidiomycetes class, colonize the outer surface of roots, penetrating only the cortex. They are proficient in absorbing phosphate, ammonium, and zinc sources, and their symbiotic relationships are limited to certain plant species. In contrast, endomycorrhizae, also known as arbuscular mycorrhizal fungi, invade plant roots entirely, penetrating cortical cells and establishing hyphal mycelium networks both internally and externally. These fungi, classified as phycomycetes, are adept at absorbing phosphate, zinc, nitrate, water, and various other nutrients.

Mycorrhizae also play a multifaceted role in plant defense against soil-borne pathogens while simultaneously facilitating nutrient and water uptake. They also assist plants during different harsh environmental conditions such as drought, salinity, high temperatures, or heavy metal contamination by providing nutrients and water to stressed roots from distant zones where plant roots can't reach. They are present in a wide range of plants, from agronomic crops to different grasses, shrubs, and trees. Many agronomic crops like Solanacea, Fabaceae, and Allium crops receive

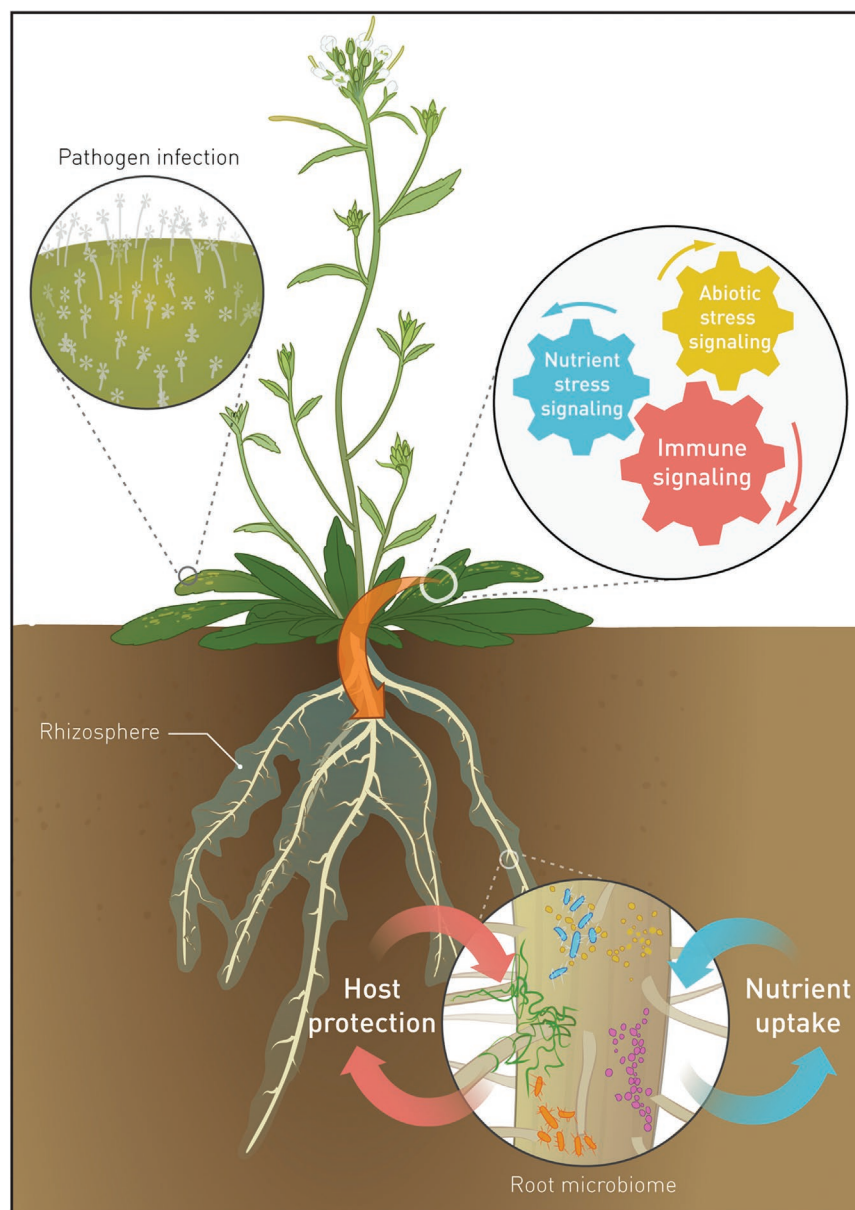
42–95% of their phosphorus needs from mycorrhizae. Variability in phosphorus acquisition among different genotypes is attributed to variations in mycorrhizal colonization levels (Elbon & Whalen, 2015). Mycorrhizae can provide up to 71% of ammonium resources to a maize crop (Tanaka & Yano, 2005).

Some of the free-living bacteria and fungi like *Pseudomonas*, *Bacillus*, *Arthobacter*, *Acinetobacter*, *Laeclercia*, and fungi like *Penicillium*, *Aspergillus* and *Trichoderma* are also considered as beneficial microbes as they can fix nitrogen and solubilize many chelated minerals into accessible forms. These microbes serve as catalysts for nutrient recycling and play an indispensable role in soil decompositions, aggregations, and nutrient provision. Their concerted efforts can lead to a potential yield increase of up to 70%.

Overall, microbial-mediated decomposition plays a crucial role in balancing the carbon and nitrogen equilibrium in the soil, thereby contributing to soil carbon storage. Approximately 80% of the 2500 gigatonnes of carbon stored in soil is directly regulated by soil microbes, underscoring their paramount importance in the global carbon pool (Gougoulas et al., 2014). Furthermore, soil microbes actively contribute to soil formation by enhancing soil aggregation, a process critical for enhancing soil fertility, porosity, water-holding capacity, and promoting seed germination and crop yield.

Rhizosphere and Microbiome Interaction

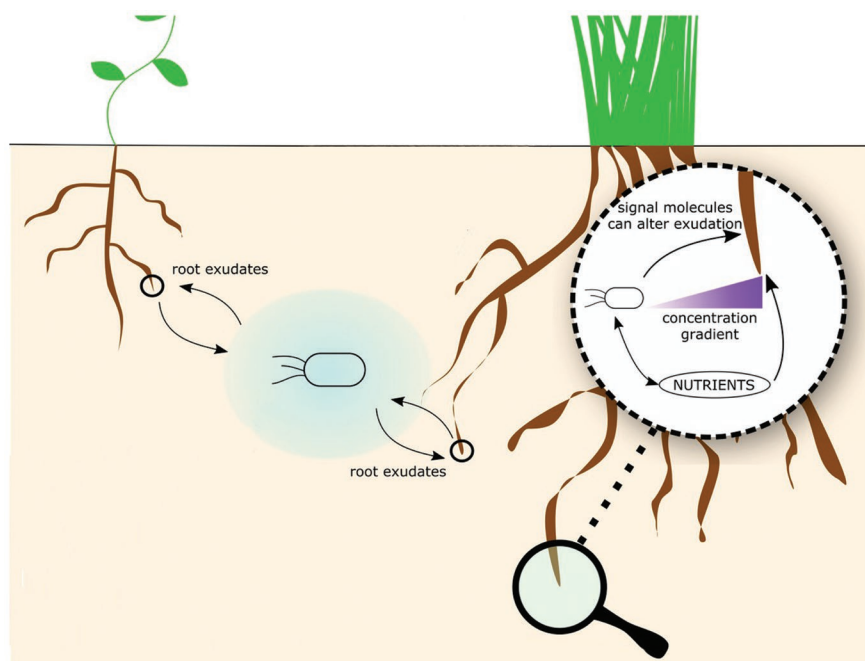
Plants, particularly their roots, forge intricate connections with



Rhizosphere microbes play a vital role in bolstering disease resistance by repelling or out-competing plant pathogens, forming physical barriers, enhancing nutrient availability, and diminishing resources accessible to pathogens. Illustration reprinted with permission from “The Soil-Borne Legacy,” by Bakker et al. (2018), originally published in the journal *Cell* (<https://doi.org/10.1016/j.cell.2018.02.024>).

microbes through the interface between the soil and roots known as rhizosphere. Rhizosphere is rich in root exudates, thereby holding higher diversity and composition of microbial communities, which thrive on carbon and metabolites released from exudates. Root exudates, comprising terpenes, flavonoids, phytohormones, amino acids, lignin, and proteins, serve as

crucial components of microbe–plant interactions. For example, terpenes, essential secondary metabolites, attract beneficial microbes such as mycorrhiza and rhizobacteria, and flavonoids released from roots act as a precursor for establishing symbiotic relationships between plants and rhizobacteria (Kumar et al., 2023). Simultaneously, the presence of microbes in the rhizosphere can



Root exudates serve as crucial components of microbe–plant interactions. While plants can regulate root exudation, soil microbes can enhance exudation rates and release molecules that affect root exudation patterns. This illustration is an adaptation from a figure originally published in the article “Root Exudation of Primary Metabolites: Mechanisms and Their Roles in Plant Responses to Environmental Stimuli,” by Canarini et al. in the journal *Frontiers*. It is published and adapted under this license: <https://creativecommons.org/licenses/by/4.0/>.

pose challenges to plant defense mechanisms. In response, plants release phytohormones, including salicylic acid, ethylene, jasmonic acid, auxin, and abscisic acid, to coordinate diverse defense mechanisms essential for safeguarding plant health and immunity against microbial presence.

Moreover, microbes possess a remarkable ability to synthesize plant hormones, including ethylene, auxins, cytokinin, abscisic acid, and gibberellins, along with their precursors, thereby influencing plant growth and hormonal signaling. The interplay among plant immunity, the release of different secondary metabolites and root exudates, and extracellular compounds by microbes, profoundly shapes microbial associations, compositions, and diversity. Additionally, microbes produce quorum-sensing compounds, including extracellular signaling

molecules like acyl homoserine lactone, oligopeptides, and gamma butyrolactones, which are essential for microbial interspecies communication (Chagas et al., 2018). Certain rhizobium bacteria secrete extracellular substances like effector proteins and exopolysaccharides to facilitate interactions between microbes and their environment as well as between different microbial species (Costa et al., 2021). Microbial biofilm is another significant component of the microbiome, providing protection and support for microbial survival and activity in diverse environmental conditions.

Thus, the rhizosphere region, as a hotspot with an abundance of root exudates, can attract varied microbes, subsequently improving the soil microbial communities and diversities. The composition of root exudates plays an important role in shaping rhizosphere microbial

communities through selective enrichment of microbes capable of utilizing exuded compounds. The types and quantities of organic molecules exuded, along with microbial metabolic versatility, determine whether epiphytic, endophytic, or free-living rhizosphere communities develop upon plant contact. Rhizosphere metabolites modulate relationships between plants and associated microbes that span pathogenic, neutral, and mutualistic. These complex and variable plant–microbe associations largely determine host plant survival and productivity. However, plant microbiome diversity and assembly rules remain poorly understood. Elucidating modulatory strategies plants utilize to optimize beneficial associations requires deeper characterization of rhizosphere community assembly principles and species interactions. This knowledge promises to enable management leveraging endogenous microbiomes for enhanced plant growth and stress resilience in agricultural systems.

Environmental Factors Determining the Soil–Microbe–Plants Interactions

Understanding the intricate interplays among soil, microbes, and plants is fundamental to ecosystem dynamics and sustainability. These interactions are heavily influenced by a myriad of environmental factors. These factors encompass a broad range of physical, chemical, biological, and climate variables that collectively share the structure and functions of soil microbial communities and their interactions

with plants. Understanding these factors is essential in elucidating the complex microbial ecology and remodeling them for agriculture and ecological advances. We will explore some of the major environmental factors that shape the soil–plant microbe interactions.

Soil Characteristics

Soil characteristics such as soil texture, structure, pH, temperature, moisture content, and nutrient availability shape the distribution and diversity of microbial communities and their activities (Girvan et al., 2003). These factors influence the microbial-mediated formation of soil aggregates in the feedback loop (Tisdall, 2020). For example, a study reported that soil moisture content exerts a higher impact on the structure of the microbial community and their metabolism and nutrient cycling ability (Singh et al., 2009). Soil pH not only directly influences nutrient availability but also serves as a crucial limiting factor for microbial soil communities (Zhalnina et al., 2015). For instance, soil pH highly determines the availability of phosphorus in soil, which in turn affects the growth of arbuscular mycorrhizal fungi and their metabolic activities. Further, soil pH influences the microbial community compositions with certain microbial species thriving in acidic soils while others prefer alkaline conditions. The abundance of mycorrhiza is directly related to crop health and productivity. Increasing atmospheric temperature can also heat up the soil; this modifies the structure of the rhizosphere microbiome and impacts the microbial activity, especially the conversion of organic



Soil microbes actively contribute to soil formation by enhancing soil aggregation, a process critical for enhancing soil fertility, porosity, water-holding capacity, and promoting seed germination and crop yield. Photo by Antonio Jordán (distributed via [imaggeo.edu.eu](https://www.imaggeo.eu)) and reprinted under this license: <https://creativecommons.org/licenses/by-sa/3.0/>.

matter to inorganic nutrients (Santoy et al., 2017).

Climate and Weather

Several studies have reported that elevated carbon dioxide reduces the microbial diversity and nitrogen fixation (Yang et al., 2019) while another study reported that elevated carbon dioxide can increase the mycorrhizal abundance and activity (Dhillon et al., 1995). Precipitation regimes also affect the soil microbial growth and metabolic activity, thus affecting diversity and composition, and altering the organic matter decomposition and nutrient recycling (Likar et al., 2013). Extreme events like droughts, floods, and heat waves can disrupt the soil microbial community and alter the plant microbial association, affecting plant productivity and ecosystem functioning. Overall, climate change exerts a significant impact in plant microbial interactions.

Land Use and Management Practices

Intensive agricultural practices, including excessive use of fertilizers and pesticides, monocropping, and

deep tillage greatly disturb soil microbial activity, composition, and diversity. Several studies have shown that monocultures reduce soil microbial diversity and increase host-specific pathogens, deep tillage alters the microbial composition by altering soil microclimate, high nitrogen deposition leads to soil acidification and reduced soil microbial biomass, and pesticides create a toxic environment for the beneficial microbes, thus impacting the overall soil microbial activity and compositions (Yang et al., 2021).

Plant Species and Diversity

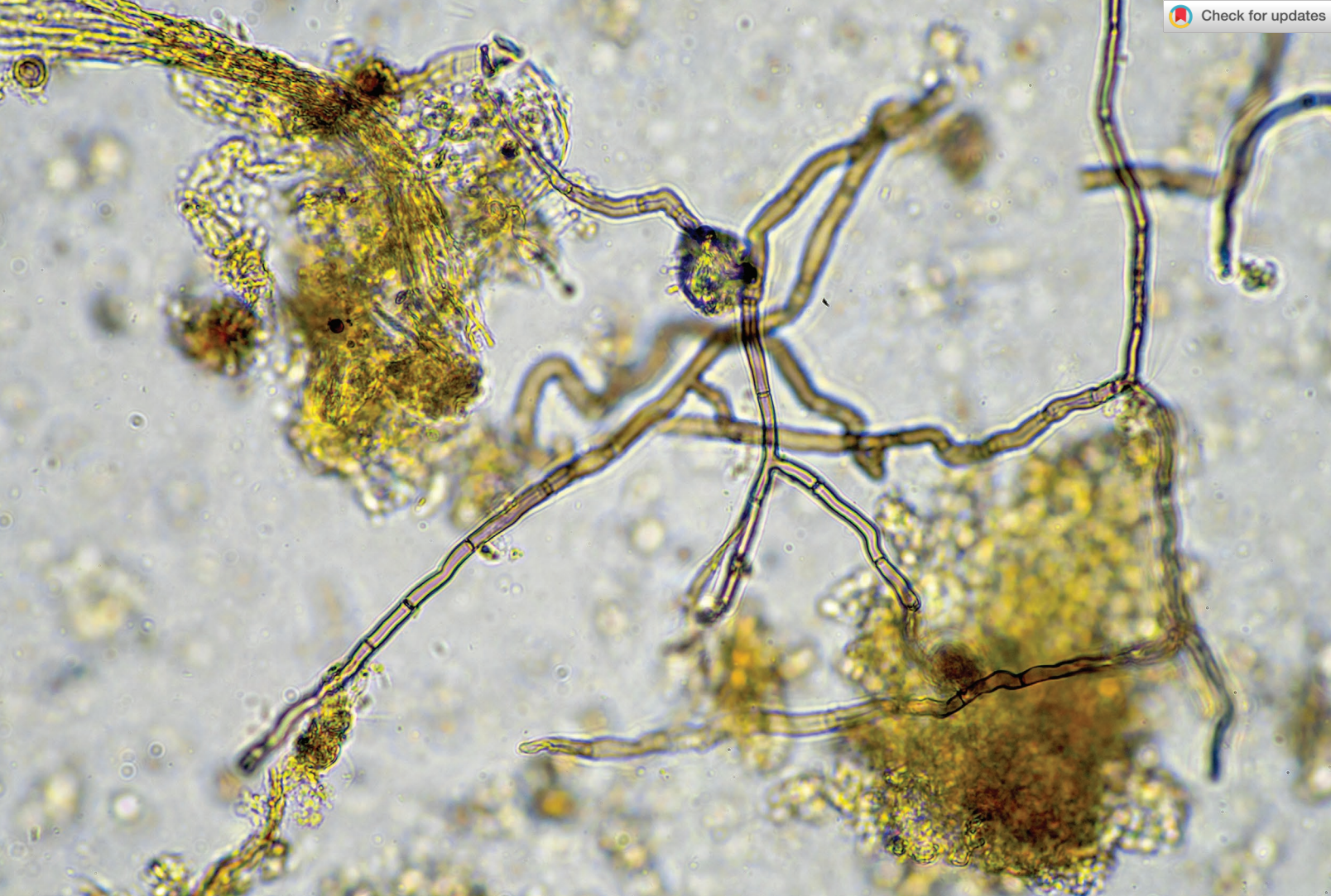
Plant species and diversity exert profound influence on soil microbial communities and their interactions with plants. Different plant species have different levels of root exudates and their compositions, thus shaping the microbial community structure and functions in the rhizosphere. High plant diversity increases rhizosphere carbon inputs into the microbial community, which results in increasing microbial activity, microbial biomass, microbial respiration and carbon storage (Lange et al., 2015; Chen et al., 2019).

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Recent studies in adopting cover crops in agricultural practices have shown significant improvement in soil microbial diversity and functional groups, thus enhancing plant–microbe interaction and plant productivity (Vukicevich et al., 2016; Finney et al., 2017).

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Microscopic view of a soil sample teeming with life. Photo courtesy of Adobe Stock/Phoebe.

Unlocking the Secrets of Soil: Exploring the Microbiome and Its Applications—Part 2

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Several studies have reported that plants can increase their tolerance towards environmental stress like drought, heat, salinity, and other abiotic and biotic stresses by changing the microbiome at the rhizosphere level. Photo courtesy of Adobe Stock/batuhan toker.

Microbiome for Plant Adaptation: A Heritable Trait

Phenotypic plasticity, a crucial trait enabling plants to adapt to diverse environments, involves the modification of their traits, which enhances the plant fitness to the environment. This has led to the evolution of many factors that contribute to phenotypic plasticity, including the alteration in the microbiome of the rhizosphere through root exudates. Several studies have reported that plants can increase their tolerance towards environmental stress like drought, heat, salinity, and other abiotic and biotic stresses by changing the microbiome at the rhizosphere level (Pascale et al., 2020; Zhang et al., 2019; Castrillo et al., 2017).

By modulating the composition and diversity of the microbiome, plants can improve the uptake of nutrients and water and harbor high mycorrhizal activity; thus, capturing the resources from distant levels, which can help with survival of different environmental stresses.

Microbes are also considered the second crop genome, regulating crop dynamics and functioning. Advancements in whole-genome sequencing and modern genomic technologies have provided insights into beneficial plant-microbe interactions in soil, offering potential crop improvement strategies.

It has been reported that plants influence the rhizosphere microbiome, showing unique microbial composition and diversity. For example, drought-tolerant crops harbor Actinobacteria, which helps combat plant drought stress (Naylor et al., 2017). Genome-wide association studies in *Arabidopsis* and other plants have revealed the strong association between host and microbial genome, revealing the heritable interactions that can be a target for future crop breeding and improvement programs. Similarly, investigations into the gut microbiomes of swine, baboons, and humans revealed high heritability of microbiomes (Grieneisen et al., 2021; Bergamaschi et al., 2020). Deng et al (2021) have reported that plant loci control rhizosphere microbiome and

cause genotype-specific microbiome composition. This has led to the development of microbiome heritability concepts.

Microbiome heritability has been defined as a deterministic component of community assembly caused by the host genetics, which can be either deterministic or stochastic over span of time and space (Wagner, 2021). The size of the microbial community has been identified as a crucial determinant of influencing whether the host phenotypes exhibit deterministic or stochastic effects, thereby significantly impacting microbiome heritability (Bisschop et al., 2022; Gao et al., 2020). Similarly, the barley domestication has harbored the microbiota positively by developing resistance against pathogens and increased nutrient and water uptake over the course of time (Bulgarelli et al., 2015). Thus, study of plant-microbe interactions and evaluating microbiome heritability will have a huge positive impact on crop productivity and soil health.

Microbiomes Drive Biogeochemical Processes in Soil Across Scales

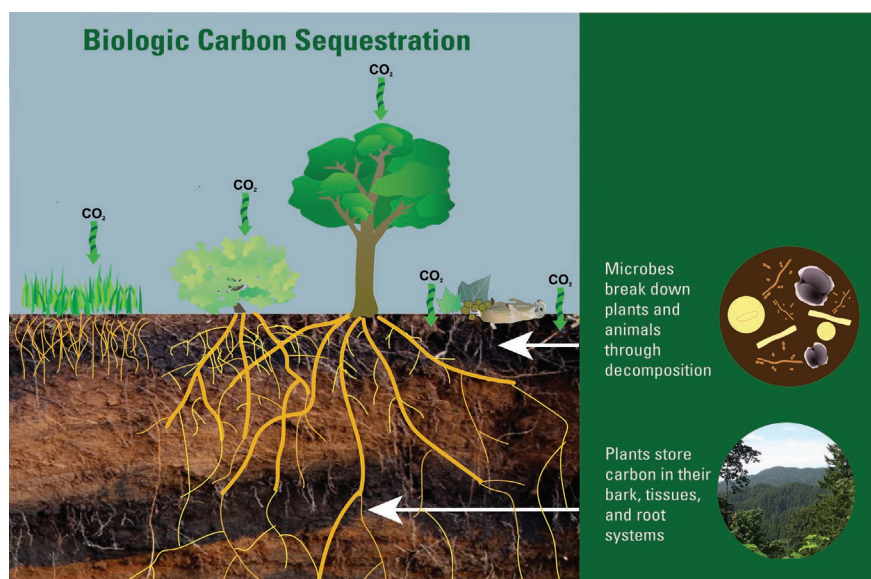
The soil biogeochemical cycling, particularly processes that mineralize nutrients bound up in carbonaceous biomass such as soil organic matter, is critical to the functioning of productive ecosystems. Microbes play a crucial role in driving these processes in the soil. Recent advancements in molecular tools and methodologies have provided deeper insights into how specific groups of microbes regulate these functions, shedding light on their activities

and abundance. Understanding the ecology of these crucial microbes is critical to establish connections among microbial communities, their activities, and mechanisms governing soil biogeochemical cycling. This comprehension is vital not only for elucidating nutrient-cycling dynamics but also for assessing the impact of human activities, such as soil, water, and air pollution, on the soil's capacity to store and sequester atmospheric carbon.

Elucidating the nutrient-cycling dynamics and ecosystem function requires examining how nutrient inputs shape soil microbial community composition and metabolic capacities. Let's delve into some of the major microbially mediated biogeochemical processes such as carbon and nitrogen cycling, which are essential for maintaining soil fertility and enhancing ecosystem productivity.

Decomposition of Organic Matter (Carbon Cycling and Sequestration)

Microbes decompose organic matter in the soil through the hydrolysis of macromolecules into lower-molecular-weight compounds that can be assimilated to support microbial metabolism. These processes are catalyzed by microbial enzymes, which are affected by microbial activity, composition, nutrient availability, substrate quality, etc. Elucidating carbon cycling principles and mechanisms governing rhizosphere microbiome assembly promises to inform integrated soil management, leveraging plant-microbe interactions to enhance agricultural productivity and sustainability. Furthermore, soil carbon sequestration is notably more



Estimates, such as those presented by Kell (2012), suggest that a 10% increase in CO₂ sequestration in soil could potentially remove up to 20% of CO₂ from the atmosphere, which shows the huge potential of microbial-mediated carbon sequestration for mitigating climate change and global warming. Illustration adapted from a USGS infographic.

reliable and stable in undisturbed environments such as grasslands and forests where root exudates serve as a resource for microbial growth and thus facilitate long-term sequestration by transitioning of carbon from labile to stable and recalcitrant pools (Panchal et al., 2022).

Increased sequestration is crucial for capturing elevated atmospheric CO₂ levels and mitigating global warming. The issue of greenhouse gas emissions has become a major global concern, underscored by initiatives highlighted at events like the United Nations climate change conferences. Estimates, such as those presented by Kell (2012), suggest that a 10% increase in CO₂ sequestration in soil could potentially remove up to 20% of CO₂ from the atmosphere, which shows the huge potential of microbial-mediated carbon sequestration for mitigating climate change and global warming.

Biological Nitrogen Fixation (Nitrogen Cycling)

Biological nitrogen fixation is a vital process that converts atmospheric

nitrogen gas into readily available nitrogen for plant uptake and growth, facilitated by the nitrogenase enzyme system produced by certain soil microbes. Symbiotic nitrogen fixation typically occurs between rhizobia bacteria and legumes while free-living nitrogen fixers like *Azotobacter*, *Clostridium*, and *Pseudomonas* independently fix nitrogen. *Pseudomonas* and symbiotic *Rhizobium* can synergistically enhance nodule formation and nitrogen fixation capacities under some conditions. Further research into microbiome assembly principles and microbial interactions governing nitrogen transformations promises to improve integrated soil management practices that optimize biological nitrogen fixation.

Phosphorus Solubilization (Phosphorus Cycling)

Understanding microbial involvement in rhizosphere phosphorus dynamics require a detailed examination of phosphorus solubilization and its modulation by microbial activities. Various bacteria

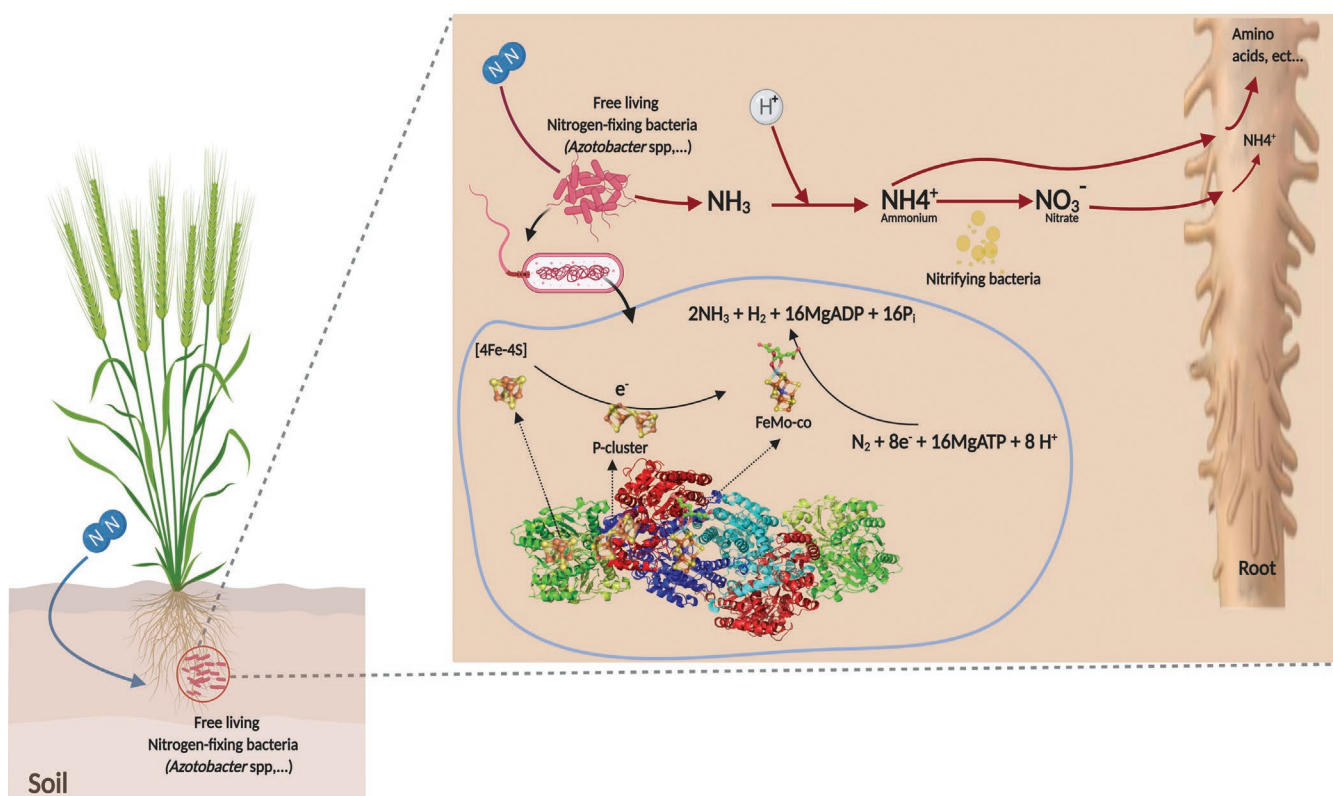


Illustration shows the mechanism of non-symbiotic fixation of atmospheric nitrogen by *Azotobacter* sp. It is reprinted under this license <https://creativecommons.org/licenses/by/4.0/> from the article in the journal *Frontiers* by Aasfar et al. (2021), “Nitrogen Fixing *Azotobacter* Species as Potential Soil Biological Enhancers for Crop Nutrition and Yield Stability.”

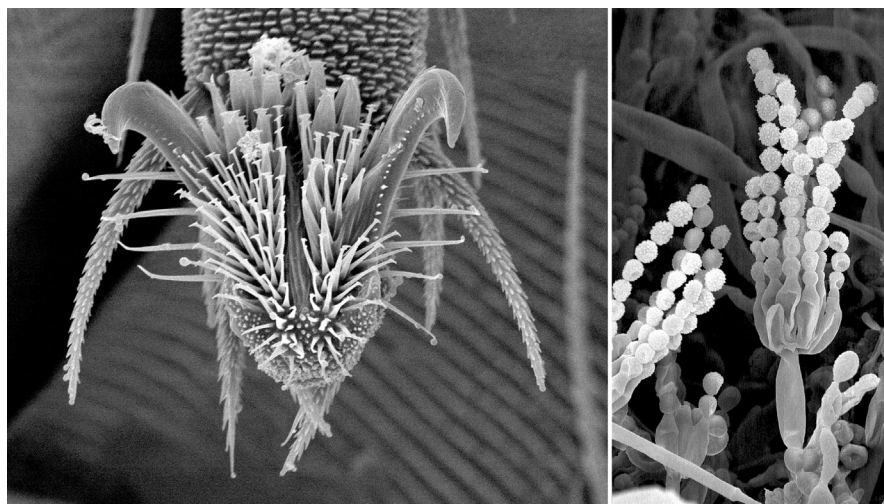
including actinomycetes, filamentous fungi, and yeasts possess the ability to solubilize both mineral and organic phosphorus forms. However, the same microbes solubilizing phosphorus, or different species, may subsequently immobilize the released phosphorus, limiting plant availability. Mycorrhizal associations are believed to play a crucial role in capturing solubilized phosphorus from the soil solution and storing polyphosphate in fungal structures in soil and roots. This underpins phosphorus–carbon exchange between fungal and plant partners. A holistic understanding of microbial phosphorus solubilization, immobilization, and facilitation of plant phosphorus uptake is needed to manage rhizosphere communities optimizing plant phosphorus acquisition.

Plant–Soil–Microbe Interactions: Mathematical Modeling Approaches

Plant–soil–microbe interactions are fundamental in shaping the rhizosphere and terrestrial ecosystems, encompassing agricultural land, forests, and grasslands, with significant implications for carbon sequestration and food production. These interactions form dynamic networks that can be mutualistic, symbiotic, or antagonistic, influencing nutrient cycling, microbial diversity and activity, soil health, and plant productivity. As global climate change accelerates, ecosystems are rapidly evolving, leading to increased carbon emissions and impacting overall ecology and agriculture. Understanding these components, their interactions,

and modeling their future consequences is vital for agricultural and conservation efforts aimed at boosting carbon sequestration and reducing emissions. Modeling these interactions offers a mechanistic understanding of their functioning and helps identify the driving factors.

Plants release exudates containing sugars, amino acids, and other metabolites, serving as energy sources for soil microbiomes. In return, microbes facilitate organic matter decomposition, provide nutrients to plants, fix atmospheric nitrogen, solubilize different nutrients, and enhance soil structure and aggregation. These activities are influenced by the dynamics of each component and the environment, creating a feedback loop where plants and soil influence microbial communities, shaping overall



A gram of soil harbors an impressive 100 million to a billion microorganisms like the purple snout mite on the left and the soil fungus on the right. Photos courtesy of USDA-ARS, Electron & Confocal Microscopy Unit, Beltsville, MD.

ecosystem dynamics. Let's see the different approaches of modeling plant–soil–microbe interactions.

We will start with a brief explanation of microbe–microbe interaction.

Advancements in DNA sequencing have revolutionized our understanding of microbe–microbe and plant–microbe interactions. Microbe–microbe interactions can be cooperative, competitive, or neutral based on the resource and environmental stimuli. Assembly theory is regarded as the primary theory for modulation of a microbiome at the community level, which is highly influenced by environmental conditions, resource availability, and interactions with other microbial species (Bai et al., 2022). Microbe–microbe interactions can be studied in general through kinetic, stochastic, and network-based models. Kinetic models, which are dynamic and deterministic, predict microbial growth, diversity, and activity using differential equations. Stochastic models describe microbial activity in scenarios with lower diversity or asymmetric distributions. The noisy patterns can be removed through Monte Carlo simulations.

Network-based methods help to find the network of interactions among microbial communication for resources and functioning. Overall, integration of theoretical and computational approaches enhances understanding of microbial ecology.

Now, let's see how we can approach plant–soil–microbe interaction as a whole process.

Modeling interactions among plants, soil, and microbes involves various biological, chemical, and physical processes that connect these systems (Beck et al., 2022). Different approaches have been applied to understand the intricacies of these interactions, ranging from simplistic compartment models to complex mechanistic models. Compartment models approach the understanding of nutrient and energy flow among different components using differential equations, aiding in understanding nutrient cycling and ecosystem dynamics. Dynamic simulation modeling simulates ecosystem dynamics over time, accounting for temporal changes in factors such as soil moisture, nutrients, plant growth, and microbial activity. Metabolic modeling helps in quantifying the stoichiometric matrix of metabolic



Modeling interactions among plants, soil, and microbes involves various biological, chemical, and physical processes that connect these systems. Photo courtesy of Flickr/Oak Ridge National Laboratory.



Maximizing the capacity and function of soil microbiomes is challenged by both natural and anthropogenic disturbances. Photo courtesy of Adobe Stock/Юрій Тарасовський.

reactions occurring at the interface of plants and microbes in the soil, elucidating plant–microbe and microbe–microbe interactions (Beck et al., 2022). Agent-based modeling, including game theory and cellular automata, can be used to study the decision-making processes by each component in the plant–soil–microbe interface, valuable for optimizing resources in crop production (Almpanis et al., 2019). Stochastic modeling aids in analyzing the diversity and structure of microbial communities at different soil depths and different levels of carbon availability, which overall affect microbial activity and the microbiome (Benucci et al., 2023). In-Silico-based modeling of interactions has given the power to derive reference models to simulate different plant–microbe interactions and extend the theoretical framework to the experimental-based framework.

With the revolution in high-throughput phenotyping and sequencing, the huge amount of data generated can be analyzed through machine-learning models. Machine-learning models perform large-scale data curation, classification and identification of hidden patterns,

and predictions through different parameter estimation and model optimization; thus, deriving hidden relations among the plant–soil–microbial interface.

Microbiome Research is Poised for Exciting Times Ahead

Plant–soil–microbe interactions are pivotal in shaping the rhizosphere and terrestrial ecosystems, spanning from agricultural land to forests and grasslands. These interactions are crucial for carbon sequestration and plant productivity. The intricate relationships among plants, soil, and microbes create a dynamic system that can be mutualistic, symbiotic, or antagonistic, influencing nutrient cycling, microbial diversity and activity, soil health, and plant productivity. With the onset of global climate change, ecosystems are rapidly evolving, leading to increased carbon emissions and affecting overall ecology and agriculture. Understanding these components, their interactions, and modeling their future consequences is essential for agriculture and conservation efforts aimed at increasing carbon sequestration and reducing emissions.

Further, maximizing the capacity and function of soil microbiomes is challenged by both natural and anthropogenic disturbances. Key challenges are discovering novel microbial species and genes governing soil health alongside developing integrated practices that nourish beneficial microbiota while reducing inputs and environmental impacts. Advancing a predictive understanding of microbiome responses to global change is critical for developing biological solutions that harness microbial potential to sustain food production.

To date, although a variety of tools, approaches, and indicators have been developed to characterize microbial composition and functions across scales, ways to integrate these measures to derive a meaningful assessment of ecosystem functioning (e.g., soil health impacts) are often inadequate and still evolving. While individual rhizosphere microorganisms' roles in biogeochemical processes are increasingly understood, interactions between beneficial groups remain less explored.

Additionally, soil fauna–microbe interactions in the rhizosphere remain relatively understudied. Further insights into microbial community assembly rules, species interactions, and functional genomics promise to inform integrated management leveraging microbial diversity. Thus, to enhance sustainable agriculture, a comprehensive understanding of rhizosphere communities is crucial, particularly regarding their impact on carbon, nitrogen, and phosphorus transformations that supports overall sustainable management of crops. While traditional concepts focus

"To enhance sustainable agriculture, a comprehensive understanding of rhizosphere communities is crucial..."

on root–microbe symbioses and microbe–microbe antagonism, there is a need to emphasize network-level interactions and move beyond binary plant–microbe relationships to incorporate multiscale relationships among plant, microbe, and environments. Exploring assembly principles, species interactions, and microbial trait-based ecology can help formulate strategies to leverage the soil microbiome for agricultural productivity and sustainability. Additionally, government-level policy and initiatives on microbiome research and funding hold the future of sustainable agriculture and ecology.

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