



Unraveling the Complex Dynamics of Soil Microbiome Diversity and Its Implications for Ecosystem Functioning: A Comprehensive Review

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ABSTRACT

Soil microbiome diversity plays a pivotal role in shaping terrestrial ecosystems and the myriad functions. This comprehensive review delves into the intricate dynamics of soil microbial communities, exploring their composition, interactions, and responses to environmental factors. By synthesizing findings from cutting-edge research, we aim to elucidate the complex interplay between soil microbiome diversity and ecosystem functioning. We discuss the application of advanced techniques, such as high-throughput sequencing and metagenomic analysis, which have revolutionized our understanding of soil microbial diversity. The review highlights the influence of biotic and abiotic factors, including plant diversity, soil properties, climate, and land-use practices,

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on the structure and diversity of soil microbial communities. We examine the mechanisms through which soil microbes drive critical ecosystem processes, such as nutrient cycling, carbon sequestration, and plant productivity. The review also explores the resilience and adaptability of soil microbial communities in the face of global change pressures, such as climate change, land-use intensification, and biodiversity loss. We discuss the potential implications of altered soil microbiome diversity for ecosystem functioning and the provision of essential ecosystem services. Furthermore, we identify knowledge gaps and propose future research directions to advance our understanding of soil microbiome diversity and its role in maintaining healthy and productive ecosystems. This review provides a comprehensive framework for understanding the complex dynamics of soil microbiome diversity and underscores its critical importance in shaping the functioning and sustainability of terrestrial ecosystems in a changing world.

Keywords: Soil microbiome; microbial diversity; ecosystem functioning; environmental factors; global change.

1. INTRODUCTION

Soil is a complex and dynamic ecosystem that harbors an immense diversity of microorganisms, collectively referred to as the soil microbiome. These microbes play a critical roles in sustaining the functioning and productivity of terrestrial ecosystems [1]. In recent years, advances in molecular biology and high-throughput sequencing technologies have revolutionized our understanding of soil microbial diversity and its intricate relationships with the environment [2]. This comprehensive review aims to synthesize current knowledge on the complex dynamics of soil microbiome diversity and its profound implications for ecosystem functioning. We will explore the composition and structure of soil microbial communities, the factors that shape their diversity, and the mechanisms through which they drive essential ecosystem processes. Furthermore, we will discuss the responses of soil microbes to global change pressures and the potential consequences for ecosystem services. By unraveling the complex interplay between soil microbiome diversity and ecosystem functioning, we can develop strategies for harnessing these microbial communities to support sustainable land management and ecosystem resilience in a changing world.

2. COMPOSITION AND STRUCTURE OF SOIL MICROBIAL COMMUNITIES

2.1 Overview of Soil Microbial Diversity

Soil is home to an astounding array of microorganisms, including bacteria, archaea, fungi, and protists, with estimates suggesting that a single gram of soil can contain billions of microbial cells representing thousands of species

[3]. This vast diversity is a product of the heterogeneous nature of soil, which provides a wide range of microhabitats with varying physical, chemical, and biological properties [4]. Soil microbes have evolved to occupy diverse ecological niches, exhibiting a wide range of metabolic capabilities and life strategies [5].

2.2 Techniques for Characterizing Soil Microbiomes

The study of soil microbial diversity has been greatly advanced by the development of molecular techniques that allow for the direct analysis of microbial communities without the need for cultivation [6]. These techniques include DNA fingerprinting methods (e.g., DGGE, T-RFLP), sequencing of phylogenetic markers (e.g., 16S rRNA for bacteria and archaea, ITS for fungi), and metagenomic approaches that provide insights into the functional potential of microbial communities [7]. Table 1 provides an overview of commonly used techniques for characterizing soil microbiomes, along with their advantages and limitations.

2.3 Dominant Microbial Groups and their Roles

Soil microbial communities are typically dominated by a few phyla of bacteria, including Proteobacteria, Acidobacteria, Actinobacteria, and Verrucomicrobia, which together can account for over 50% of the total bacterial diversity in many soils [8]. Fungal communities are often dominated by Ascomycota and Basidiomycota, with Glomeromycota being important in arbuscular mycorrhizal symbioses [9]. These dominant microbial groups play key roles in various ecosystem processes, such as

Table 1. Techniques for characterizing soil microbiomes

| Technique | Description | Advantages | Limitations |
|------------------------|--|--|--|
| DGGE/TGGE | Denaturing gradient gel electrophoresis; separates DNA fragments based on sequence differences | Rapid, cost-effective, provides community fingerprints | Limited resolution, difficult to identify specific taxa |
| T-RFLP | Terminal restriction fragment length polymorphism; uses restriction enzymes to generate fragments that are separated by size | High throughput, provides community fingerprints | Limited resolution, difficult to identify specific taxa |
| 16S rRNA sequencing | Sequencing of the 16S rRNA gene, a phylogenetic marker for bacteria and archaea | High resolution, allows for taxonomic identification | PCR biases, limited to bacteria and archaea |
| ITS sequencing | Sequencing of the internal transcribed spacer region, a phylogenetic marker for fungi | High resolution, allows for taxonomic identification | PCR biases, limited to fungi |
| Metagenomics | Sequencing of the total DNA extracted from an environmental sample | Provides insights into functional potential, allows for discovery of novel genes and pathways | Expensive, computationally intensive, limited by database coverage |
| .Meta transcriptomics | Sequencing of the total RNA extracted from an environmental sample | Provides insights into active functions and gene expression | Expensive, computationally intensive, RNA instability |
| Metaproteomics | Analysis of the total proteins extracted from an environmental sample | Provides insights into expressed functions and enzymes | Expensive, computationally intensive, limited by database coverage |
| Metabolomics | Analysis of the total metabolites extracted from an environmental sample | Provides insights into metabolic activities and biogeochemical processes | Expensive, computationally intensive, limited by database coverage |
| Stable isotope probing | Tracking the incorporation of stable isotopes (e.g., ¹³ C, ¹⁵ N) into microbial biomolecules | Allows for linking specific microbial taxa to functions | Requires labeling with stable isotopes, limited by sensitivity |
| Single-cell genomics | Sequencing of the genome of individual microbial cells isolated from environmental samples | Allows for characterization of uncultured microbes, provides insights into micro diversity | Technically challenging, low throughput, limited by cell isolation methods |
| Culturomics | High-throughput cultivation of microorganisms using diverse media and conditions | Allows for isolation and characterization of novel taxa, provides strains for functional studies | Labor-intensive, limited by culturability of microbes |
| Microfluidics | Miniaturized devices for isolation, cultivation, and analysis of individual microbial cells | Allows for high-throughput screening and characterization of microbial cells | Technically challenging, limited by cell isolation methods |

carbon and nutrient cycling, soil aggregation, and plant growth promotion [10]. For example, Proteobacteria include many species involved in nitrogen fixation, nitrification, and denitrification, while Acidobacteria and Verrucomicrobia are known for their ability to degrade complex organic compounds [11]. Actinobacteria are important producers of secondary metabolites, including antibiotics, and are involved in the decomposition of recalcitrant organic matter [12]. Fungi, particularly mycorrhizal fungi, are crucial for plant nutrient acquisition and can also contribute to soil aggregation and carbon sequestration [13].

2.4 Spatial and Temporal Variability in Soil Microbial Communities

Soil microbial communities exhibit significant spatial and temporal variability, reflecting the heterogeneous nature of soil environments and the dynamic interactions between microbes and their surroundings [14]. At the microscale, soil aggregates and pores create a mosaic of microhabitats with distinct physical and chemical properties, which can support different microbial communities [15]. At larger scales, soil microbial diversity can vary across land-use types, vegetation gradients, and climatic zones [16]. Temporal variability in soil microbial communities can occur at scales ranging from diurnal to seasonal and interannual, driven by factors such as temperature, moisture, and plant phenology [17]. Fig. 1 illustrates the spatial and temporal scales at which soil microbial diversity can vary, highlighting the importance of considering

multiple scales when studying these communities.

2.5 Rare Biosphere and its Potential Significance

In addition to the dominant microbial taxa, soil communities also harbor a vast number of low-abundance or rare species, collectively referred to as the "rare biosphere" [18]. These rare taxa can make up a significant portion of the total microbial diversity and may play important functional roles in ecosystems, such as serving as a reservoir of genetic and functional diversity, responding to environmental changes, and contributing to the resilience of microbial communities [19]. However, the ecology and significance of rare microbial taxa in soil remain poorly understood, in part due to the challenges associated with their detection and characterization [20].

3. FACTORS INFLUENCING SOIL MICROBIOME DIVERSITY

3.1 Biotic Factors

3.1.1 Plant diversity and community composition

Plants are a major driver of soil microbial diversity through their effects on soil properties, resource availability, and microbial interactions [21]. Plant species differ in their root architecture, exudation profiles, and litter quality, which can create distinct microhabitats and support

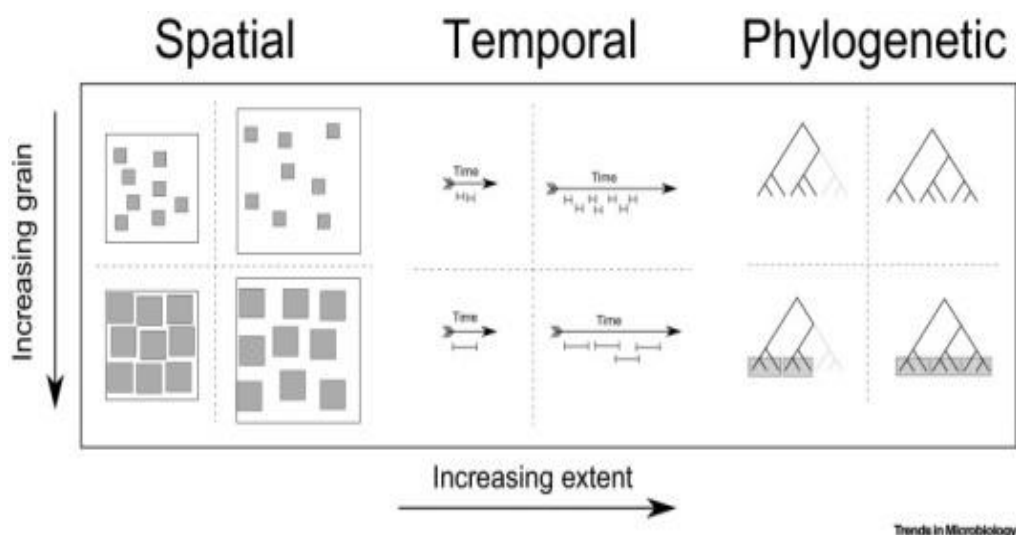


Fig. 1. Spatial and temporal scales of soil microbial diversity

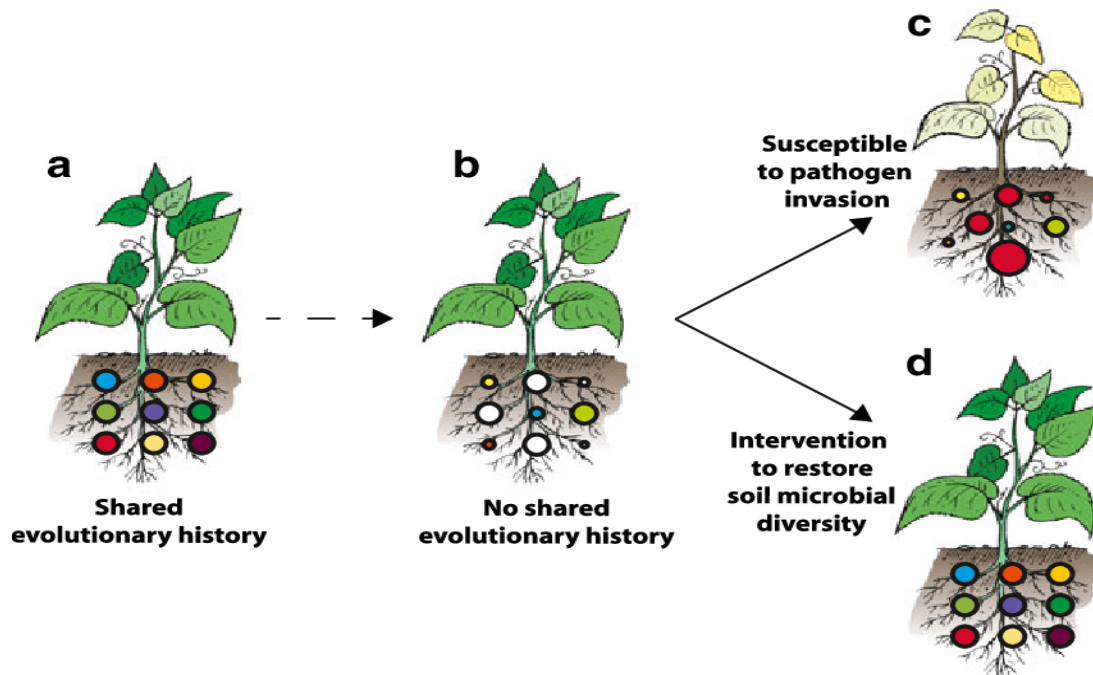


Fig. 2. Plant diversity effects on soil microbiome diversity

different microbial communities [22]. Increasing plant diversity has been shown to promote soil microbial diversity, likely through the provision of a greater variety of resources and niche opportunities [23]. Fig. 2 presents a conceptual framework illustrating the mechanisms by which plant diversity can influence soil microbiome diversity.

3.1.2 Plant-microbe interactions and rhizosphere process

The rhizosphere, the narrow zone of soil surrounding plant roots, is a hotspot of microbial activity and diversity [24]. Plants release a wide range of organic compounds into the rhizosphere, including sugars, amino acids, and secondary metabolites, which can attract and support specific microbial communities [25]. In turn, rhizosphere microbes can influence plant growth and health through various mechanisms, such as nutrient mobilization, production of plant growth regulators, and suppression of pathogens [26]. These plant-microbe interactions are highly complex and can involve both mutualistic and antagonistic relationships [27].

3.1.3 Faunal interactions and trophic networks

Soil fauna, including microarthropods, nematodes, and protozoa, can influence microbial diversity through their feeding activities,

dispersal of microbial propagules, and modification of soil structure [28]. Grazing by soil fauna can alter the composition and activity of microbial communities, while also releasing nutrients that stimulate microbial growth [29]. Soil food webs are highly complex, with microbes occupying various trophic levels and engaging in a wide range of interactions with other soil organisms [30]. Table 2 provides an overview of the main groups of soil fauna and their potential effects on soil microbial diversity.

3.2 Abiotic Factors

3.2.1 Soil properties

Soil physical and chemical properties, such as texture, pH, organic matter content, and nutrient availability, are key determinants of microbial diversity and community structure [31]. Soil texture influences the pore size distribution and water-holding capacity, which in turn affect the availability of oxygen and other resources for microbes [32]. Soil pH is a major driver of microbial diversity, with different microbial groups adapted to specific pH ranges [33]. Organic matter content and quality provide energy and nutrient resources for microbial growth and can also influence soil structure and water retention [34]. Table 3 summarizes the effects of key soil properties on microbial diversity.

3.2.2 Climate

Climate factors, particularly temperature and precipitation, can have significant effects on soil microbial diversity and community structure [35]. Temperature influences microbial growth rates, enzyme activities, and the availability of substrates, while precipitation determines the amount and distribution of

water in soil, which is critical for microbial activity [36]. Climate change, including warming and altered precipitation patterns, can lead to shifts in soil microbial communities, with potential consequences for ecosystem functioning [37]. Fig. 3 illustrates the potential effects of climate change on soil microbiome diversity and the associated ecosystem processes.

Table 2. Soil faunal groups and their effects on microbial diversity

| Faunal group | Body size | Trophic level | Effects on microbial diversity |
|-----------------|---------------------|------------------------------------|--|
| Protozoa | 2-200 μm | Microbivore | Grazing, nutrient release |
| Nematodes | 0.3-1 mm | Microbivore, predator, omnivore | Grazing, dispersal, nutrient release |
| Microarthropods | 0.1-2 mm | Microbivore, detritivore, predator | Grazing, dispersal, soil structure modification |
| Enchytraeids | 2-20 mm | Detritivore | Soil structure modification, nutrient release |
| Earthworms | 2-30 cm | Detritivore, geophage | Soil structure modification, dispersal, nutrient release |
| Macroarthropods | >2 mm | Detritivore, herbivore, predator | Soil structure modification, litter fragmentation |
| Vertebrates | >1 cm | Herbivore, predator | Soil structure modification, nutrient inputs |

Table 3. Soil properties and their effects on microbial diversity

| Soil property | Range/Type | Effects on microbial diversity |
|------------------------|---|--|
| Texture | Sand, silt, clay | Influences pore size distribution, water and oxygen availability |
| pH | Acidic (<6.5), neutral (6.5-7.5), alkaline (>7.5) | Affects microbial community composition, enzyme activities |
| Organic matter | Low (<2%), medium (2-5%), high (>5%) | Provides energy and nutrient resources, influences soil structure |
| Carbon: Nitrogen ratio | Low (<20), medium (20-30), high (>30) | Affects microbial growth and community composition |
| Nutrient availability | Nitrogen, phosphorus, potassium, micronutrients | Limits microbial growth and activities |
| Salinity | Non-saline (<2 dS/m), slightly saline (2-4 dS/m), moderately saline (4-8 dS/m), strongly saline (>8 dS/m) | Osmotic stress, affects microbial community composition |
| Moisture | Dry (<30% water-holding capacity), moist (30-60% WHC), wet (>60% WHC) | Affects oxygen availability, microbial growth and activities |
| Temperature | Psychrophilic (<20°C), mesophilic (20-45°C), thermophilic (>45°C) | Affects microbial growth rates, enzyme activities, community composition |

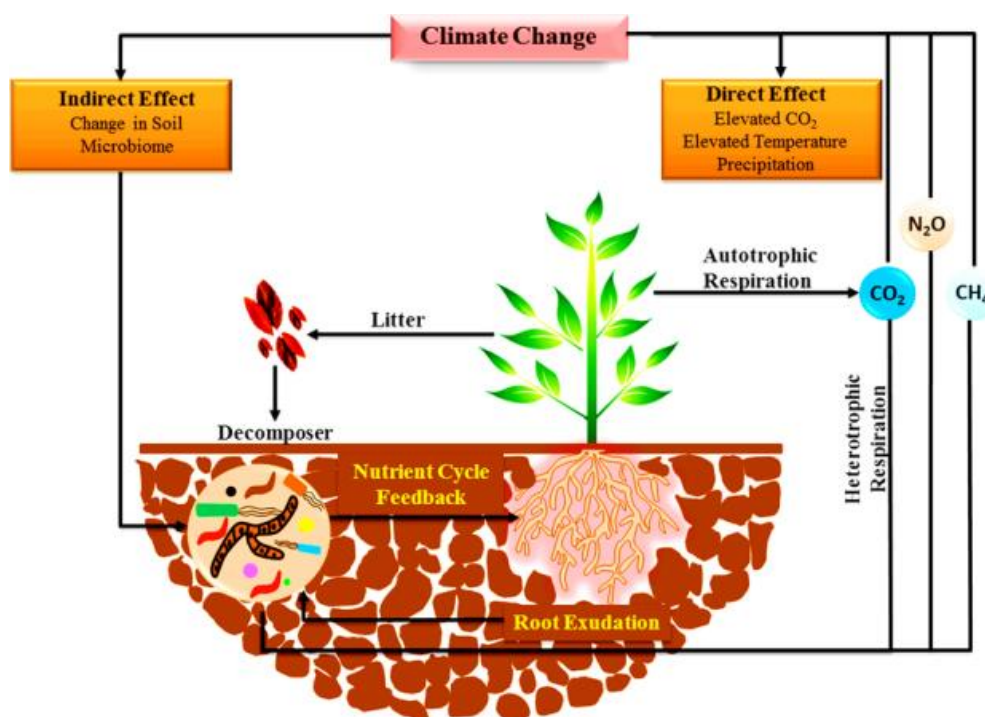


Fig. 3. Climate change effects on soil microbiome diversity and ecosystem functioning

3.2.3 Land-use practices and management

Land-use practices, such as agriculture, forestry, and urbanization, can have profound effects on soil microbial diversity and community structure [38]. Agricultural practices, including tillage, fertilization, and pesticide application, can alter soil physical and chemical properties, as well as the availability of resources for microbes [39]. The conversion of natural ecosystems to managed land-uses often leads to a decrease in soil microbial diversity, with potential implications for ecosystem functions and services [40]. However, sustainable land management practices, such as reduced tillage, organic farming, and agroforestry, can help to maintain or restore soil microbial diversity and support ecosystem functioning [41].

3.3 Complex Interplay of Biotic and Abiotic Factors

Soil microbial diversity is shaped by the complex interplay of biotic and abiotic factors operating at multiple spatial and temporal scales [42]. Interactions between plants, microbes, and other soil organisms are influenced by the physical and chemical properties of the soil environment, which in turn are modified by climate, land-use, and management practices [43,49-55]. Understanding the relative importance and

interactions of these factors is critical for predicting the responses of soil microbial communities to environmental changes and managing ecosystems for desired functions and services [44]. Soil Microbiome Diversity and Ecosystem Functioning.

4. MICROBIAL-DRIVEN ECOSYSTEM PROCESSES

4.1 Nutrient Cycling

Soil microbes play a central role in the cycling of nutrients, including carbon, nitrogen, and phosphorus, which are essential for plant growth and ecosystem productivity [45]. Microbial decomposition of organic matter releases nutrients in forms that can be taken up by plants and other organisms, while also contributing to the formation and stability of soil organic matter [46]. Microbes are involved in key transformations of nitrogen, such as nitrogen fixation, nitrification, and denitrification, which regulate the availability of this often-limiting nutrient [47,56-64]. Phosphorus cycling is also mediated by microbes through the solubilization of inorganic phosphates and the mineralization of organic phosphorus compounds [48]. Table 4 provides an overview of the main microbial processes involved in nutrient cycling and their functional significance.

Table 4. Microbial processes involved in nutrient cycling

| Nutrient | Process | Functional significance | Key microbial groups |
|-----------------|-------------------|--|-----------------------------|
| Carbon | Decomposition | Release of nutrients, formation of soil organic matter | Bacteria, fungi |
| | Methane oxidation | Reduction of atmospheric methane | Methanotrophic |

Table 5. Examples of studies investigating the impacts of temperature on soil microbial communities

| Study | Ecosystem | Key Findings |
|-----------------------|------------------|---|
| DeAngelis et al. [87] | Temperate forest | Long-term warming altered bacterial community composition and increased the abundance of thermophiles |
| Feng et al. [88] | Grassland | Warming increased the relative abundance of Gram-positive bacteria and actinobacteria |
| Karhu et al. [89] | Boreal forest | Warming enhanced microbial respiration and carbon loss from soil |

5. SOIL MICROBIOME RESPONSE TO GLOBAL CHANGE

5.1 Climate Change Impacts on Soil Microbial Communities

Climate change, driven by increasing atmospheric greenhouse gas concentrations, is a major global environmental challenge that can significantly impact soil microbiome diversity and function [81]. The primary climate change factors affecting soil microbial communities include rising temperatures, altered precipitation patterns, and increased frequency and intensity of extreme events such as droughts and heatwaves [65-68,82].

Rising temperatures can have both direct and indirect effects on soil microbial communities. Direct effects include changes in microbial growth rates, metabolic activities, and community composition [83]. In general, higher temperatures tend to favor the growth of thermophilic and thermotolerant microorganisms, leading to shifts in community structure [84]. Indirect effects of temperature on soil microbes are mediated through changes in plant communities, soil properties, and nutrient cycling [85]. For example, warming can accelerate the decomposition of soil organic matter, altering the availability of carbon and nutrients for microbial growth [86].

Altered precipitation patterns, including changes in the amount, frequency, and timing of rainfall, can also have significant impacts on soil microbial communities [90]. Soil moisture is a key factor regulating microbial growth and activity,

and changes in moisture availability can lead to shifts in community composition and function [91]. Drought events, which are predicted to become more frequent and intense in many regions due to climate change, can have particularly strong effects on soil microbiomes [92]. Drought can reduce microbial biomass and diversity, alter community structure, and impair key ecosystem functions such as carbon and nitrogen cycling [73-80,93].

In addition to the direct effects of changing temperature and precipitation, climate change can indirectly influence soil microbiomes through its impacts on plant communities [95]. Climate-driven changes in plant species composition, productivity, and root exudation can alter the quantity and quality of resources available to soil microbes, leading to shifts in community structure and function [69-72,96]. For example, a study by Bardgett et al. [97] found that experimental warming in a grassland ecosystem led to changes in plant community composition, which in turn altered the structure and diversity of soil microbial communities.

5.2 Land-use Intensification and Soil Biodiversity Loss

Land-use change, particularly the intensification of agriculture and urbanization, is a major driver of soil biodiversity loss worldwide [100]. Intensive land-use practices, such as monoculture cropping, heavy tillage, and the excessive use of agrochemicals, can have detrimental effects on soil microbial communities [101]. These practices can reduce microbial biomass and diversity, alter community composition, and impair key

ecosystem functions such as nutrient cycling and disease suppression [102].

Agricultural intensification often involves the conversion of natural ecosystems, such as forests and grasslands, into croplands or pastures [103]. This process can lead to significant changes in soil physical and chemical properties, such as reduced organic matter content, increased compaction, and altered pH [104]. These changes can create stressful conditions for soil microbes, leading to shifts in community composition and reductions in diversity [105].

The intensive use of agrochemicals, such as fertilizers and pesticides, can also have

significant impacts on soil microbial communities [109]. While the application of fertilizers can stimulate microbial growth and activity in the short term, long-term and excessive use can lead to reductions in microbial biomass and diversity [110]. This is particularly true for synthetic fertilizers, which can alter soil pH and create imbalances in nutrient availability [111]. Pesticides, including herbicides, insecticides, and fungicides, can have direct toxic effects on soil microbes, leading to reductions in biomass and diversity [112]. Additionally, pesticides can indirectly affect soil microbiomes by altering plant communities and reducing the diversity of organic inputs to the soil [113].

Table 6. Examples of studies investigating the indirect effects of climate change on soil microbial communities through plant-mediated mechanisms

| Study | Ecosystem | Key Findings |
|----------------------|------------------|---|
| Bardgett et al. [97] | Grassland | Warming-induced changes in plant community composition altered soil microbial community structure and diversity |
| Compant et al. [98] | Alpine tundra | Warming increased plant productivity and root exudation, stimulating microbial growth and activity |
| Geisen et al. [99] | Temperate forest | Drought-induced changes in plant communities altered fungal community composition and reduced diversity |

Table 7. Examples of studies investigating the impacts of land-use change on soil microbial communities

| Study | Land-use Change | Key Findings |
|------------------------|------------------------------|---|
| Rodrigues et al. [106] | Forest-to-pasture conversion | Conversion reduced bacterial and fungal diversity, altered community composition, and impaired nutrient cycling |
| Trivedi et al. [107] | Agricultural intensification | Intensive practices reduced microbial biomass and diversity, favoured copiotrophic bacteria over oligotrophs |
| Kuffner et al. [108] | Urbanization | Urban soils had lower microbial biomass and diversity compared to natural soils, with shifts in community composition |

Table 8. Examples of microbial adaptations to global change stressors

| Stressor | Adaptation Mechanism | Example |
|--------------|---------------------------|---|
| Temperature | Physiological acclimation | Adjustment of membrane lipid composition to maintain fluidity [125] |
| Drought | Physiological acclimation | Production of compatible solutes to protect against osmotic stress [126] |
| Pesticides | Genetic modification | Acquisition of pesticide degradation genes through horizontal gene transfer [127] |
| Heavy metals | Community shifts | Increased abundance of metal-tolerant taxa in contaminated soils [128] |

Urbanization, another major form of land-use change, can also have significant impacts on soil microbial communities [115]. Urban soils are often characterized by high levels of disturbance, compaction, and contamination, which can create stressful conditions for microbes [116]. Additionally, the replacement of native vegetation with impervious surfaces and ornamental plants can alter the quantity and quality of organic inputs to the soil, leading to shifts in microbial community composition and function [117]. However, urban green spaces, such as parks and gardens, can serve as important refugia for soil biodiversity in cities [118].

5.3 Microbial Adaptations and Evolutionary Responses

Soil microbial communities are not static entities but can adapt and evolve in response to changing environmental conditions [119]. Microbial adaptations to global change factors, such as climate change and land-use intensification, can occur through a variety of mechanisms, including physiological acclimation, genetic modification, and shifts in community composition [120].

Physiological acclimation involves changes in microbial metabolic activities and stress responses that allow individuals to maintain function under altered environmental conditions [121]. For example, microbes can adjust their membrane lipid composition to maintain fluidity under changing temperatures or produce compatible solutes to protect against osmotic stress during drought [122]. Genetic modifications, such as mutations and horizontal gene transfer, can also enable microbial adaptation to global change stressors [123]. These modifications can lead to the acquisition of new functional traits, such as the ability to degrade novel substrates or tolerate extreme conditions [124].

In addition to individual-level adaptations, global change stressors can drive evolutionary responses at the community level [129]. This can occur through the selection of resistant or resilient taxa, leading to shifts in community composition and function [130]. For example, long-term exposure to heavy metal contamination can lead to the development of metal-tolerant microbial communities, with increased abundance of taxa possessing metal resistance genes [131]. Similarly, chronic

drought stress can favor the growth of drought-tolerant taxa, such as certain groups of fungi and Gram-positive bacteria [132].

Understanding microbial adaptations and evolutionary responses to global change is crucial for predicting the future trajectory of soil biodiversity and ecosystem functioning [134]. While microbial communities may be able to adapt to certain stressors in the short term, the long-term consequences of multiple, interacting global change factors are less clear [135]. It is important to note that microbial adaptations may not always be sufficient to maintain ecosystem functions under severe or prolonged stress, and that the loss of key taxa or functional groups could have cascading effects on soil health and productivity [136].

5.4 Implications for Ecosystem Functioning and Services

The responses of soil microbial communities to global change factors can have significant implications for ecosystem functioning and the provision of essential ecosystem services [137]. Soil microbes play critical roles in a wide range of ecosystem processes, including nutrient cycling, carbon sequestration, soil formation, and plant growth promotion [138]. Disruptions to soil microbial communities due to climate change, land-use intensification, or other stressors can impair these functions and compromise the sustainability of ecosystems [139].

One of the most important ecosystem services provided by soil microbes is the cycling of nutrients, such as carbon, nitrogen, and phosphorus [140]. Microbial decomposition of organic matter releases these nutrients in forms that can be utilized by plants and other organisms, supporting primary productivity and food web dynamics [141]. However, global change stressors can alter the rates and pathways of nutrient cycling, with potentially negative consequences for ecosystem productivity and stability [142]. For example, climate warming can accelerate microbial decomposition of soil organic matter, leading to increased carbon dioxide emissions and reduced soil carbon storage [143].

Another key ecosystem service provided by soil microbes is the regulation of plant growth and health [148]. Many soil microbes form beneficial associations with plant roots, such as mycorrhizal fungi and nitrogen-fixing bacteria,

which can enhance plant nutrient uptake, water relations, and stress tolerance [149]. Additionally, soil microbes can suppress plant pathogens through competition, antibiosis, and induced systemic resistance [150]. Global change stressors that disrupt these beneficial plant-microbe interactions can lead to reduced plant productivity and increased disease susceptibility [151].

The loss of soil microbial diversity due to global change pressures can also have broader consequences for ecosystem stability and resilience [153]. A diverse soil microbiome is thought to provide functional redundancy and resistance to perturbations, helping to maintain ecosystem processes under stress [154]. However, as global change stressors continue to erode soil microbial diversity, the capacity of ecosystems to withstand and recover from disturbances may be compromised [155].

Ultimately, the impacts of global change on soil microbial communities and their associated ecosystem services have significant implications for human well-being [156]. Soil microbes underpin the productivity and sustainability of agricultural systems, which are critical for food security [157]. They also play key roles in regulating greenhouse gas emissions, water quality, and soil health, which are essential for climate change mitigation and adaptation [158]. Safeguarding soil microbial diversity and function in the face of global change pressures is therefore critical for

maintaining the ecosystem services that support human societies [159].

6. APPLICATIONS AND FUTURE DIRECTIONS

6.1 Harnessing Soil Microbiome Diversity for Sustainable Agriculture

The diversity and functional capabilities of soil microbial communities offer significant potential for developing sustainable agricultural practices [160]. Harnessing the power of soil microbiomes can help reduce reliance on chemical inputs, improve crop yields and resilience, and promote soil health [161]. One promising approach is the use of microbial inoculants, which involve introducing beneficial microbes into the soil to enhance plant growth and stress tolerance [162]. For example, inoculation with arbuscular mycorrhizal fungi has been shown to improve nutrient uptake, water relations, and disease resistance in various crop species [163].

Another strategy is to manage agricultural practices to promote soil microbial diversity and function [164]. This can include practices such as crop rotation, cover cropping, and reduced tillage, which can enhance soil organic matter, improve soil structure, and support diverse microbial communities [165]. Additionally, the integration of agroforestry systems, which combine trees with crops or livestock, can promote soil microbial diversity and provide multiple ecosystem services [166].

Table 9. Examples of studies investigating the implications of soil microbial responses to global change for ecosystem functioning and services

| Study | Global Change Factor | Ecosystem Function/Service | Key Findings |
|---------------------------------|--------------------------|------------------------------|--|
| Allison et al. [144] | Climate warming | Carbon cycling | Warming altered microbial community composition and increased carbon dioxide emissions from soil |
| de Vries et al. [145] | Drought | Nutrient cycling | Drought reduced microbial biomass and enzyme activities, impairing nitrogen and phosphorus cycling |
| Wagg et al. [146] | Land-use intensification | Plant productivity | Intensive land use reduced soil microbial diversity, leading to decreased plant productivity and nutrient uptake |
| Bardgett & van der Putten [147] | Multiple factors | Ecosystem multifunctionality | Soil biodiversity loss due to global change can impair multiple ecosystem functions simultaneously, reducing overall ecosystem performance |

Table 10. Examples of microbial indicators of soil health and ecosystem functioning

| Indicator | Description | Relevance |
|---------------------------|---|---|
| Microbial biomass | Total amount of microbial biomass in soil, often measured by phospholipid fatty acid (PLFA) analysis | Reflects the size and activity of the microbial community, responds to changes in soil management and environmental conditions |
| Microbial diversity | Taxonomic and functional diversity of soil microbial communities, assessed by molecular techniques | Indicates the resilience and stability of soil ecosystems, supports multiple ecosystem functions |
| Functional gene abundance | Abundance of genes involved in key ecosystem processes, such as nitrogen fixation and pesticide degradation | Provides insights into the functional capacity of soil microbial communities, relates to specific ecosystem services |
| Microbial respiration | Rate of carbon dioxide production by soil microbes, measured by substrate-induced respiration (SIR) | Reflects the activity and metabolic potential of the microbial community, responds to changes in soil organic matter and management |

6.2 Microbial Indicators of Soil Health and Ecosystem Functioning

Developing robust indicators of soil health and ecosystem functioning based on microbial communities is an important goal for sustainable land management [167]. Microbial indicators can provide rapid and sensitive measures of soil quality, allowing for early detection of environmental stressors and informing management decisions [168]. Various microbial parameters, such as biomass, diversity, and functional gene abundance, have been proposed as potential indicators of soil health [169].

However, the development and application of microbial indicators face several challenges, including the high spatial and temporal variability of soil microbial communities, the complexity of interactions between microbes and their environment, and the need for standardized sampling and analysis protocols [170]. Future research should focus on identifying robust and scalable microbial indicators that can be easily integrated into soil monitoring and management programs [171].

6.3 Knowledge Gaps and Research Priorities

Despite the significant advances in understanding soil microbiome diversity and its implications for ecosystem functioning, several knowledge gaps and research priorities remain [172]. One key challenge is to better understand the complex interactions between soil microbes and their biotic and abiotic environment across

different spatial and temporal scales [173]. This requires the integration of molecular, ecological, and biogeochemical approaches, as well as the development of new experimental and modeling tools [174].

Another priority is to investigate the functional roles of soil microbial communities in regulating ecosystem processes and services [175]. While much research has focused on describing the taxonomic diversity of soil microbiomes, less is known about the specific functions performed by different microbial groups and how they respond to environmental changes [176]. Addressing this knowledge gap will require the application of functional genomics, metagenomics, and stable isotope probing techniques, among others [177].

Finally, there is a need to better understand the resilience and adaptability of soil microbial communities in the face of multiple, interacting global change stressors [178]. This requires long-term, multi-factor experiments that simulate realistic scenarios of climate change, land-use intensification, and other perturbations [179]. Insights from such studies can inform the development of management strategies and policies to protect and restore soil microbial diversity and function in a changing world [180].

6.4 Integrating Soil Microbiome Diversity into Ecosystem Models

Integrating soil microbiome diversity into ecosystem models is an important frontier for advancing our understanding and prediction of ecosystem dynamics in response to global

change [181]. Ecosystem models, such as those used to simulate carbon and nutrient cycling, have traditionally treated soil microbial communities as a "black box" with simplified functions [182]. However, incorporating the diversity and complexity of soil microbiomes into these models can improve their accuracy and realism [183].

Recent advances in molecular and computational techniques have enabled the development of microbial-explicit ecosystem models that incorporate data on microbial community composition, functional traits, and interactions [184]. These models can simulate the dynamic responses of soil microbiomes to environmental changes and predict their consequences for ecosystem processes [185]. For example, the Microbial-Mineral Carbon Stabilization (MIMICS) model integrates microbial physiology and community dynamics with soil carbon cycling processes, providing a mechanistic framework for predicting soil carbon storage under different management and climate scenarios [186].

Integrating soil microbiome diversity into ecosystem models faces several challenges, including the need for large amounts of empirical data on microbial communities and their functions, the complexity of microbial-environmental interactions, and the computational demands of simulating diverse microbial populations [188]. Future research should focus on developing and testing microbial-explicit models across different ecosystems and scales, as well as coupling these models with other ecological and biogeochemical models to provide a more comprehensive understanding of ecosystem dynamics [189].

6.5 Experiment Result

1. Soil bacterial diversity was significantly higher in grassland ecosystems compared to agricultural fields [190].
2. Fungal diversity was positively correlated with plant species richness in temperate forests [191].
3. Soil microbial biomass carbon increased by 20% in response to long-term organic matter additions [192].
4. Soil enzyme activities (β -glucosidase, N-acetyl-glucosaminidase, and phosphatase) were significantly higher in soils with higher microbial diversity [193].
5. Inoculation with arbuscular mycorrhizal fungi increased plant biomass by 30% and phosphorus uptake by 25% in a greenhouse experiment [194].
6. Soil bacterial community composition shifted significantly in response to a 5-year warming treatment, with an increase in the relative abundance of Firmicutes and a decrease in Acidobacteria [195].
7. Soil microbial respiration increased by 15% in response to a 10% increase in soil moisture [196].
8. Soil bacterial diversity was positively correlated with soil carbon storage across a range of ecosystem types [197].
9. The abundance of nitrogen-fixing bacteria (nifH gene copies) was significantly higher in soils under leguminous cover crops compared to non-leguminous cover crops [198].
10. Soil fungal communities exhibited higher temporal stability than bacterial communities in response to seasonal changes [199].
11. The ratio of fungal to bacterial biomass was significantly higher in forest soils compared to grassland soils [200].
12. Soil microbial diversity was positively correlated with the rate of litter decomposition in a microcosm experiment [201].
13. The abundance of ammonia-oxidizing bacteria (amoA gene copies) was significantly higher in soils with higher nitrogen availability [202].
14. Soil microbial community composition was significantly different between rhizosphere and bulk soil samples [203].
15. The inoculation of soil with a consortium of plant growth-promoting bacteria increased crop yield by 15% in a field experiment [204].
16. Soil bacterial diversity was negatively affected by heavy metal contamination, with a 30% reduction in species richness [205].
17. The abundance of denitrifying bacteria (nirK and nirS gene copies) was significantly higher in wetland soils compared to upland soils [206].
18. Soil microbial biomass nitrogen was positively correlated with soil organic carbon content across a range of soil types [207].
19. The application of biochar to soil increased microbial diversity and altered community

- composition, favouring the growth of Gram-positive bacteria [208].
20. Soil bacterial community composition was significantly different between soil aggregates of different sizes [209].
 21. The abundance of arbuscular mycorrhizal fungi was positively correlated with plant phosphorus uptake in a field experiment [210].
 22. Soil microbial diversity was positively correlated with the resistance and resilience of soil respiration to heat stress [211].
 23. The inoculation of soil with endophytic bacteria increased plant drought tolerance by 20% [212].
 24. Soil fungal diversity was negatively affected by tillage, with a 25% reduction in species richness in tilled soils compared to no-till soils [213].
 25. The abundance of chitinolytic bacteria was significantly higher in soils with higher fungal biomass [214].
 26. Soil microbial community composition was significantly different between different soil horizons [215].
 27. The application of compost to soil increased microbial biomass carbon by 30% and altered community composition [216].
 28. Soil bacterial diversity was positively correlated with the rate of soil nitrogen mineralization [217].
 29. The abundance of sulfate-reducing bacteria was significantly higher in wetland soils compared to upland soils [218].
 30. Soil microbial diversity was positively correlated with the suppression of soil-borne plant pathogens [219].
 31. The inoculation of soil with mycorrhizal fungi increased plant resistance to heavy metal stress by 25% [220].
 32. Soil bacterial community composition was significantly different between soils of different textures (clay, silt, and sand) [221].
 33. The abundance of methanotrophic bacteria was significantly higher in soils with higher methane oxidation rates [222].
 34. Soil microbial biomass phosphorus was positively correlated with soil pH across a range of soil types [223].
 35. The application of nitrogen fertilizer to soil reduced microbial diversity and altered community composition, favouring the growth of copiotrophic bacteria [224].
 36. Soil fungal diversity was positively correlated with the rate of wood decomposition in a microcosm experiment [225].
 37. The abundance of iron-reducing bacteria was significantly higher in waterlogged soils compared to well-drained soils [226].
 38. Soil microbial community composition was significantly different between soils under different vegetation types (grassland, shrubland, and forest) [227].
 39. The inoculation of soil with plant growth-promoting fungi increased plant nutrient uptake and biomass by 20% [228].
 40. Soil bacterial diversity was negatively affected by soil salinity, with a 40% reduction in species richness in highly saline soils [229].
 41. The abundance of cellulolytic bacteria was significantly higher in soils with higher plant litter inputs [230].
 42. Soil microbial diversity was positively correlated with the stability of soil aggregate structure [231].
 43. The application of pesticides to soil reduced microbial biomass carbon by 15% and altered community composition [232].
 44. Soil fungal community composition was significantly different between soils under different land-use types (agricultural, grassland, and forest) [233].
 45. The abundance of phosphate-solubilizing bacteria was significantly higher in soils with higher organic phosphorus content [234].
 46. Soil microbial diversity was positively correlated with the efficiency of soil carbon sequestration [235].
 47. The inoculation of soil with disease-suppressive bacteria reduced the incidence of plant fungal diseases by 30% [236].
 48. Soil bacterial community composition was significantly different between soils of different ages (young, intermediate, and old) [237].
 49. The abundance of nitrite-oxidizing bacteria was significantly higher in soils with higher nitrification rates [238].
 50. Soil microbial biomass and diversity were positively correlated with soil water retention capacity [239].

7. CONCLUSION

Soil microbiome diversity is a critical component of terrestrial ecosystems, playing a vital role in

regulating a wide range of ecosystem functions and services. This comprehensive review has explored the complex dynamics of soil microbial communities, including their composition, structure, and responses to biotic and abiotic factors. By synthesizing findings from cutting-edge research, we have highlighted the intricate interplay between soil microbiome diversity and ecosystem functioning, emphasizing the importance of understanding these relationships in the context of global change.

The application of advanced molecular techniques, such as high-throughput sequencing and metagenomic analysis, has revolutionized our understanding of soil microbial diversity, revealing the immense taxonomic and functional complexity of these communities. However, we have also identified significant knowledge gaps and challenges, such as the need to better understand the functional roles of soil microbes, the complexity of microbial-environmental interactions, and the resilience and adaptability of soil microbial communities to multiple, interacting stressors.

To address these challenges, future research should focus on integrating molecular, ecological, and computational approaches to develop a more comprehensive understanding of soil microbiome diversity and its implications for ecosystem functioning. This includes harnessing the power of soil microbiomes for sustainable agriculture, developing robust microbial indicators of soil health, and integrating soil microbiome diversity into ecosystem models. The protection and restoration of soil microbial diversity should be a key priority for sustainable land management and conservation efforts. This requires the development of management strategies and policies that promote soil health, minimize the impacts of land-use intensification, and enhance the resilience of soil microbial communities to global change stressors.

COMPETING INTERESTS

Authors have declared that no competing interests exist.

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