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Review Paper

Influence of Sustainable Agricultural Practices on Microbial Aspects of Soil

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ABSTRACT

Soil is a non-renewable natural resource essential for supporting plants, animals, and microorganisms. The intensification of conventional agriculture has substantially affected soil health, including its microbial component. This review evaluates how sustainable agricultural practices, including crop rotation, intercropping, cover cropping, organic amendments, and agroforestry, influence microbial aspects of soil health, with particular emphasis on microbial biomass, diversity, community composition, and functions related to nutrient cycling. Peer-reviewed studies published up to 2025 were identified through Web of Science, PubMed, and Google Scholar using combinations of terms describing individual agricultural practices and microbial soil health parameters. The reviewed evidence indicates that crop diversification can enhance microbial biomass and modify microbial community composition through changes in soil properties, nutrient cycling, root exudation, and organic inputs, although responses vary among cropping systems and environmental conditions. Organic amendments generally increase microbial biomass and can promote microbial diversity by supplying organic and mineral nutrients and providing favorable microhabitats, with the magnitude of these effects strongly dependent on the amendment type and soil conditions. Agroforestry practices can also modify microbial biomass and diversity through increased plant diversity, rhizodeposition, and organic matter inputs, but responses depend on plant species, management, climate, and soil properties. Overall, sustainable agricultural practices show considerable potential to support the microbial component of soil health; however, their effects are context-dependent and cannot be generalized across all production systems. Further long-term and function-oriented research is needed to link changes in microbial communities with soil processes, crop performance, and ecosystem services.

Key words:
agroforestry, microbial biomass, microbial diversity, organic, sustainable agriculture

Abbreviations:
MBC – Microbial biomass carbon; MBN – Microbial biomass nitrogen; MBP – Microbial biomass phosphorus; SOC – Soil organic carbon; PLFA – Phospholipid fatty acid; AMF – Arbuscular mycorrhizal fungi; FAME – Fatty acid methyl ester; OA – Organic amendment; ITS – Internal transcribed spacer; TC – Total carbon; HS – Humic substances; Ha – Humic acid; PGPM (B) – Plant growth promoting microorganisms (bacteria)

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INTRODUCTION

Soil, a complex system composed of solid (mineral and organic matter), liquid, and gaseous phases, forms the foundation of terrestrial life by supporting plants, animals, and microorganisms. As a non-renewable resource on a

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human timescale, its preservation is critical (Van Camp et al., 2004). Following World War II, the rapid growth of the global population and rising food demands intensified conventional agricultural practices, with extensive physical and chemical manipulations of soils (Lehman et al., 2015). While these practices boosted short-term productivity, they also undermined soil health and long-term sustainability. With the global population projected to reach 8.9 billion by 2050 (Tahat et al., 2020), agriculture faces the urgent challenge of meeting food demand sustainably, without jeopardizing essential ecosystem services such as carbon sequestration, nutrient cycling, and water regulation (Cárceles Rodriguez et al., 2022).

Kibblewhite et al. (2008) define a healthy agricultural soil as one capable of sustaining food and fiber production at levels sufficient to meet human needs, while simultaneously delivering essential ecosystem services that support human well-being and biodiversity conservation. The key functions of such soils include regulating water flow and retention, facilitating solute transport, maintaining physical integrity, cycling and retaining nutrients, remediating potentially toxic elements, and providing habitats that sustain biodiversity (Lehman et al., 2015).

Beyond physical and chemical properties, soil biology represents a fundamental dimension of soil health. It encompasses the total biomass present in soil, including bacteria, archaea, and microscopic eukaryotes such as fungi, algae, protozoa, and nematodes, as well as larger invertebrates and vertebrates (Lehman et al., 2015). Among these, microorganisms are the most abundant and diverse, with estimates of up to 10^9 cells and 10^4 species per gram of soil (Griffiths and Philippot, 2013). The soil microbial community is considered the most genetically diverse ecosystem on Earth (Kendzior et al., 2022). Biodiversity is even greater in the rhizosphere, where root exudates enrich microbial communities with nutrients and signaling compounds (Araujo, 2022). Owing to their abundance and diversity, soil microorganisms play roles in virtually every soil process (Table 1).

Table 1. The role of soil microorganisms

Roles of soil microorganisms	Reference
Biogeochemical cycles of carbon, nitrogen, sulfur, hydrogen, uranium, manganese and iron.	Madsen, 2011
Solubilization of phosphorus and potassium from minerals	Pang et al., 2024 Youssef et al., 2023
Excreted biopolymers, filamentous fungi and actinomycetes contribute to soil aggregate stability and prevent soil erosion.	Tecon and Or, 2017
Bioremediation of pollutants	Vogt and Richnow, 2013
Biostimulation[1]	Ansari et al., 2023
Pathogen and pest biocontrol	Fira et al., 2018 Soumia et al., 2021
Control of atmospheric trace gases	Conrad, 1996

Legend: [1] Soil microorganisms can modify plant physiological processes and mitigate biotic and abiotic stress conditions through secretion of various biologically active compounds like sugars, enzymes, volatile compounds, exopolysaccharides and phytohormones (Ansari et al., 2023).

Sustainable agriculture is a sum of productive and profitable practices that do not impair soil health (Cárceles Rodriguez et al., 2022). Sustainable agriculture incorporates various methods including the use of microorganisms and the enhancement of indigenous soil species activity. It is straightforward that the preservation and potential enhancement of soil microbial biomass and diversity should be achieved with natural-based solutions and in the presence of appropriate plants or plant-/animal- based residues.

Crop rotation is one of the oldest agricultural practices, traditionally used to prevent yield decline caused by soil sickness, a phenomenon linked to the accumulation of autotoxins under monocropping systems (Huang et al., 2013). Beyond mitigating soil sickness, crop rotation improves the overall soil health by enhancing microbial diversity and biomass (McDaniel et al., 2014; Dias et al., 2015). Similarly, cover cropping is a widely adopted practice for soil conservation and improvement, particularly in annual cropping systems, with significant benefits for soil biological properties (Castellano-Hinojosa and Strauss, 2020) (Table 2). Another early diversity-based approach is intercropping, which has been shown to increase yield, improve nutrient use efficiency, suppress weeds, pests, and diseases, and reduce runoff and erosion (Mousavi and Eskandari, 2011; Xiao et al., 2023). Moreover, intercropping can indirectly influence microbial diversity and ecosystem functioning through its effects on soil properties (Xiao et al., 2023).

Table 2. Benefits of cover crops in agriculture

Benefits of cover crops	Reference
Increase SOC stocks in agricultural soils.	Poeplau and Don, 2015
Improving soil nitrogen content[2]	Ketterings et al., 2015
Soil structure improvement	Gentsch et al., 2024
Reducing soil erosion	Kaspar and Singer, 2011
Improve soil fertility	Scavo et al., 2022
Conserving soil moisture	Fageria et al., 2005
Weed suppression	Teasdale et al., 2007
Improve yield of subsequent crops	Chahal and Van Eerd, 2023

Legend: [2] Improving soil nitrogen content can be done with N-fixation by legume winter cover crops or residual N immobilization by cereal grains and prevent leaching.

Organic amendments are biodegradable materials that decompose gradually, releasing nutrients that can be absorbed by plants and soil organisms (Singh et al., 2020). In addition to nutrient supply, these amendments create favorable microhabitats for microorganisms and stimulate their proliferation, particularly in the upper soil layers where aerobic decomposition predominates (Diacono and Montemurro, 2011).

Agroforestry encompasses a range of long-established practices, some of which have been used for centuries, though systematic research and promotion have intensified over the past 50 years. This approach not only meets human needs for food, fiber, and fuel but also contributes to restoring degraded soils, supporting biodiversity, and delivering a wide array of ecosystem services (Udawatta et al., 2017).

The aim of this article is to provide essential insights into how sustainable, nature-based practices influence the soil microbiome, particularly microbial biomass and diversity, in agricultural soils, and to what extent these effects occur. Three groups of practices are discussed: those based on crop diversity, organic amendment application, and agroforestry practices. As the roles of sustainable practices in improving crop yields and preserving soil quality are well established, our study focuses exclusively on their interaction with the soil microbiome. We hypothesize that sustainable management practices enhance soil microbial biomass and diversity by promoting favorable physicochemical conditions and providing continuous organic inputs that stimulate microbial activity and functional diversity. This study synthesizes findings from previous research, recent field experiments, and long-term trials to provide an integrated understanding of how these practices shape soil microbial communities and contribute to maintaining soil health.

This review was based on a literature search conducted using Web of Science, PubMed, and Google Scholar. Search terms were combined according to the general principle of sustainable agricultural practice + microbial soil health parameter. Agricultural practices included crop rotation, cover cropping, intercropping, organic amendments, manure, compost, biochar, humic substances, seaweed extracts, peat, PGPR, AMF, cyanobacteria, biocrusts, riparian buffers, windbreaks, alley cropping, silvopasture, and forest farming. These terms were combined with microbial indicators such as microbial biomass, MBC, MBN, MBP, microbial abundance, bacterial diversity, fungal diversity, microbial community composition, microbial activity, functional diversity, PLFA, FAME, and microbial functional genes. Additional searches targeting microbial functions related to carbon, nitrogen, and phosphorus cycling were performed where relevant. The literature search included peer-reviewed studies published up to 2025, without a predefined lower publication-year limit.

PRACTICES BASED ON CROP DIVERSITY

By examining the effects of crop rotation, intercropping, and cover cropping on microbial biomass and diversity, this section highlights how practices based on crop diversity contribute to achieving the overarching aim of understanding sustainable practices' influence on the soil microbiome.

Crop rotation

Crop rotation is one of the earliest sustainable practices known to improve soil physicochemical properties, particularly by enhancing carbon and nitrogen accumulation (McDaniel et al., 2014; Wang et al., 2023). It also contributes to plant pathogen suppression through the stimulation of beneficial microbial communities (Pavković et al., 2025; Peralta et al., 2018), helps alleviate drought stress effects on crops (Bowles et al., 2020), and positively influences the total number of bacteria and aminoheterotrophs (Stamenov et al., 2016). Microbial biomass in crop rotation systems increases significantly due to the continuous input of organic compounds from plant residues, which serve as nutrient sources for soil biota and subsequent crops (Figure 1). McDaniel et al. (2014) reported that

introducing one or more crops into rotation increased MBC by 20.7 percent and MBN by 26.1 percent. Similarly, Wang et al. (2023) found that MBC and MBN concentrations were significantly higher in maize (*Zea mays* L.)–garlic (*Allium sativum* L.) and maize–annual ryegrass (*Lolium multiflorum* Lam.) three-year rotations compared to maize monocropping. Microbial biomass phosphorus was also greater in maize–garlic and maize–rape (*Brassica napus* L.) rotations than in maize monocropping. In addition, bacterial and fungal PLFA content tends to increase with more diverse crop rotations, although microbial community composition varies among soil aggregate sizes (Tiemann et al., 2015). Specifically, bacterial abundance is greater in micro-aggregates (0.05–0.25 mm), whereas fungi dominate in macro-aggregates (0.25–2 mm) and play a key role in aggregate stability. Overall, crop rotation strongly influences soil microbial biomass by enhancing soil properties and increasing organic inputs.

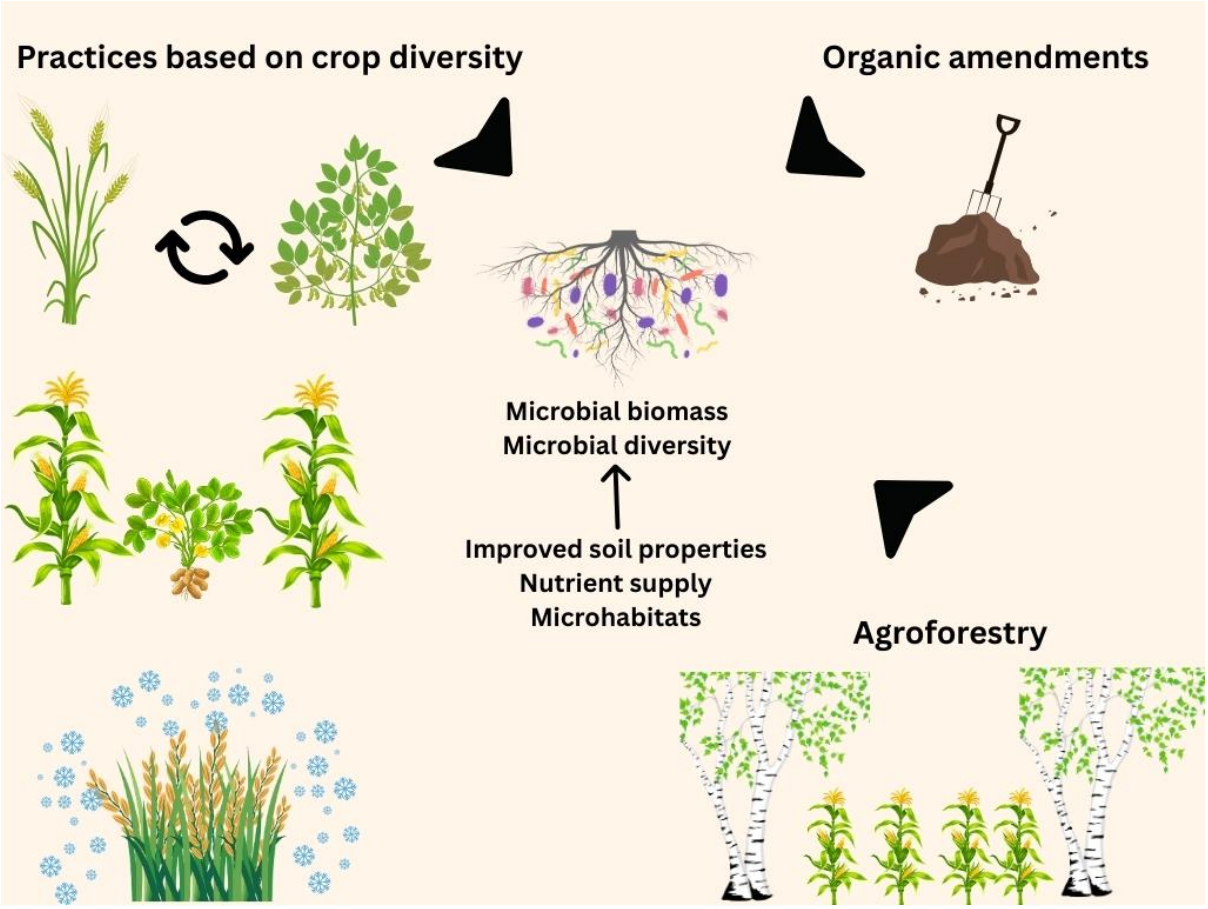


Figure 1. Effect of sustainable agricultural practices on soil microbial biomass and diversity

Microbial diversity is generally enhanced by organic farming practices such as crop rotation (Mäder et al., 2002; Woo et al., 2022). The diversification of organic inputs, together with the release of distinct root exudates and signaling molecules by different crops, promotes a more diverse soil microbial community, which may exert legacy effects on subsequent crops (Williams et al., 2023). A diverse microbial community contributes to soil aggregate stability, nutrient cycling, and overall crop productivity (D'Acunto et al., 2018). For instance, rapeseed–potato (*Solanum tuberosum* L.) rotations increased microbial community diversification, and when combined with conifer-based compost, these practices had a complementary effect on soil microbiota (Bernard et al., 2012). Crop rotation can also alter the structure and complexity of symbiotic microbial community networks (Zong et al., 2024). Such networks represent not only microbial diversity but also interactions among taxa, which may be positive (mutualism), negative (parasitism), or neutral (Faust and Raes, 2012). Zong et al. (2024) reported that symbiotic network density was lower in tobacco (*Nicotiana tabacum* L.) rotation systems compared to gramineous rotations. Conversely, Wang et al. (2023) found that bacterial and fungal diversity declined in maize–garlic and maize–annual ryegrass rotations relative to maize monocropping, even though soil quality improved significantly under these rotations. These findings highlight that while crop rotation generally enhances soil quality, not all rotation patterns positively affect microbial diversity. This outcome may be linked to specific interactions between root exudates and

microbial communities, which can exert a stronger influence on microbial diversity than soil physicochemical properties alone.

Rotations between Leguminosae and Gramineae crops have long been considered optimal for maintaining soil nutrient cycles (Zhang et al., 2019). While Gramineae–Leguminosae rotations can positively affect soil microbial communities, these effects are not always consistent (Woo et al., 2022). In a 13-year study, pulse-inclusive rotations increased MBC and MBN by 31–36 percent and 50–61 percent, respectively, compared to a maize–wheat (*Triticum aestivum* L.) rotation (Borase et al., 2020). Crop rotation can selectively enhance certain microbial groups while reducing others. For example, soybean (*Glycine max* L.)–maize rotations combined with organic fertilizers increased the Gram-positive bacterial abundance but decreased the fungal abundance relative to continuous maize cropping (Zhang et al., 2019). Similarly, Sun et al. (2023) reported that soybean–maize rotations increased the bacterial diversity, particularly Proteobacteria, while reducing the fungal diversity. Soybean–wheat rotations also shifted microbial composition, increasing *Proteobacteria*, *Firmicutes*, and *Bacteroidetes*, while decreasing *Actinobacteria*, *Verrucomicrobia*, and *Chloroflexi* (Yu et al., 2021). The synergistic effects of crop rotation with other sustainable practices can be substantial: no-tillage in a maize–soybean system enhanced fungal abundance and the fungal-to-bacterial ratio in the 0–5 cm soil layer compared to no-till maize monocropping (Sun et al., 2016). Nitrogen fixed by Leguminosae benefits subsequent cash crops and supports soil microbiota, further increasing microbial biomass.

While microbial diversity is widely recognized as a key indicator of soil health, examining functional genes instead of solely taxonomic composition can provide a more meaningful understanding of the overall functional potential of microbial communities, and thus better reflect their role in maintaining soil health (Jia et al., 2025). For instance, the introduction of alfalfa into a tomato–maize rotation proved beneficial for the subsequent tomato crop due to reduced nitrogen loss through denitrification, as the abundance of denitrification genes decreased compared to the rotation without alfalfa. Additionally, some beneficial microbial communities that thrived on legume residues with a low C/N ratio were transferred to the following tomato crop (Samaddar et al., 2021). Similarly, a wheat–soybean rotation followed by wheat–maize showed promise as a rotational pattern, as it increased the abundance of nitrification genes while reducing denitrification genes (Yu et al., 2024). Furthermore, the introduction of soybean enhanced the soil's potential for phosphorus solubilization (e.g., *gcd* gene) and organic phosphorus mineralization, such as phosphodiester degradation (e.g., *ugp*Q gene) (Yu et al., 2021). In contrast, Wang et al. (2024) reported that phosphorus solubilization genes were less abundant in a wheat–soybean rotation compared to a wheat–corn system. Overall, functional gene analysis reveals that plant residues with a low C/N ratio can stimulate diverse microbial communities that, in turn, enhance nutrient availability and improve soil health for subsequent crops.

The available evidence indicates that crop rotation generally promotes soil microbial biomass, while its effects on microbial diversity and community composition are less consistent and depend strongly on the crops included in the rotation. Leguminosae–Gramineae rotations frequently increased microbial biomass and altered microbial communities, likely through complementary nutrient inputs and differences in rhizodeposition; however, positive responses were also reported when Gramineae crops were rotated with non-leguminous species such as garlic and ryegrass. Importantly, improvements in soil properties do not necessarily coincide with increased microbial diversity, indicating that crop-specific root exudates and residue characteristics may exert a stronger influence on microbial community structure than crop diversification alone. The reviewed studies also suggest that interactions with other management practices, including no-tillage, organic amendments, reduced mineral fertilization, and cover cropping, can further modify microbial responses, making it difficult to attribute changes in the soil microbiome exclusively to crop rotation.

Cover crops

Understanding how cover crops affect soil microbial communities is essential for clarifying their role in shaping subsequent crop productivity and the overall functioning of agroecosystems (Castellano-Hinojosa and Strauss, 2020) (Table 2). Cover cropping generally enhances microbial abundance parameters, including MBC, MBN, and PLFA content, though the magnitude of these effects depends on climate, soil type, cover crop species, tillage, and termination methods (Kim et al., 2020). Cover cropping had more pronounced positive effects on microbial abundance in Oxisols, Ultisols, and Entisols compared to Mollisols (except for MBN), with increases ranging from 14.5 to 40.7 percent. Consistently, Daryanto et al. (2018) reported significant enhancements under cover cropping: MBC (+64 percent), MBN (+79 percent), and MBP (+26 percent). Cover crops also improve AMF colonization in cash crop roots, with Daryanto et al. (2018) noting a 40 percent increase relative to fallow systems, and Bowles et al. (2017) reporting a 28.5 percent increase following winter cover crops. Legume cover crops combined with no-till systems showed the strongest positive effects on soil AMF colonization.

Microbial diversity is strongly influenced by cover cropping. In a 10-year maize–cover crop study, Hontoria et al. (2019) reported that a barley (*Hordeum vulgare* L.) cover crop promoted AMF communities that persisted into the

subsequent maize crop, unlike vetch cover crops. This effect may be due to specific host–AMF interactions, facilitated by the phylogenetic similarity between maize and barley. Overall, cover crops increased soil Gram-positive bacteria, Gram-negative bacteria, and actinomycetes by 17 percent, 11 percent, and 23 percent, respectively, compared to fallow systems (Muhammad et al., 2021). Actinomycetes were particularly influenced by the type of cover crop, especially legumes, whereas Gram-positive and Gram-negative bacterial populations were less dependent on cover crop species. In a tomato (*Solanum lycopersicum* L.) system, cover crops (rye, *Secale cereale* L., or a rye–vetch, *Vicia sativa* L., mixture) combined with organic compost enhanced soil microbial biomass and functional diversity more than cover crops alone (Nair and Ngouajio, 2012). Continuous rhizodeposition from both cash crops and cover crops throughout the year provides nutrients and stable microhabitats, promoting a rapid increase in microbial biomass in spring as temperatures rise. Additional effects of cover crops on soil microbial diversity and biomass are summarized in Table 3.

Table 3. Effects of cover crops on soil microbial diversity and biomas

Cover crop type	Cover crop effect on soil microorganisms	Reference
Multi-mix cc (Japanese Millet (*Echinochloa esculenta* Braun), Sorghum-Sundan Grass (Sorghum x Drumondi), Pearl Millet (*Pennisetum glaucum* R. Br), Soybeans, Sunnhemp (*Crotalaria juncea* L.), Cowpea (*Vigna unguiculata* Walp.), and Buckwheat (*Fagopyrum esculentum* Hill.)) Singe-species cc (buckwheat) Control (no cc)	Microbial abundance and diversity declined across all three treatments; however, both the control and the multi-species mixture were more effective at preserving overall microbial abundance and diversity than the single-species mixture.	Wang et al., 2020
Residues of buckwheat, clover (*Trifolium sp.* L.), sunflower (*Helianthus annuus* L.), radish (*Raphanus sativus* L.) and a mixture containing 25% of all four residues.	All residues increased microbial biomass, particularly biomass of fungi, gram-positive, gram-negative bacteria and Cyanobacteria. Mixture of residues enhanced microbial activity more compared to each treatment alone, but microbial community composition wasn't changed.	Shu et al., 2021
Three sole cover crops of pea (*Pisum sativum* L.), oat (*Avena sativa* L.), and canola; Four mixtures of pea + oat, pea + canola, pea + oat + canola, and pea + oat + canola + hairy vetch + forage radish + barley; and a fallow (no cover crop). Cover crops were implemented between winter wheat and sorghum (*Sorghum bicolor* Moench.) rotation.	In semiarid conditions, the use of multispecies cover crops resulted in larger populations of AMF, saprophytic fungi, total fungal communities, and Gram-negative bacteria, increasing by 20.5%, 12.7%, 13.3%, and 16.1%, respectively, relative to monoculture cover cropping systems.	Thapa et al., 2021
Fallow (zero species), old radish (one species) and mixtures of BetaSola (five species), SolaRigol and BetaMaxx (seven species), AquaPro (eight species) and MaizePro (13 species). Cover crops treatments are applied in silage maize-rye-potato-triticale (*Triticale* Wittmack.)-sugar beet (*Beta vulgaris* L.) rotation in cambisol.	Relative to the fallow treatment, oil radish, SolaRigol, MaizePro, AquaPro, and BetaMaxx led to significant increases in soil bacterial populations. Among the mixtures, MaizePro and AquaPro notably enhanced Gram-positive and Gram-negative bacteria, as well as actinobacteria and AMF. In contrast, an increase in saprotrophic fungi was observed only under the MaizePro treatment compared with fallow.	Di Rauso Simeone et al., 2020
Sorghum alternating with winter cover crops: rye + vetch, rye, vetch, rye fertilized with 40 kg/ha of urea–nitrogen, and a control without CC.	Compared with no-till sorghum grown alone or in combination with rye cover crops, vetch cover cropping resulted in higher net N mineralization rates and supported a more diverse, bacteria-dominated microbial community. This system also promoted	Frasier et al., 2016

	greater sequestration of carbon and nitrogen within stable soil organic matter fractions after three years, whereas the sorghum-based systems exhibited lower nitrogen turnover.	
In oat–corn cash crop rotation 8 monoculture cover crops (Sunn hemp, Soybean, Red clover (*Trifolim pratense* L.), Hairy vetch, Forage radish, Oat, Canola and Cereal rye) and 6 cover crop mixtures were implemented.	Specific cover crop promoted abundance of specific microbial communities. Cereal rye and Oat increased abundance of AMF. Hairy vetch, and to a smaller degree red clover, promoted a higher abundance of non-AMF. Eight species mix had the most potent influence on Gram-negative bacteria and total bacterial abundance, while Canola and 8 species mix increased gram-positive bacterial biomass much more compared to other cover crops 9 months following cover crop planting.	Finney et al., 2017
The cover crop species evaluated included oat, vetch, and radish. These were established as mixtures of oat/radish and oat/radish/vetch. Soybean monoculture and a soybean–corn rotation were used as the cash cropping systems, while plots without cover crops served as the control.	Cover crops inclusion notable increased total bacteria PLFA content, particularly for Gram positive bacteria. Oat/radish/vetch mixture is highly recommended for improving soil biological processes and N content of soil.	Chavarria et al., 2016
Cover crops included in this 6-year study were: legume-oat mixture (planted every 4th winter or annually), mustard (planted annualy) and rye (planted annualy). Cash crops were the lettuce in spring and spinach or broccoli in the summer. Yard-waste compost was applicated annualy.	MBC and MBN was 2-4 times greater in cropping systems with annually applied cover crops and compost compared to cropping systems which have only one cover crop winter period. Across all systems, bacterial indicators exhibited a general increase in abundance over time, averaging 21–23%, with the most pronounced rise observed among Gram-positive bacteria. The influence of frequent cover cropping on soil microbial communities was greater than that of compost application, and this effect was consistent across different cover crop types, including legume–rye mixtures, mustard, and rye.	Brennan and Acosta-Martinez, 2017
Rye, vetch or black polyethylene mulch were used as cover crops in tomato production system.	Vetch cover cropping increased fungal and eubacterial biomass compared to black polyethylene mulch. Moreover, the results indicated that seasonal variation exerted the strongest influence on soil microbial community structure, as anticipated, with sample location (bulk versus rhizosphere soil) representing the next most important factor. No significant effect of the preceding cover crop on soil microbial community structure was observed.	Maul et al., 2014
The cover crop treatments was planted on spring and consisted of a fallow treatment, a 10-species cover crop mixture of oat, pea, flax (*Linum usitatissimum* L.), rapeseed, lentil (*Lens culinaris* Medik.), vetch, clover, barley (*Hordeum vulgare* L.), safflower (*Carthamus tinctorius* L.), and phacelia	The greatest total FAME (Fatty Acid Methyl Ester) concentration at wheat maturity stage indicated that longer period of roots growth favored increasing of soil MB. Compared with single-species cover crops, mixtures did not provide any further improvement in microbial community composition or activity. Water had a high impact on microbial activity, especially	Calderon et al., 2016

(*Phacelia tanacetifolia* Benth.), and single species plantings of flax, oat, pea, and rapeseed. Cash crop was winter wheat, planted in september. Irrigation effect on microbial community is also examined.	in semiarid areas.

Overall patterns suggest that cover cropping generally increases microbial biomass by maintaining rhizodeposition and organic inputs during periods when cash crops are absent. However, responses of microbial diversity and community composition are less consistent and depend on cover crop species, soil fertility, climate, tillage, termination method, and interactions with other management practices. Although multispecies mixtures can promote particular microbial groups, they do not consistently provide greater benefits than single-species cover crops, suggesting that species identity and compatibility with the cropping system may be more important than species richness alone. The combination of cover crops with organic amendments can further enhance microbial biomass and functional diversity, particularly under frequent cover-cropping regimes, but these responses are also strongly context-dependent. Further research should therefore move beyond general measures of microbial biomass and diversity and determine whether cover-crop-induced changes in specific microbial groups translate into ecosystem functions such as nutrient cycling and pathogen suppression.

Intercropping

Intercropping is a cropping practice in which two or more crop species or genotypes grow together and coexist for a period of time (Brooker et al., 2015). While many studies have focused on above-ground plant–plant interactions for light, temperature, and space, below-ground interactions with soil biota are equally important for both crop productivity and soil microbial diversity and biomass (Brooker et al., 2015; Li et al., 2018). For example, Li et al. (2018) demonstrated that maize/peanut (*Arachis hypogaea* L.) intercropping provided multiple benefits for soil health. This intercropping system increased the abundance of *Firmicutes* and *Actinobacteria* in the maize rhizosphere, and *Proteobacteria* in the peanut rhizosphere. Moreover, populations of beneficial bacteria such as *Bacillus*, *Burkholderia*, *Pseudomonas*, and *Rhizobium*, along with nitrogen-cycling genes, were enhanced. These changes in the soil microbiome positively influenced the yield of both intercropped maize and peanut.

Intercropping systems provide a greater diversity of root exudates, including amino acids and organic acids, along with varied crop residues, which enhance the energy supply for soil microbial biomass (Lai et al., 2022). Cereal–legume intercropping has been shown to increase MBC and MBP, particularly in the rhizosphere, compared to sole crops (Tang et al., 2014). This effect is attributed to rhizodeposition of carbon compounds, which boosts microbial biomass and promotes microbial phosphorus mineralization to meet nutrient demands. Similarly, MBC in the rhizosphere of alfalfa (*Medicago sativa* L.) increased in alfalfa/Siberian wild rye (*Elymus sibiricus* L.) intercropping, with even greater effects after inoculation with *Sinorhizobium meliloti* (Sun et al., 2009). Potato–legume intercropping enhanced soil MBC by 15–38 percent compared to sole potato production, with macro-aggregates supporting the highest microbial biomass and microbial carbon use efficiency (MBC/SOC) (Nyawade et al., 2019).

However, intercropping does not always increase microbial biomass. In some cases, sole crops can support higher MBC or MBN than intercropped systems, for example, MBC was higher in sole faba bean (*Vicia faba* L.) compared to faba bean–maize or faba bean–wheat intercropping, and MBN was greater in sole wheat relative to wheat intercropped with faba bean or maize (Song et al., 2007). Zhou et al. (2019) also reported that Chinese milk vetch (*Astragalus sinicus* L.) reduced microbial biomass in the rape rhizosphere, with higher abundance of bacteria, fungi, actinomycetes, and AMF in fully separated plants compared to non-separated plants. Overall, intercropping generally increases microbial biomass, but exceptions can occur when root exudates suppress each other's rhizobiome or when soil and climatic conditions are unfavorable for microbial growth.

Intercropping can influence soil microbial diversity and ecosystem functions by modifying soil properties (Nyawade et al., 2019; Xiao et al., 2023). For example, intercropping maize with sesame (*Sesamum indicum* L.), peanut, soybean, or sweet potato (*Ipomoea batatas* L.) increased the richness of bacterial and fungal species and enhanced ecosystem functions such as soil nutrient availability, crop nutrient uptake, enzyme activity, MBC, and MBN compared to maize monocropping (Xiao et al., 2023). In contrast, Zhao et al. (2022) reported that maize/peanut intercropping did not significantly increase overall bacterial and fungal diversity relative to sole cultivation; however, the abundance of certain beneficial bacteria increased, and fungal community composition shifted, with a reduction in pathogenic fungi and enrichment of saprotrophic fungi. Similarly, cucumber (*Cucumis sativus* L.) intercropped with trifolium or mustard (*Brassica juncea* Czern.) substantially enhanced bacterial and fungal diversity, particularly *Actinobacteria*, *Chloroflexi*, and *Bradyrhizobium*, compared to sole cucumber cropping (Li

and Wu, 2018). These effects are largely attributed to the diverse root exudates released by coexisting crops, which modify soil properties in the rhizosphere and create a variety of niches that support different microbial communities.
In perennial tree crop production, crops are sown between tree rows, and they are also known as cover crops, although this is an intercropping approach (Castellano-Hinojosa and Strauss, 2020). Plant diversity of cover crops in perennial systems can enhance the heterogeneity of soil microbial communities, which further could improve soil organic carbon, total nitrogen content and, ultimately, tree production (Vukicevich et al., 2016; Castellano-Hinojosa and Strauss, 2020).
Evidence across different cropping systems shows that intercropping can modify soil microbial communities while contributing to nutrient complementarity and disease management, although these responses depend strongly on crop combination and environmental conditions (Nyawade et al., 2019). Legume-based intercropping is the most extensively studied pattern, but changes in microbial biomass, diversity, and community composition have also been reported in systems involving Brassicaceae, Cucurbitaceae, and other plant families. Importantly, greater crop diversity does not necessarily result in consistent benefits to the soil microbiome, as plant–plant competition and species-specific effects on rhizodeposition and nutrient availability can modify microbial responses. These limitations may become particularly important in arid and semi-arid environments, where competition for water can constrain the benefits of intercropping and influence the associated soil microbial community. In such environments, the selection of compatible crop combinations and appropriate management practices appears to be particularly important for reducing interspecific competition (Zhang et al., 2025b).

ORGANIC AMENDMENTS

The discussion on organic amendments demonstrates how the addition of manure, compost, biochar or other organic amendments not only improves soil fertility but also aligns with our aim of elucidating the specific mechanisms through which sustainable practices shape microbial communities.
Organic amendments (OAs) are derived from once-living materials, such as manure, compost, or biostimulants (Aytenew and Bore, 2020) (Table 4). They influence soil life both directly, by supplying nutrients and creating favorable microhabitats for soil biota, and indirectly, by modifying soil physicochemical properties. OAs generally enhance nutrient availability, improve soil texture and water retention, and reduce soil erosion and nutrient leaching (Singh et al., 2020). One notable effect of OAs is the stimulation of soil microbial biomass. In a meta-analysis of 41 studies, Kallenbach and Grandy (2011) reported that organic amendment applications increased MBC by 36 percent and MBN by 27 percent, with high rates of cattle manure sometimes boosting MBC by more than 60 percent.
Different composted materials, including urban organic waste, cattle manure, green waste, and sewage sludge, have been shown to enhance soil MBC under crop rotations such as maize/wheat/barley, with even greater increases when combined with 80 kg N/ha fertilizer (Ros et al., 2006). Sewage sludge compost mixed with rice husk or sawdust compost also significantly increased MBC and MBN compared to conventional NPK fertilization (Zaman et al., 2004). Cotton gin crushed compost, alone or combined with beet vinasse compost in a 1:1 ratio, increased MBC several-fold relative to control soils, while beet vinasse compost alone did not, suggesting that not all composts exert equal benefits on soil microbiomes (Tejada et al., 2006).
Poultry manure compost increased MBC, 16S rRNA gene abundance by 76 percent, and ITS copy number by two orders of magnitude in bulk soil compared to mineral fertilizer treatment (Wang et al., 2022a). Beyond microbial biomass, composts can suppress root diseases by promoting a larger and more diverse microbial community, often fungal-dominated, which enhances disease suppression (Leon et al., 2006). Similarly, bio-composts composed of straw, wheat bran, chicken manure, and cottonseed meal increased microbial diversity and the abundance of beneficial bacteria (e.g., *Skermanella*, *Sphingomonas*, *Actinobacteria*, *Bacteroidetes*, *Firmicutes*) and fungi (e.g., *Chrysosporium*, *Chaetomium*, *Acremonium*, *Trichoderma*, *Metarhizium*), while reducing pathogenic fungi such as *Aspergillus* and *Stachybotrys* (Liu et al., 2022b). Also composted manure promoted abundance of phosphorus solubilization genes, by modifing physicochemical properties of soil for beneficial bacteria that participate in phosphorus geochemical cycle (Wang et al., 2025).
Long-term studies confirm these benefits: over 21 years, combined composted pig manure and NPK fertilization significantly increased total, bacterial, gram-negative, and actinobacterial PLFA content in degraded soils compared to unfertilized or synthetically fertilized soils. Compost alone improved gram-positive bacterial, anaerobic, and fungal PLFA content relative to synthetic fertilizers (Zhong et al., 2009).
The use of manure in agriculture has been a long-standing sustainable practice that continues to benefit soil health and the soil microbiome (Ren et al., 2019; Kallenbach and Grandy, 2011). In a meta-analysis of 103 peer-reviewed studies, Ren et al. (2019) reported that manure application increased MBC and MBN by 40 percent and 55 percent, respectively, compared to mineral fertilizers across major cultivation systems in China. The magnitude of these

effects depends on several factors: manure type (cattle manure has shown the greatest effect on MBC with a 69 percent increase, while sheep manure increased MBN by 169 percent, followed by horse manure at 118 percent; farmyard manure had no significant effect), soil type (soils with higher clay content >30 percent show smaller MBC increases), duration of application (long-term application of 25–30 years yields stronger impacts than short-term treatments), and climate (higher temperatures and precipitation generally favor microbial growth).

From the standpoint of microbial functional gene profiles, abundance of genes associated with carbon decomposition and fixation, nitrogen mineralization, and phosphorus solubilization was increased after manure application. This parameter was also identified as a major driver of yield under organic treatment (Li et al., 2022). Furthermore, incorporating cattle manure into vegetable production systems can enhance yield, as microorganisms involved in the phosphorus cycle thrive under such conditions (Mao et al., 2025). These microorganisms exhibited increased production of organic acids important for the solubilization of inorganic phosphorus (e.g., *gcd* gene) and elevated expression of the *pho*D gene, which encodes alkaline phosphatase.

Table 4. Organic amendments that are reviewed in this article

Organic amendment	Definition	Reference
Composted material	Compost is partially decomposed organic matter. During the initial stages of organic matter decomposition, fungi tend to dominate due to the relatively high lignin-to-nitrogen ratio, while bacteria typically act as secondary colonizers in later stages.	Singh et al., 2020
Manure	A complex organic material derived from the combined excreta (dung and urine) of farm animals, which improves tilth and fertility of the soil. Can menace environment due to presence of heavy metals and pathogenic bacteria.	Kumar et al., 2013
Biochar	A carbon-dense, porous substance generated by thermochemical processing of organic materials (woody biomass, crop residues, animal wastes, and sewage sludge) under oxygen-limited conditions (pyrolysis).	Li et al., 2020
Humic-based substances	Humic-based materials are carbon-rich organic amendments derived from extracted humic fractions of manure and compost, as well as from both raw and processed forms of lignite, coal, and peat.	Lumactud et al., 2022
Seaweed extracts	Complex mixtures that possess assorted biostimulatory compounds such as various forms of carbohydrates, amino acids, small quantities of phytohormones, osmoprotectants, and proteins.	Ali et al., 2021
Peat moss	Partially degraded plant material (e.g. Sphagnum moss) under wet, low oxygen and low temperature conditions.	Gong et al., 2018; Le Geay et al., 2024
Plant growth promothing microorganisms (PGPM)	Microorganisms isolated from soil, water, air, extreme habitats, enriched in laboratory and applied to soil as bio-amendment to provide one or more ecosystem services (Table 1).	
Biocrust	Soil biocrusts consist of communities of	Coe et al., 2014

	cyanobacteria, green algae, fungi, lichens, and mosses that are adapted to arid and semi-arid (dryland) environments and contribute a wide range of ecosystem functions in those regions.	

In a century-long experiment, cattle manure application enhanced soil bacterial diversity and promoted a more even microbial distribution compared to chemical fertilizer-treated or untreated soils (Sun et al., 2004). However, a critical drawback of manure use is the potential presence of pathogenic bacteria, such as *Pseudomonas* and *Staphylococcus*, which can pose risks to human health through contaminated food or water (Faissal et al., 2017).

Green manure is undercomposed plant material which is integrated into the soil system to enhance nutrient status and fertility (Singh et al., 2020). Cover crops, or crops grown in rotation with cash crops, or crops intercropped with cash crops, can enhance soil microbial biomass and diversity during their growth stage through rhizodeposition or by incorporation of their residues into the soil. Overall, partially decomposed plant residues, such as compost or manures, provide initial boost of microbial biomass due to presence of readily utilizable components of polysaccharides (e.g. glucose from cellulose) and proteins compared to the green manures.

Biochar is an important soil amendment that offers multiple benefits for the soil microbiome. It provides stable microhabitats within its porous structure (charosphere), supplies nutrients, including labile carbon fractions readily accessible to microorganisms and contains specific organic compounds (e.g., xylenols and polycyclic aromatic hydrocarbons) that can serve as carbon sources for specialized microbial populations. Additionally, biochar can increase soil pH, enhance moisture retention, and immobilize contaminants (Bolan et al., 2024).

Several studies have shown that biochar positively affects soil microbial biomass, increasing MBC by 21.7 percent (Pokharel et al., 2020) or 26 percent (Zhou et al., 2017), and MBN by 21 percent (Zhou et al., 2017). However, the effects of biochar on microbial biomass are highly dependent on factors such as pyrolysis temperature, feedstock material and application rate (see Table 5). Some biochars, such as eucalyptus wood biochar pyrolyzed at 600 °C, can even decrease MBC (Dempster et al., 2012).

Labile carbon fractions from manure can increase MBC by promoting the expression of carbon-decomposing genes in tea plantations. In contrast to manure, which enhances soil respiration and CO_2 emissions through increased labile carbon availability and microbial activity, biochar amendment exerts minimal influence on soil respiration, thereby contributing to improved carbon sequestration in agricultural soils (Han et al., 2023).

Table 5. Factors that affect biochar effect on soil microbial biomass (MB)

Factors	Effect on MB	Reference
Experiment duration	Increase of MBC tended to decrease with increasing duration, particularly in experiments that were prolonged up to 12 months. Reason for that could be depletation of labile and extrectable carbon pool in soil.	Zhou et al., 2017
Soil characteristics	MBC increased significantly across soils differing in pH, TC, and texture. The increase was 16.6% in acidic soils and 38.7% in alkaline soils; 23.6% in soils with TC < 10 g/kg and 23.2% in soils containing 10–20 g/kg TC; and 22.1% in coarse-textured soils compared with 18.6% in fine-textured soils.	Pokharel et al., 2020
Biochar characteristics	MBC was signifcantly increased by biochars produced from urban wastes and crop residues and by biochars with high pH (> 10) and low C/N ratios (< 50), applied in field conditions. Different particle size biochar had effect on different communities, e. g. biochar with a smaller particle size (<1 mm) tended to favor the development of bacterial communities, whereas larger particles were more conducive to fungal growth. In addition, biochar derived from manure and produced at relatively low temperatures (<300 °C) exerted the strongest effect on MBC.	Pokharel et al., 2020; Li et al., 2020
Method used for determining MBC	MBC determined by fumigation-extraction method showed a greater overall response to biochar application	Li et al., 2020

	compared to PLFA method. PLFA method was more used in analyzed studies.

Overall, biochar addition also increased microbial diversity (soil bacterial Shannon diversity index by 0,99 percent and Chao1 richness index by 6,45 percent) (Xiang et al., 2023). Specifically, biochar application at lower rates and over a longer experiment duration resulted in higher soil microbial diversity. However overall effect of biochar on soil microbiome diversity was highly dependent on soil properties, rather than biochar properties (Li et al., 2020).
Several factors influence how biochar affects soil microbial diversity. Climatic conditions play a role: significant increases in Shannon diversity indices were noted in regions with mean annual precipitation above 800 mm or mean annual temperatures above 13 °C. Experimental duration also matters; bacterial richness increased significantly under short-term biochar application (<6 months), whereas this effect was less pronounced with longer exposure periods (6–30 months). Land use and system type influence outcomes as well, with bacterial richness increasing by 15 percent, 5.74 percent, and 2.87 percent in horticultural systems, farmland, and forestland, respectively. Edaphic factors are important: while bacterial diversity generally increased with biochar application, this effect was less pronounced in rhizosphere soils, subsoils (0–30 cm), alkaline soils, or soils with SOC > 20 g/kg. Biochar properties also determine its impact: high application rates (C > 700 kg/ha), elevated nitrogen content (>7 kg/ha), low C/N ratios (<60), or high pyrolysis temperatures (>600 °C) may reduce or prevent increases in microbial diversity (Xiang et al., 2023).
Humic substances (HS) enhance plant growth, development, and productivity, which in turn stimulate the rhizosphere microbiome through increased root exudation (Bezuglova and Klimenko, 2022; Yang et al., 2021). In addition, HS can directly stimulate soil microbial communities through multiple mechanisms (Table 6). In a seven-year experiment, Lei et al. (2022) reported that bentonite-humic acid application increased MBC, MBN and MBP by 38 percent, 84 percent, and 43 percent at 0–10 cm depth, and by 40 percent, 93 percent, and 45 percent at 10–20 cm depth, respectively. Microbial biomass increased continuously during the first five years and then stabilized for the remainder of the study. Comparatively, municipal solid waste compost, bovine manure, and sewage sludge significantly enhanced MBC more than commercial humic acid (Albiach et al., 2000), likely due to the higher application rates possible with lower-cost organic residues. HS also influence bacterial community composition, increase microbial diversity, and promote the growth of beneficial bacteria. Furthermore, combining HS with other organic amendments can have synergistic effects on the soil microbial community (Lumactud et al., 2022). Both heterotrophic and hemolytotrophic bacteria benefit from compost-derived humic acids because HS adsorb mineral nutrients and release them gradually, providing a sustained nutrient supply (Valdrighi et al., 1996).

Table 6. Stimulatory action of HS on soil microorganisms (Source: Bezuglova and Klimenko, 2022)

Causes of the stimulatory action of HS on Microorganisms	**Effect**
HSs stimulate the processes of respiration and nitrogen fixation in bacteria	Enhanced growth of the bacterial community, primarily azotobacter
Capacity of humic acid (ha) to chelate trace nutrients	Increased availability of trace nutrients
HS is a source of carbon and energy in the humus mineralization process	Release of bound elements of mineral nutrition
The effect of HS on the membranes of microorganisms (higher permeability)	Slower plasmolysis and deplasmolysis in the *Saccharomyces cerevisiae* yeast
	Improved conditions for the penetration of nutrients into the cell
Ha sorbs substances inhibiting the growth of nitrifying bacteria and trigger their switch to heterotrophic growth	Stimulation of the growth of nitrifying bacteria
Sorption of ha on the cell walls of bacteria creates a protective layer contributing to withstanding higher concentrations of toxicants, the resistance of bacteria to toxicants improves	Copper oxide nanoparticles, heavy metal salts, radionuclides, phenolic compounds, atrazine and quinoline
Penetration of ha into bacterial cells is enhanced under stress caused by salinity	Reduction of the negative effects of stress
Ha, as well as malic and succinic acids, increase the content of sugars and organic acids in the rhizosphere of maize	Growing population of soil microbial communities

Seaweed extracts provide numerous benefits for plant growth, vigor, and tolerance to pests, diseases, and abiotic stresses, ultimately enhancing overall productivity (Ali et al., 2021). They also influence the soil microbiome positively. For example, extracts from two brown seaweeds, *Ascophyllum nodosum* and *Durvillaea potatorum*, slightly increased the abundance of total active fungi, yeast, and plant growth-promoting bacteria in the tomato rhizosphere (Hussain et al., 2021). Moreover, these extracts significantly enriched eight bacterial families (Nakamurellaceae, Cytophagaceae, Sterolibacteriaceae, Archangiaceae, Moraxellaceae, Brevibacteriaceae, Chlorobiaceae, and Dermatophilaceae), some of which contribute to improved soil properties and plant growth. Similarly, Wang et al. (2018) demonstrated that *Sargassum horneri* extract enhanced bacterial diversity and richness in tomato rhizosphere, which correlated with higher plant yield and quality. In apple (*Malus hupehensis*) seedlings, extracts from *Lessonia nigrescens* and *L. flavicans* alleviated replanting stress by promoting a more favorable environment for beneficial microorganisms (Wang et al., 2017). The highest application rate (40 g/kg soil) increased bacterial, fungal, and actinomycete abundance by 172 percent, 67 percent, and 57 percent, respectively, compared to untreated soil. Pigments, polysaccharides, and nutrients in seaweed extracts stimulate both crop growth and rhizobiome activity, particularly at higher application rates. However, accessibility and cost may limit their use in developing countries, reducing economic feasibility for smallholder farmers.

Peatlands support highly diverse microbial communities that form a complex trophic network and participate in the biogeochemical C cycle (Le Geay et al., 2024). Moreover, peat, applied as an OA, shows beneficial effects on soil microbial diversity (Pan et al., 2020). Peat and bentonite were appropriate for assisting soilless revegetation in heavy metal contaminated sites (Liu et al., 2022a). These amendments increased microbial species richness and increased relative abundance of PGPB (plant growth promoting bacteria) including *Arthrobacter*, *Altererythrobacter* and *Bacillus*. Further, peat and vermiculite combined with chemical fertilizer increased bacterial diversity, but did not have a remarkable effect on MBC and MBN compared to manure + chemical fertilizer application (Pan et al., 2020). This phenomenon was caused by the potential of manure to provide a high nutrient input, which further favored a less metabolically diverse microbial community. On the other hand well-humified natural peat decreased MBC, MBN and AMF abundance in soils under strawberry in Finland (Vestberg et al., 2009). The reason for this could be poor utilization of peat substrate by soil microorganisms, particularly in a cold climate.

PGPM support processes such as biofertilization (increase nutrients content through solubilization and nitrogen fixation); biostimulation (see Table 1); bioprotection (direct biocontrol of pests and pathogens or induction of plant resistance system) and bioremediation of polutants. Through these processes, PGPM increase plant health, and consequently soil health (Khatoon et al., 2020). PGPM application can also promote soil biota. Biofertilization process provides nutrients for soil biota as well, thereby increasing their growth. In addition, the reduction of pollutants concentration prevents their detrimental effect on soil biota also. Vigorous and healthy plants, influenced by PGPM, can also positively affect rhizosphere biota through increased secretion of root exudates. The combination of NPK fertilizer and PGPB, such as *Serratia marcescens*, or *Enterobacter* sp., or *Burkholderia cepacia*, or *Klebsiella* sp. Increased MBC, MBN and MBP compared to treatments without fertilization or PGPB application alone under ginger (*Zingiber officinale* Roscoe.) cultivation (Dinesh et al., 2013). Furthermore, PGPB application attenuated the negative effect of NPK fertilizers on MBC and biochemical processes, indicating that reducing the NPK fertilization rate was unnecessary. Biofilm forming *Bacillus* sp. HW27 with abilities to produce Indol-acetic acid and siderophores while also solubilizing phosphate, combined with spent mushroom substrate, increased abundance of Bacillus and Pseudomonas bacteria in tomato rhizosphere by 148,4 percent and 70,1 percent and reduced the abundance of pathogenic *Fusarium oxysporum* by 52,1 percent relative to the control (Wang et al., 2022b). Additionally, combination of PGPB and spent mushroom supstrate had the most potent influence on abundance of total bacteria, gram positive, gram negative and Actinobacteria.

AMF is one important group of soil microorganisms that have beneficial effects on other soil biota. Secretions of AMF and root exudates of symbiotic plant positively affect Pseudomonads, Rhizobia, saprotrophic fungi, *Bacillus* spp. and other PGPM (Fall et al., 2022). Moreover, cyanobacteria-based inoculants can improve soil fertility, provide N for crops and soil biota, and stimulate growth with exopollysacharides, plant hormones, vitamins, etc. Supporting this, Alvarez et al. (2024) showed that cyanobacterial inoculants (*Anabaena cylindrica* or *A. Cylindica* + *Chlamydomonas* sp.) improved MBC, MBN, and microbial activity, especially under wheat cultivation. Effect of PGPM on crop growth and health is highly dependent on environmental factors and therefore focus should be on strains adapted on specific soil, climate and crop.

Biocrusts provide many benefits for underlying soils in arid climates, such as reducing erosion, improving primary production, enhancing nutrient storage, increasing aggregate stability and water content (Miralles et al., 2020). The same authors found that microbial species diversity and richness in soil under biocrusts were significantly increased compared to biocrusts colonized by lichens, since lichens could produce secondary antibiotic metabolites that reduced the growth of bacteria and fungi, while preventing their degradation of lichen thalli. A quite opposite trend is

noticed in the Xiao and Veste (2017) experiment, where the moss biocrust on loess plateu in China had higher MBC, MBN, bacterial and fungal densities and microbial diversity relative to biocrust fixed and mobile sand. These contrasting results could be due to differences in climate, soil structure and biocrust-forming organisms. Biocrusts are complex systems, in wich every component is essential for their proper functioning. Therefore excluding even one component can significantly reduce influence of biocrusts on ecosystem services (Cheng et al., 2021). The same authors noticed that removal of biocrust-forming mosses reduced the bacterial abundance and diversity in soil under the biocrust. In addition, biocrust-forming mosses minimized aridity detrimental effect on soil microbial comunity composition and diversity (Delgado-Baquerizo et al., 2018). Biocrusts also affect the microbiome of agricultural soils, but the effect is dependent on the presence of crops (Zou et al., 2024) .The biocrust presence led to a dramatic shift in a microbial community composition, characterized by a dominance of Cyanobacteria. Adapted to extreme conditions, this cyanobacterial community possibly outcompeted other microbes, or alterations in soil physicochemical properties induced by biocrusts favored specific microbial groups. Conversely, biocrust-associated pepper (*Capsicum annuum* L.) rhizosphere soil showed higher diversity that might be attributed to the combined effects of biocrust-associated microorganisms and plant root exudates, creating a more heterogeneous environment that supports a wider range of microbial species.

Responses of soil microbial communities to organic amendments vary considerably with amendment type and application conditions, although increases in microbial biomass and, in many cases, microbial diversity are frequently reported. Combining organic amendments with mineral fertilizers can provide benefits related to crop productivity, soil properties, biodiversity, waste management, and soil C sequestration (Ros et al., 2006). Similarly, combinations of different organic amendments may provide more diverse nutrient sources and microhabitats, potentially producing stronger microbial responses than individual amendments. However, these effects are highly dependent on amendment characteristics; for example, biochar properties are influenced by feedstock and pyrolysis conditions, while biocrust-forming mosses and lichens can differently affect microbial communities. Soil type, climate, application rate, and interactions with existing management practices further contribute to variability among studies. Importantly, higher application rates do not necessarily produce stronger beneficial responses and may adversely affect particular microbial groups, emphasizing the need to evaluate organic amendments within specific soil and production contexts.

AGROFORESTRY

Insights from agroforestry practices illustrate the role of diversified plant inputs and rhizodeposition in modulating microbial biomass and diversity, further reinforcing the study's focus on linking sustainable practices to soil microbial health.

Agroforestry is an "intensive land-use management that optimizes the benefits (physical, biological, ecological, economic, and social) from biophysical interactions created when trees and/or shrubs are intentionally integrated with crops and/or livestock" (Gold and Garrett, 2009). Major agroforestry practices are listed and defined in Table 7. Agroforestry also can be studied from a landscape perspective, and in that approach, the biodiversity of macrobiota is mainly influenced by provided secondary habitats and microclimate of agroforestry systems (McNeely and Schroth, 2006). Soil microbiome is affected by plants diversification, which involves the secretion of various root exudates and the promotion of growth of different microbial communities. Plant diversity is increased by introducing trees and shrubs in agricultural systems, which indicates that the soil microbiome should also become more diverse.

Table 7. Major agroforestry practices and their definitions (adapted from Gold and Garrett, 2009)

Agroforestry practice	Definition
Riparian buffers	Strips of permanent vegetation (trees, shrubs and grasses) placed between agricultural land and water bodies to suppress runoff and nonpoint source pollution, stabilize streambanks, improve aquatic and terrestrial habitats, and provide harvestable products.
Windbreaks	Barriers consisted of trees and shrubs that reduce wind speed; protect wind-sensitive crops and livestock; control erosion and improve bee polination.
Alley cropping	This practice combines trees planted in single or multiple rows with agricultural or horticultural crops.
Silvopasture	Adding trees to existing pasture, or by thinning an existing forest stand and adding (or improving) a forage component. The trees provide shelter for livestock, protecting them from temperature stresses and reducing food and water consumption.

Forest farming	Crops are cultivated under the protection of a forest overstory that has been modified and managed to provide the appropriate microclimate conditions.

In the soils of riparian buffers, microbial species richness and evenness are generally enhanced (Martin et al., 1999; Ducey et al., 2013). Microbial communities are affected by many factors including: groundwater that provides nutrients and minerals, the roots of overlying vegetation that provide carbohydrates, amino acids and organic acids; and chemical and physical soil properties. The uneven distribution of those factors reflects heterogeneity of species richness, evenness and diversity in the riparian zone (Martin et al., 1999). Proteobacteria, Acidobacteria, Planctomycetes, Verrucomicrobia and Actinomycetes were the most dominant groups in the riparian zone, and a factor that influenced this composition might be effluent from a swine lagoon (Ducey et al., 2013). Rahman et al. (2014) highlighted that MBN, microbial diversity, and microbial activity were increased in riparian zone compared to soil outside the zone, but these parameters decreased with soil depth, which further indicates that plant organic matter had a more potent influence on the microbial community than nutrients carried by groundwater. Vegetation composition of the riparian zone is an important factor affecting the soil microbiome (Cardinali et al., 2014). The highest MBC content was detected in riparian zones that contained a 6 m wide grass zone and 2 rows of trees and shrubs, but MBN showed the highest increase in a 3 m wide grass riparian zone only. A posible reason for that could be the presence of grasses, a fast growing plants with dense, tangled roots, which provides more organic content for the soil microbiome in shorter period of time compared to trees and schrubs.

In riparian buffer zones, different plant species can exert distinct effects on the soil microbiome. A thriving microbial community enhanced nitrogen uptake in *Pennisetum alopecuroides*, whereas *Cynodon dactylon* increased the abundance of denitrifying bacteria. Both plant species, however, played a significant role in reducing nitrogen pollution (Zhang et al., 2025a).

Fast-growing trees that are planted between crops in alley cropping systems can positively influence the soil microbial population size and increase microbial diversity due to the presence of specific rhizosphere microbiome compared to monocropping systems (Beule et al., 2022). Further, the quality and amount of plant litter and N input can also alter microbial functional diversity (Mungai et al., 2005). Functional diversity can indicate a higher microbiome capability to use various substrates which might further influence nutrient cycling in alley cropping systems (Beuschel et al., 2019). In addition, Seiter et al. (1999) highlighted that green manure in the form of leaf fall of alder trees (*Alnus rubra* Bong.), additional below ground substrate from tree roots and untilled soil increased bacterial and fungal counts in and near the tree rows. The abundance of gram negative bacteria was higher in hybrid walnut (*Juglans nigra* L.) rows compared to gram positive and Actinobacteria abundance, which was higher in wheat rows. This could indicate that copiotrophic microorganisms were favored in tree rows, compared to interrows of alley cropping system (Guillot et al., 2021). Also, microbial parameters gradually decreased from the tree rows to the crop row, which was a trend in many studies (Beuschel et al., 2019; Guillot et al., 2021). This indicates that trees promote a stable and rich rhizobiome over the years, which cannot be maintained further from the tree root zone due to the lower concentration of root exudates.

Similar to other agroforestry systems, silvopasture implemenattion drastically modificates soil microbiome due to changes in the microenvironmental conditions and the quantity and quality of organic matter entering the soil (Gonzalez-Polo et al., 2019). A long-term (15 years) application of silvopastural management restored degraded soil and improved soil health indicators after extensive pasture in the Amazon region (Silva-Olaya et al., 2021). Ramakrishnan et al. (2021) highlighted that guava (*Psidium guajava* L.) pasture was a favourable combination for most of the soil physical, chemical and biological properties, but bael (*Aegle marmelos* Correa.) pasture could be a promising alternative in terms of MBC, bacteria and cellulolytic bacteria counts. In contrast to previous studies, Gonzalez-Polo et al. (2019) emphasized that the introduction of pine (*Pinus ponderosa* Laws.) in a silvopastoral system decreased microbial biomass and microbial enzymatic activity under pine cover. This might be caused by the introduction of unique pine rhizobiome, the specific quality of litter and a 13-year experiment duration may not be enough to show the effect of pine afforestation on soil processes. According to a previous study, Viruel et al. (2021) showed that the *Prosopis alba* (Griseb.) tree increased microbial activity and MBC, however, the *Leucaena leucocephala* (de Wit.) tree decreased these parameters, possibly due to specific rhizodeposits. Further, the Leucaena tree promoted a unique bacterial community, including Streptococcus and Clostridum genera, by producing amino acids like mimosine.

The available evidence indicates that agroforestry practices can influence soil biological processes and associated ecosystem services, although the magnitude and direction of these effects are strongly context-dependent (Vranešević et al., 2025). The introduction of trees into croplands and pastures can increase microbial biomass and diversity, particularly within the tree rhizosphere; however, contrasting responses among tree species have also been reported, likely due to differences in rhizodeposition and the quantity and quality of organic matter inputs (Gonzalez-

Polo et al., 2019; Viruel et al., 2021). Therefore, the effects observed in individual agroforestry systems cannot be generalized across all agricultural settings, as their applicability and impact depend on climate, production system, tree–crop or tree–livestock compatibility, and available land and resources. Further studies across contrasting climates and production systems are needed to clarify these interactions and determine under which conditions agroforestry provides consistent benefits to the soil microbiome.

SUGGESTIONS FOR FUTURE RESEARCH

Future research could focus on identifying suitable plant varieties used in sustainable practices, with diverse root exudates as a key selection criterion. Elucidating the interactions between specific root-exuded metabolites and microbial communities may facilitate the preservation of beneficial taxa that enhance the performance of subsequent cash crops.

Further investigations should go beyond assessing microbial functional gene abundance, as genes alone do not fully reflect microbial activity. Integrating transcriptomics, proteomics, and metabolomics can reveal which genes are actively expressed and how microbial functions respond to sustainable agricultural practices. Coupling these molecular tools with predictive modeling will improve our ability to forecast microbial responses to management strategies, environmental changes, and crop rotations. Such multi-omics approaches, particularly in long-term field trials, are essential for linking potential microbial functions to actual soil processes, ultimately supporting the design of practices that optimize soil health, nutrient cycling, and ecosystem services.

Climate and soil characteristics are critical determinants influencing the effectiveness of sustainable practices in enhancing the soil microbiome. Therefore, such information should be consistently reported in studies involving the application of sustainable practices. Moreover, predicting the effectiveness of a given practice is not feasible without detailed information on the climate and soil characteristics of the specific region.

Ultimately, changes in the soil microbiome should be evaluated in terms of their impact on key ecosystem services, such as nutrient mineralization. It is insufficient to assess only the influence of sustainable practices on microbial communities; it is equally important to determine whether these microbial changes translate into measurable effects on soil functioning and the performance of subsequent cash crops.

CONCLUSION

The evidence synthesized in this review indicates that sustainable agricultural practices can substantially influence the microbial component of soil health, although the magnitude and direction of these responses vary among practices and environmental conditions. Increases in microbial biomass are relatively consistently reported following crop diversification, organic amendment application, and agroforestry, whereas responses of microbial diversity and community composition are more variable. These differences highlight that changes in microbial biomass or taxonomic diversity alone cannot be considered universal indicators of improved soil health.

The effects of crop rotation, cover cropping, intercropping, organic amendments, and agroforestry are strongly context-dependent and are influenced by factors such as crop and tree species, soil properties, climate, amendment characteristics and application rates, and interactions with other management practices. Consequently, positive responses observed under particular experimental conditions cannot necessarily be generalized across different agricultural systems. Furthermore, much of the available evidence focuses on changes in microbial biomass, abundance, and taxonomic diversity, while direct links between these changes and microbial functions, crop performance, and ecosystem services remain less well established. Recognizing these limitations is essential for interpreting microbial responses to sustainable agricultural practices and for identifying the conditions under which these practices can most effectively support soil health.

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