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REVIEW

Biochar as a Modulator of Soil Microbial Diversity and Enzymatic Function: Critical Insights and Ecological Implications

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Abstract

Biochar amendments can modify soil microbial communities and extracellular enzyme activities, but reported responses remain heterogeneous across soils, biochar types, and management contexts. This review critically synthesises current evidence to identify the conditions under which microbial and enzymatic responses to biochar are most likely. A structured literature search in Web of Science and Scopus was combined with citation tracking of key reviews, meta-analyses, and mechanistic studies. Evidence was synthesised qualitatively, with emphasis on microbial biomass, bacterial and fungal diversity, extracellular enzyme activities, and links with broader soil functions. Microbial biomass carbon responds more consistently to biochar than diversity metrics. Bacterial community composition often shifts, especially in acidic, coarse-textured, nutrient-poor, or otherwise constrained soils, whereas fungal responses are more variable. Potential activities of C-, N-, and P-cycling enzymes are commonly neutral to moderately positive, but interpretation is complicated by assay artefacts, substrate sorption, and co-varying changes in soil pH, nutrient availability, moisture, and microhabitat structure. Evidence supports recurring response windows, defined by combinations of baseline soil constraints, biochar functional traits, application context, and time since application. Biochar effects on soil biological functioning are best interpreted through boundary conditions rather than universal mean responses. Benefits are most predictable when biochar properties are matched to site-specific constraints, whereas risks mainly arise from very high application rates, poorly characterised materials, or mismatched biochar–soil combinations.

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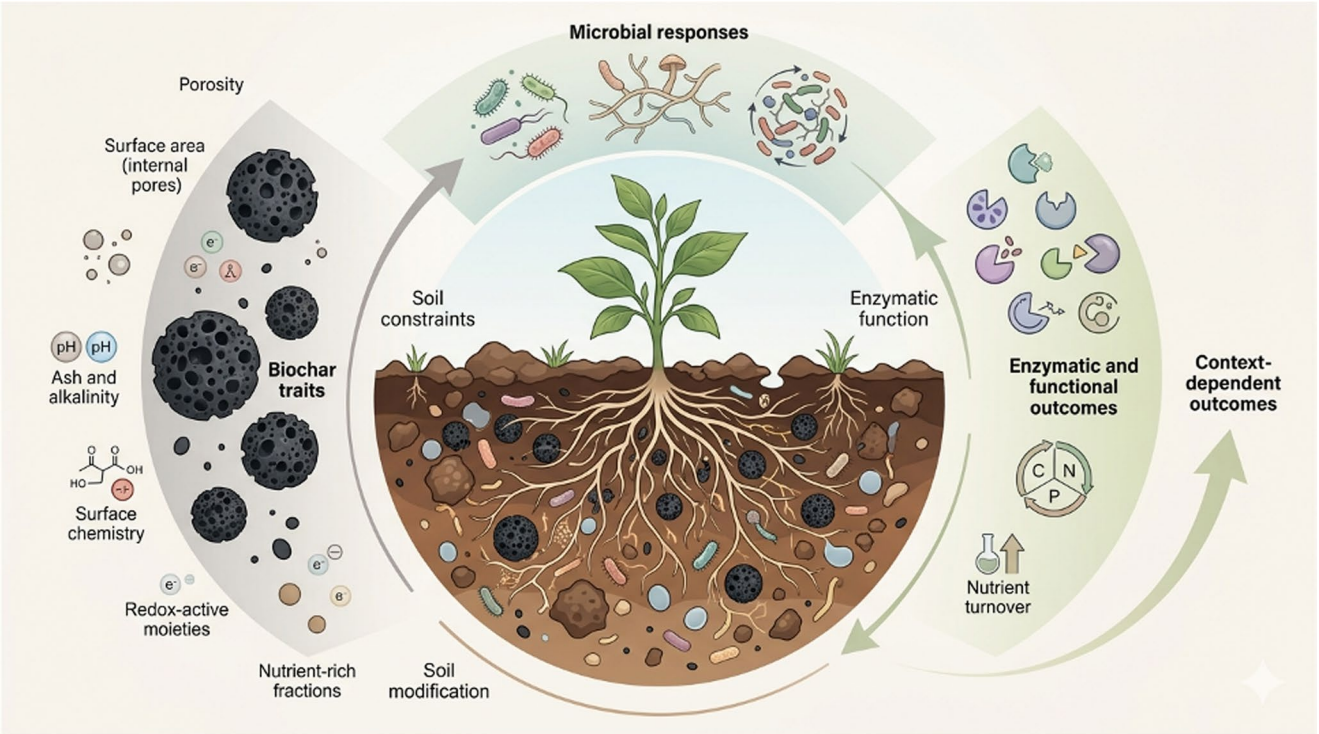
Graphical Abstract



Keywords Soil microbiome · Soil microbial diversity · Extracellular enzyme activities · Nutrient cycling · Greenhouse-gas emissions · Response windows.

1 Introduction

Biochar is a carbonaceous material produced by pyrolysis of biomass under limited oxygen supply. It has been widely investigated as a soil amendment because it can contribute to long-term soil carbon storage through the accumulation of relatively persistent pyrogenic C pools (Kuzyakov et al. 2014; Schmidt et al. 2021; Singh et al. 2012; Woolf et al. 2010, 2021). Biochar can also modify key physicochemical soil properties, including pH, cation exchange capacity, water-holding capacity, and nutrient retention (Lehmann et al. 2011; Librici et al. 2026; Palansooriya et al. 2019a, b; Zhu et al. 2025). However, the magnitude and direction of these effects vary with pedo-climatic conditions, biochar feedstock, pyrolysis conditions, and application rate (Bolan et al. 2024; Deshoux et al. 2023). Application rate is particularly important when interpreting experimental evidence, because many studies, especially those reporting N_2O emission reductions, have used rates of 10–100 t ha^{-1}, whereas field use in practice is often closer to 0.5–1 t ha^{-1} yr^{-1} (Major et al. 2012; Schmidt et al. 2021).

Beyond these physicochemical effects, biochar can influence the biotic component of soils. Soil microorganisms, including bacteria, archaea, fungi, and microbial eukaryotes, regulate nutrient cycling, organic matter turnover, and plant health (Huang et al. 2023; Lehmann et al. 2011; Palansooriya et al. 2019a, b). Biochar-driven changes in soil habitat conditions may therefore co-occur with shifts in microbial community structure, nutrient cycling, and plant–soil interactions. A central interpretative challenge is to distinguish biologically mediated responses from direct physicochemical effects, such as pH correction, sorption, nutrient retention, or altered water availability (Deshoux et al. 2023; Lehmann et al. 2011; Palansooriya et al. 2019a, b). Some biochars also possess redox-active surface moieties that may modify the redox microenvironment experienced by soil microorganisms (Klüpfel et al. 2014; Leng et al. 2022), as discussed further in Sect. 5.

Despite extensive research, biochar effects on the soil microbiome remain difficult to predict across systems (Bolan et al. 2024; Deshoux et al. 2023; Li et al. 2020). Several experiments and meta-analyses report increases in microbial biomass and, under specific conditions, microbial diversity, whereas other studies show negligible responses or declines in selected groups (Kumar et al. 2025; Li et al. 2020; Wang et al. 2023a, b; Xu et al. 2023; Yue et al. 2023).

These contrasting outcomes are commonly associated with differences in baseline soil constraints, biochar feedstock and pyrolysis temperature, application rate, plant presence, and study duration, indicating that microbial responses are strongly conditioned by soil-biochar interactions rather than representing universal effects (Dai et al. 2021; Huang et al. 2023; Khan et al. 2024).

Bacterial and fungal communities may respond differently to the same biochar-induced environmental shifts. These differences reflect contrasting trophic strategies, carbon substrate use, and sensitivity to pH and nutrient availability (Gao et al. 2021; Kracmarova-Farren et al. 2024; Sharma et al. 2025; Wang et al. 2023a, b). Increases in bacterial biomass or diversity are reported more frequently than comparable increases in fungal indicators, and several studies report a higher bacteria-to-fungi ratio after biochar addition, as inferred from PLFA biomarkers, qPCR marker genes, or molecular proxies (Chen et al. 2013; Dai et al. 2021; Kabir et al. 2023; Sharma et al. 2025). Recent meta-analyses are consistent with this pattern: bacterial taxonomic diversity tends to increase on average, whereas fungal diversity often remains unchanged, although between-study heterogeneity remains substantial (Deshoux et al. 2023; Wang et al. 2023a, b; Xu et al. 2023). This apparent contrast may also reflect differences in study coverage, marker choice, and analytical resolution between bacterial and fungal datasets.

In some systems, biochar appears to favour fast-growing and resource-responsive microbial groups, including copiotrophic bacterial taxa, relative to fungi (Sharma et al. 2025; Wang et al. 2023a, b). Under specific crop-pathogen contexts, these shifts may coincide with lower plant disease incidence or severity, especially when biochar-induced changes in soil chemistry, plant nutrition, and rhizosphere microbiota act together (Bhatt et al. 2024; Iacomino et al. 2022). This outcome, however, is not consistently observed and should be interpreted in relation to the targeted pathosystem and management context.

Long-term systems enriched in pyrogenic carbon, such as Amazonian Dark Earths and fire-impacted forest soils, provide a different perspective. In these systems, some studies report stronger shifts in fungal diversity than in bacterial diversity (Glaser et al. 2001; Lucheta et al. 2016). These systems are not directly comparable to most short-term agricultural biochar amendments, but they show that sustained pyrogenic C inputs can be associated with bacterial–fungal balances that differ from those observed in shorter experiments.

Overall, this heterogeneity highlights the need to identify the boundary conditions that delineate benefit and risk windows for biochar effects on soil microbial communities. Benefit windows occur when soil constraints, biochar traits, and management context combine in ways that make microbial responses more likely to be positive than neutral or adverse. In this review, biochar effects are therefore interpreted through soil-biochar interactions, namely how soil conditions, such as pH, texture, organic matter status, and nutrient availability, intersect with biochar functional traits, such as alkalinity, ash content, surface chemistry, redox properties, and porosity (Conte et al. 2021). Although biochar addition increases total soil C stocks and can alter the bulk soil C/N ratio, the pyrogenic C fraction is largely biologically unavailable. Its direct relevance to the microbial C/N balance should therefore be interpreted cautiously (Dai et al. 2021; Palansooriya et al. 2019a, b; Xu et al. 2023).

The aim of this review is to provide a critical and up-to-date synthesis of the understanding of soil-biochar-microbe interactions, with particular emphasis on: (i) biochar-induced shifts in soil microbial communities and biodiversity patterns; (ii) effects on soil enzyme activities involved in major biogeochemical cycles; (iii) relationships between microbial community changes and soil ecosystem functions; (iv) environmental implications in terms of soil health, fertility, and carbon and nutrient fluxes; and (v) current knowledge gaps and future research priorities.

To reconcile heterogeneous findings, we synthesise the evidence using a response-window framework. In this review, response windows denote recurring combinations of baseline soil constraints, biochar functional traits, application context, and time-dependent ageing processes that jointly shape microbial endpoints and functional responses. Baseline constraints include acidity, low resource availability, coarse texture with limited water retention, and poor drainage associated with periodic waterlogging and oxygen limitation. Relevant biochar traits include ash content and alkalinity, residual nutrients and accessible organic fractions, porosity and surface area, and surface chemistry. Application context includes application rate, time since application, observation duration, plant presence, and experimental scale.

The framework is not a predictive model. Rather, it is an organising approach based on moderators repeatedly identified in quantitative syntheses (Table 2). It distinguishes benefit windows, where constraint alleviation drives measurable microbial or enzymatic responses, from risk windows, where trade-offs become more probable, for example when very high application rates or high-EC materials are used in weakly buffered systems. In this sense, the purpose of the review is not simply to summarise mean biochar effects, but to identify the combinations of soil constraints, biochar functional traits, and time-dependent processes under which microbial and functional responses become more or less predictable.

This conceptual framework is summarised in Fig. 1, which illustrates how baseline soil constraint level, biochar

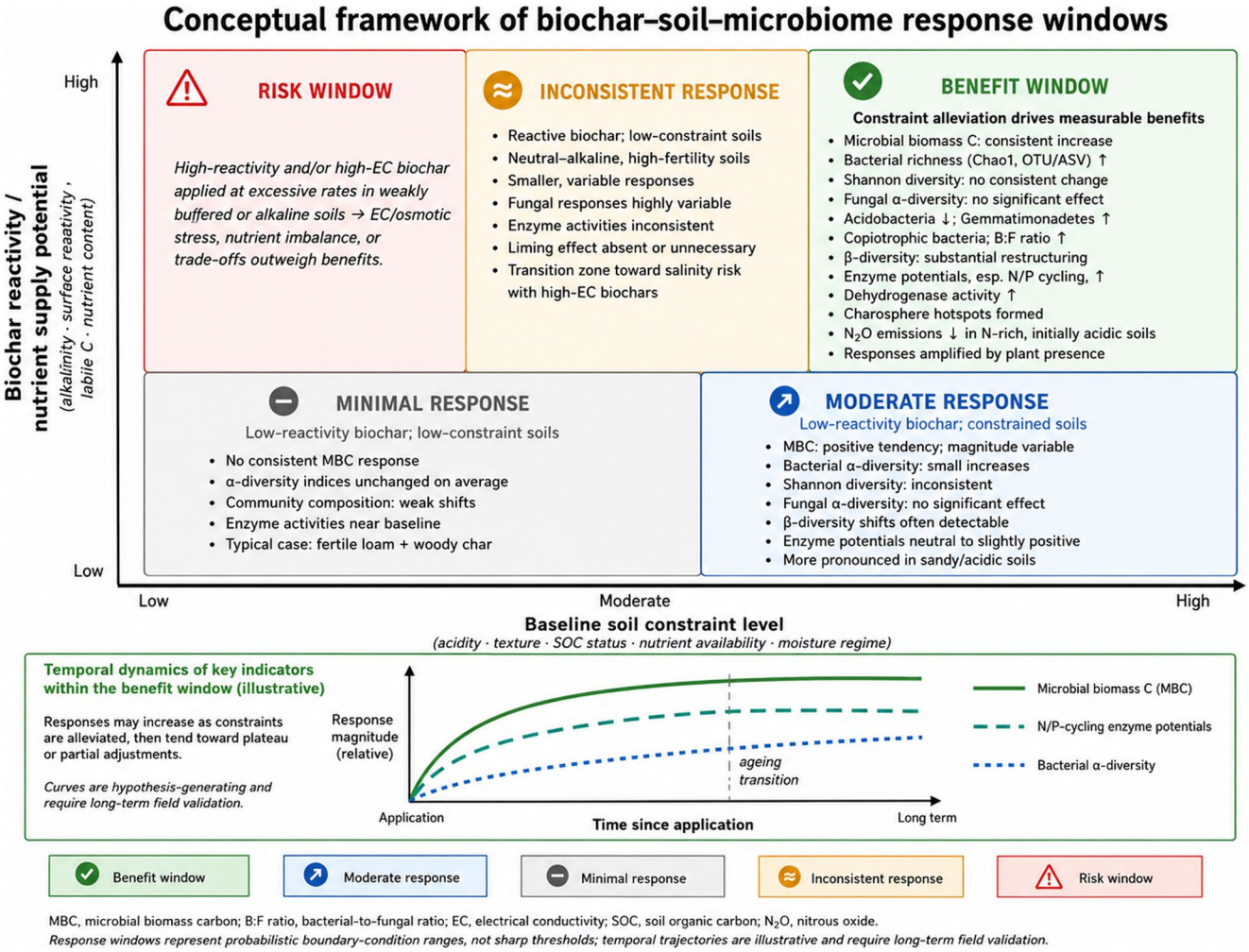


Fig. 1 Conceptual framework of biochar–soil–microbiome response windows. Microbial and enzymatic responses to biochar are represented as a function of baseline soil constraint level (x-axis) and biochar reactivity and nutrient-supply potential (y-axis), with application rate and time-dependent ageing as additional modulating factors. The five domains distinguish conditions under which biochar is more likely to generate beneficial, neutral, inconsistent, or adverse responses. The lower panel is illustrative and hypothesis-generating, showing expected temporal trajectories within the benefit window that still require long-term field validation. Response windows should be interpreted as probabilistic boundary-condition ranges rather than sharp thresholds

reactivity and nutrient-supply potential, application rate, and time since application jointly define benefit windows, risk windows, and intermediate response domains for microbial and enzymatic outcomes.

2 Research Approach and Literature Search

2.1 Search Strategy

This review was developed as a critical narrative synthesis supported by a structured literature search. The search strategy was designed to identify studies examining the effects of biochar on soil microbial communities, microbial diversity, and extracellular enzyme activities, as well as studies linking these responses to broader soil biological functions. The purpose of the search was to assemble a broad and mechanistically informative evidence base for critical synthesis across a heterogeneous literature, rather than to generate a formal quantitative dataset for pooled effect-size estimation.

The core database search was conducted in Web of Science Core Collection and Scopus and was last updated in January 2026. Searches covered publications from 2010 to 2025, consistent with the January 2026 literature update, and were restricted to English-language articles and reviews. In Web of Science Core Collection, the search was performed using the Topic field; in Scopus, the equivalent search was performed using the TITLE-ABS-KEY field. The core search string was: biochar AND soil* AND ("microbial communit*" OR microbiome OR bacteria OR bacterial OR fungi OR fungal OR rhizosphere OR charosphere) AND ("microbial biomass" OR

"extracellular enzyme*" OR "enzyme activit*" OR diversity OR "community composition").

The database search retrieved 2,160 records from Web of Science Core Collection and 2,098 records from Scopus, for a total of 4,258 records. After duplicate removal based primarily on DOI and, where DOI was unavailable, on normalised title matching, 2,876 unique records formed the title-and-abstract screening pool. Records were screened for relevance to biochar application in terrestrial soils and for the presence of microbial, enzymatic, or soil-biological endpoints. The final synthesis cited 184 items, selected because they provided quantitative syntheses, field-based evidence, mechanistic insight, technical or conceptual support, or representative examples of the boundary conditions underlying biochar-microbiome and biochar-enzyme responses.

The core database search was complemented by backward and forward citation tracking of key reviews, meta-analyses, and influential primary studies. This step was used to identify additional relevant publications not captured by the core search string, including selected studies on functional genes, metagenomic or metatranscriptomic approaches, greenhouse-gas dynamics, disease suppression, remediation, and other environmental implications. Citation tracking was also used to retain a small number of seminal pre-2010 studies, recent directly relevant records outside the database time window, and technical standards or certification guidelines where these were needed to support historical, conceptual, or quality-standard statements.

2.2 Scope, Study Selection and Synthesis Approach

The review focused primarily on peer-reviewed studies conducted on terrestrial soils and reporting microbial community endpoints or functional biological indicators. Eligible evidence included studies assessing microbial community composition or diversity through approaches such as amplicon sequencing, shotgun metagenomics, PLFA, and qPCR, as well as studies reporting extracellular enzyme activities, nutrient transformations, greenhouse-gas fluxes, disease suppression, contaminant biodegradation, or other soil-biological outcomes. Relevant technical standards and certification guidelines were also retained when needed to support statements on biochar quality, safety thresholds, or agronomic applicability.

Studies were considered eligible when they met the following criteria: (i) they examined biochar application to terrestrial soils; (ii) they reported microbial, enzymatic, or soil-biological endpoints, including microbial biomass, bacterial or fungal diversity, microbial community composition, PLFA, qPCR, 16 S/ITS amplicon sequencing, metagenomics, metatranscriptomics, extracellular enzyme activities, nutrient transformations, greenhouse-gas fluxes, disease suppression, or contaminant biodegradation; and (iii) they provided sufficient information on soil context, biochar properties, application rate, experimental setting, or time since application to support interpretation of the reported response.

Studies were excluded when they focused exclusively on biochar production without soil application, hydrochar or activated carbon without clear relevance to soil biochar amendment, non-soil systems, purely engineering or wastewater applications, or agronomic and physicochemical outcomes without any microbial, enzymatic, or soil-biological component.

Within this broad evidence base, priority was given to recent meta-analyses and systematic reviews because they provide the strongest basis for identifying recurring moderators and average response directions across heterogeneous studies. These syntheses were complemented by long-term field experiments, multi-site studies, and mechanistic primary studies explicitly linking microbial or enzymatic responses to biochar functional traits, including feedstock, pyrolysis temperature, ash content, alkalinity, nutrient release, porosity, surface chemistry, redox properties, and ageing processes. Primary studies were therefore used mainly when they provided mechanistic insight, representative examples of structure-function coupling, or evidence for specific boundary conditions not sufficiently resolved in quantitative syntheses.

Given the marked heterogeneity of study designs, analytical methods, soil conditions, biochar materials, application contexts, and reported response variables across the literature, this work was not conceived as a meta-analysis. Instead, the evidence was synthesised qualitatively, with emphasis on recurring tendencies, direction of response, magnitude when robustly supported, and the boundary conditions under which specific outcomes were more likely to occur. When findings were inconsistent, discrepancies were interpreted in relation to baseline soil constraints, biochar functional traits, application rate, time since application and associated biochar ageing, plant presence, and study scale (from laboratory incubations to field conditions), rather than being attributed to random variability or treated as universally transferable effects. This framework was used throughout the review to reconcile contrasting findings and to identify the conditions under which biochar is more likely to generate beneficial, neutral, or adverse microbial and biochemical responses.

2.3 Terminology

Several terms are used with specific meanings throughout this review and are defined here to avoid ambiguity. Soil microbial community refers to the taxonomic assemblage

of microorganisms in a soil sample, characterised through composition and diversity metrics. Soil microbiome is reserved for contexts in which the community is considered together with its functional genetic potential or associated metabolic processes, as resolved by shotgun metagenomics or related approaches.

α-diversity denotes within-sample diversity, encompassing both taxon richness and evenness as captured by indices such as Chao1 (richness) or Shannon (richness and evenness). β-diversity describes compositional dissimilarity between samples and is typically assessed through ordination methods and permutational multivariate analysis (PERMANOVA). Unless otherwise specified, reported changes in bacterial or fungal α-diversity refer to these indices; it should be noted that α-diversity indices and community composition (β-diversity) can respond independently to the same treatment.

The bacteria-to-fungi ratio (B: F) is used as a proxy for the relative dominance of bacterial versus fungal biomass. When derived from sequencing-based data (e.g., 16 S rRNA gene versus ITS amplicon read counts), B:F values reflect relative abundances and cannot be interpreted as absolute biomass ratios; PLFA-based estimates are comparably subject to methodological constraints.

Enzyme activities reported in this review are potential activities measured under standardised laboratory conditions (defined substrate concentration, temperature, and pH) and should not be interpreted as direct estimates of in situ process rates. Biochar can sorb enzyme substrates or fluorescent probes, and can interfere with colorimetric detection, potentially causing assay artefacts that are difficult to distinguish from genuine biological responses.

When we use terms such as "increase" or "decrease" in reference to biochar effects, these are shorthand for mean tendencies observed under specified conditions and should not be read as universal predictions. Unless stated otherwise, reported effects are mean directions across studies or within a defined boundary-condition range; individual study outcomes may deviate substantially from these central tendencies.

3 Biochar-Induced Shifts in Soil Microbial Communities

The application of biochar can measurably influence the composition, diversity, and biomass of soil microbial communities. Global meta-analyses report, on average, a positive mean effect of biochar on soil microbial biomass carbon (MBC). Larger responses are generally associated with lower pyrolysis temperatures, nutrient-rich feedstocks, and strongly constrained baseline soils, particularly acidic, sandy, arid, or SOC-poor soils (Kumar et al. 2025; Li et al. 2020; Liao et al. 2016; Pokharel et al. 2020). The quantitative evidence is summarised in Table 2; the following paragraphs focus on the mechanisms and boundary conditions that modulate these responses.

Mechanistically, these patterns are consistent with biochar-driven amelioration of key constraints: in acidic soils, the liming effect can shift pH towards ranges favourable to many neutrophilic taxa, whereas in coarse-textured soils the porous structure and additional sorption sites can enhance water and nutrient retention, thereby supporting microbial proliferation (Premalatha et al. 2023; Singh et al. 2022; Wang et al. 2023a, b). Because biochar can simultaneously alter pH, nutrient availability, and moisture or aeration, attributing biomass changes to direct habitat effects remains difficult. Experimental designs should therefore isolate co-varying drivers through pH-matched or nutrient-matched controls, which are still largely absent from most published studies. Several syntheses indicate that biochar-associated increases in MBC are detectable across study types and tend to be more pronounced in sandy than in clay soils, though magnitudes remain strongly context-dependent (Li et al. 2020; Wang et al. 2023a, b). Under field conditions, effects on the soil microbiota are detectable particularly in degraded or strongly constrained soils and are often of the same order of magnitude as those reported in controlled studies, although their expression is more strongly modulated by site-specific soil, climatic, and management conditions (Kumar et al. 2025; Premalatha et al. 2023).

Biochar effects on soil microbial diversity, typically assessed through α- and β-diversity metrics, are also widely reported; across meta-analyses, bacterial α-diversity shows more frequent but generally small mean increases, whereas fungal α-diversity responses remain inconsistent and strongly context-dependent (Deshoux et al. 2023; Wang et al. 2023a, b). A global meta-analysis across 165 study sites reported a modest but statistically detectable increase in bacterial richness and taxonomic diversity, with substantial heterogeneity across soils, biochar types, application rates, and study durations; mean increases in Chao1 and in richness estimated as operational taxonomic units (OTUs) or amplicon sequence variants (ASVs) were on the order of 4–8%, whereas Shannon diversity showed no consistent change (Xu et al. 2023). The same synthesis documented consistent compositional shifts at the phylum level: Acidobacteria declined by approximately 14%, whereas Gemmatimonadetes increased by approximately 19%, without overall negative effects on bacterial richness. The decline of Acidobacteria is consistent with biochar-induced improvements in soil pH and fertility, because this phylum is typically associated with acidic, low-resource conditions. The increase in Gemmatimonadetes likely reflects pH normalisation rather

than a copiotrophic response, as this phylum is generally associated with neutral-to-alkaline, well-structured soils rather than with high-resource environments (Kalam et al. 2020; Mujakić et al. 2022).

Consistent with these patterns, a meta-analysis across 196 datasets concluded that biochar significantly increases bacterial diversity while having no significant overall effect on fungal diversity (Wang et al. 2023a, b). Fungal communities generally appear less responsive than bacterial communities with respect to α-diversity indices: many studies report no appreciable change in indices such as Shannon following biochar addition, even when substantial compositional shifts occur within fungal assemblages (Deshoux et al. 2023; Wang et al. 2023a, b). This apparent stability at the whole-community level, however, can obscure divergent responses within specific fungal functional guilds, including mycorrhizal symbionts, saprotrophic decomposers, and soil-borne pathogens, which may respond differently and even in decoupled directions from the bacterial component (He et al. 2024).

Mycorrhizal fungi show responses that depend strongly on the soil nutrient context and on the nutrient status conferred by the applied biochar. Biochar may indirectly favour mycorrhizal functioning when it alleviates constraints such as acidity, poor soil structure, limited water retention, or restricted nutrient diffusion, thereby improving root growth and rhizosphere conditions. Conversely, where nutrient-rich biochars, especially P-rich waste-derived materials, substantially increase plant-available P, plant dependence on mycorrhizal nutrient acquisition may decline, potentially reducing mycorrhizal colonisation or fungal abundance. For example, Kolton et al. (2017) found that biochar addition modulated the rhizosphere microbial community, with improved plant performance co-occurring with higher microbial diversity and metabolic potential. Nie et al. (2018), however, observed a decline in fungal populations, attributed to high phosphorus availability released by the biochar, which may disadvantage mycorrhizal associations where P is no longer limiting. It should be noted that the high P availability described in that study is a property specific to biochars derived from P-rich feedstocks such as sewage sludge and organic wastes; biochars produced from primary plant biomass, including wood, straw, and crop residues, generally contain negligible amounts of plant-available P and would not be expected to induce this type of response (Nie et al. 2018; Warnock et al. 2007).

Saprotrophic fungi, which contribute to litter decomposition, organic matter turnover, and extracellular enzyme production, remain comparatively understudied at the guild level within the biochar literature. Biochar can simultaneously affect saprotrophic niches by modifying pH, aeration, moisture, nutrient availability, labile C inputs, and sorption processes. Low-temperature or nutrient-rich biochars may transiently favour fast-growing decomposer fungi by supplying accessible substrates or nutrients, whereas highly carbonised woody biochars may mainly provide habitat structure with limited directly available C. However, because many studies report fungal communities at broad taxonomic or diversity levels, direct evidence separating saprotrophic responses from other fungal guilds remains limited. This represents an important evidence gap, and guild-level interpretations should therefore be supported, where possible, by enzyme activities, decomposition measurements, or functional annotation tools rather than inferred from fungal α-diversity alone (Dai et al. 2021; Nguyen et al. 2016; Zhang et al. 2025).

Plant-pathogenic fungi represent a third guild with direct agronomic relevance. Several studies report that biochar amendment can reduce disease severity or modify the relative abundance of soil-borne pathogens, but these effects are highly pathosystem-specific. Apparent suppression of fungal pathogens may arise from multiple interacting mechanisms, including changes in rhizosphere microbiota, enrichment of antagonistic bacterial populations, sorption or deactivation of pathogen-derived toxins and enzymes, and induction of plant defence responses. Several studies report biochar-induced declines in the relative abundance or activity of specific soil-borne fungal pathogens, including *Rhizoctonia solani* and *Fusarium* spp., often coinciding with reduced disease severity (Bhatt et al. 2024; Bonanomi et al. 2015; Iacomino et al. 2022; Jaiswal et al. 2014, 2017; Jin et al. 2022). However, the underlying mechanisms are frequently multifactorial, involving induction of plant systemic resistance, deactivation of pathogen-derived toxins and enzymes, and shifts in antagonistic rhizosphere populations, rather than a simple compositional decline of the pathogen itself (Elad et al. 2010; Graber et al. 2014; Jaiswal et al. 2018, 2020). Reductions in putative fungal pathogens should therefore not be interpreted as evidence of disease suppression unless supported by direct disease assessments or pathogen-specific measurements. At the broader community level, these guild-specific responses may contribute to shifts in the relative balance between bacteria and fungi. Biochar amendment frequently shifts the community towards bacterial dominance, as reflected by an increase in the bacteria-to-fungi (B: F) ratio inferred from PLFA biomarkers, qPCR marker genes, or molecular proxies (Chen et al. 2013; Dai et al. 2021; Kabir et al. 2023; Sharma et al. 2025). However, this pattern is highly dependent on soil type, application rate, biochar feedstock, nutrient status, plant presence, and time since application. Therefore, fungal responses should be interpreted not only through total fungal α-diversity, but also through guild-level changes and

their links with mycorrhizal functioning, decomposition, disease regulation, and plant-soil feedbacks.

Importantly, this tendency towards bacterial dominance is not universal: in a long-term semiarid farmland experiment, very high application rates (up to 50 t ha^{-1}) were associated with a relatively greater increase in fungal than bacterial diversity (Luo et al. 2017), and comparative experiments confirm that both soil type and application rate substantially modulate the emerging community structure and the abundance of functional groups such as nitrifying and denitrifying bacteria (Hu et al. 2023; Zhong et al. 2022). Taken together, these findings reinforce that biochar effects on soil microbial communities are strongly context dependent and help explain the wide variability reported across studies (Dai et al. 2021; Wang et al. 2023a, b). Compartment-specific patterns and their main moderators are summarised in Table 1.

Beyond α-diversity, β-diversity shifts significantly following biochar addition, reflecting a substantial restructuring of community composition (Deshoux et al. 2023; Wang et al. 2022, 2023a, b). These compositional shifts co-occur with changes in soil pH/alkalinity and labile C and nutrient availability, though causal attribution requires pH-matched or nutrient-matched controls. In the presence of plants, effects tend to be more pronounced, reflecting differential effects between the rhizosphere and bulk soil, and are further modulated by biochar feedstock and pyrolysis temperature (Kolton et al. 2017; Kracmarova-Farren et al. 2024; Li et al. 2020; Palansooriya et al. 2019a, b).

Table 1 Compartment-specific patterns of biochar effects on soil microbial communities and on the bacteria-to-fungi ratio

Microbial compartment/indicator*	Common biochar-driven response	Main moderators	Notes/limitations	Key references
Bulk soil	Community composition (16 S/ITS; β-diversity) often shifts even when α-diversity changes are small, with recurrent enrichment of resource-responsive bacterial taxa and groups linked to C/N/P cycling.	Biochar feedstock and pyrolysis temperature; application rate; baseline soil conditions (pH, texture, fertility, SOC); ageing and study duration.	Direction and magnitude are context-dependent; fungal α-diversity responses are frequently weak/non-significant, even when composition changes. In the large majority of available studies, pH-matched or nutrient-matched controls are absent, making it difficult to attribute observed responses specifically to biochar as a habitat material rather than to indirect pH or nutrient effects.	(Li et al. 2020; Xu et al. 2023; Wang et al. 2023a, b; Kracmarova-Farren et al. 2024; Deshoux et al. 2023)
Rhizosphere	Plant-mediated compositional shifts are often stronger than in bulk soil; biochar can intensify spatial heterogeneity by creating 'charosphere' microhabitats and by modifying root-microbe interactions.	Plant species/genotype; soil nutrient status and root exudation; biochar alkalinity/ash and porosity; application rate; time since application.	Effects can be particularly pronounced in soils with strong baseline limitations; fungal responses are often more variable than bacterial responses.	(Kolton et al. 2017; Kracmarova-Farren et al. 2024; Ran et al. 2023; He et al. 2024; Li et al. 2023)
Root endosphere	Endophytic prokaryote composition can change indirectly via rhizosphere filtering; effects are typically smaller than rhizosphere responses and can be soil-dependent.	Plant genotype; soil type; rhizosphere conditions; time; biochar properties that shape the rhizosphere niche.	Evidence base is still limited compared with bulk soil and the rhizosphere; responses are often specific to particular microbial taxa and are not consistent across soils.	(Kracmarova-Farren et al. 2024)
Bacteria-to-fungi ratio (B: F)*	Frequently increases (more bacteria-dominated communities), as inferred from PLFA, qPCR marker genes, or sequencing proxies; not universal.	Application rate; pyrolysis temperature and ash/liming potential; nutrient inputs; time/ageing; baseline soil conditions.	B: F values derived from sequencing data reflect relative abundances, not absolute biomass; PLFA-based estimates are subject to different methodological constraints. Some studies report relatively stronger fungal responses under high application rates or after longer observation periods, but this pattern is not universal and should be interpreted alongside soil pH, soil nutrient status, and plant presence.	(Chen et al. 2013; Dai et al. 2021; Sharma et al. 2025; Wang et al. 2023a, b; Luo et al. 2017)

* The bacteria-to-fungi ratio (B: F) is not a soil compartment sensu stricto but is included here as a widely reported community-level indicator for comparative purposes

A key spatial concept in this context is the "charosphere", the microbial hotspot that forms around biochar particles and was first described by Quilliam et al. (2013). Several studies have documented the formation of microhabitats with sharp pH gradients and locally elevated concentrations of nutrients and labile C, which drive community reorganisation at the particle scale (Pietikäinen et al. 2000; Ran et al. 2023; Thies and Rillig 2012). In acidic soils, these microhabitats can selectively favour neutrophilic bacteria over acidophilic taxa such as Acidobacteria. In nutrient-poor soils amended with nutrient-rich biochars, they may also stimulate resource-responsive taxa, including copiotrophic representatives within Actinobacteriota and Firmicutes (Deshoux et al. 2023; Kalam et al. 2020; Mujakić et al. 2022). Beyond their role as microhabitats for colonisation, biochar pores have been proposed to provide partial refuges for bacteria against predation by protists and nematodes. This mechanism, often described as the shelter effect, remains supported by limited direct experimental evidence. If present, it may partly decouple increases in microbial biomass from functional activity (Asiloglu 2022; Asiloglu et al. 2021). These recurrent patterns are sometimes associated with functional shifts in soil processes, as discussed in Sect. 4, though the strength of microbiome-function coupling remains context-dependent. A concise overview of relevant quantitative syntheses and their reported moderators is provided in Table 2.

Taken together, the evidence is consistent with recurring response windows. The most frequently reported microbial biomass and compositional responses occur when biochar alleviates strong baseline constraints, most commonly acidity and low resource availability. These responses are especially likely in coarse-textured or SOC-poor soils amended with biochars that supply alkalinity, ash, accessible nutrients, or labile C fractions.

Plant presence often amplifies these shifts through rhizosphere feedbacks, whereas neutral-to-alkaline, high-fertility soils more frequently show smaller and less consistent responses. By contrast, very high application rates or biochars with high soluble ash content can cause sharp increases in soil salinity, particularly in weakly buffered or already alkaline soils. Under these conditions, trade-offs and occasional declines in selected microbial or enzymatic indicators become more likely (Librici et al. 2026).

4 Biochar-Induced Changes in Soil Extracellular Enzyme Activities

Beyond changes in microbial community composition, biochar can influence potential soil enzyme activities, particularly extracellular hydrolases involved in C, N, and P cycling and proxy indicators of microbial oxidative activity such as dehydrogenase (Bolan et al. 2024; Liao et al. 2022; Sharma et al. 2025). Across studies, key soil enzymes show neutral to moderately positive mean responses to biochar application, consistent with the alleviation of limiting conditions such as acidity, low nutrient availability, low labile C, or limited moisture. Meta-analytic evidence indicates mean increases in urease, alkaline phosphatase, and

Table 2 Overview of quantitative syntheses (meta-analyses) of biochar effects on soil microbial biomass and diversity, and typical moderators reported across studies.

Endpoint	Evidence base	Mean direction/magnitude (overall)	Key moderators/boundary conditions	Notes	Reference(s)
Microbial biomass carbon (MBC)	72 studies; 964 observations	+21.7% vs. control	Stronger responses in low-fertility or otherwise strongly constrained soils; magnitude also varies with application rate	High between-study heterogeneity; effect sizes represent global averages	Pokharel et al. (2020)
Total microbial biomass (various metrics)	999 experimental comparisons	Increase on average (magnitude context-dependent)	Biochar pyrolysis temperature; biochar ash and nutrient content; soil properties (pH, texture, SOC status)	The use of different biomass proxies (e.g., fumigation-extraction, PLFA) limits comparability	Li et al. (2020)
Bacterial α-diversity (Chao1; OTU/ASV richness; Shannon)	165 study sites	+4–8% for Chao1 and OTU/ASV richness; Shannon generally not significant	Edaphic context and soil management influence magnitude; responses often linked to pH and resource availability shifts	Phylum-level averages: Acidobacteria − 14.6%; Gemmatimonadetes + 19.8%	Xu et al. (2023)
Bacterial vs. fungal diversity (overall)	196 datasets	Increased bacterial diversity; no significant overall change in fungal diversity	Soil constraints and biochar traits modulate responses; fungal indices often less responsive on average	Fungal community structure may shift even when α-diversity indices do not	Wang et al. (2023a, b)

Percentage values summarise mean relative changes versus controls as reported in the cited meta-analyses. Because effect-size metrics and inclusion criteria differ across syntheses (e.g., ln response ratios vs. weighted mean differences; field vs. laboratory balance), these magnitudes should be interpreted as indicative and used primarily to compare direction and boundary conditions, rather than as directly interchangeable universal effect sizes. Reported precision and significant figures follow the original publications

MBC microbial biomass carbon, *OTU* operational taxonomic unit, *ASV* amplicon sequence variant, *SOC* soil organic carbon

dehydrogenase following biochar amendment, although enzyme- and site-specific decreases can still occur under particular boundary conditions. Reported changes should be interpreted as shifts in functional potential rather than direct in situ process rates, not least because most assays are subject to artefacts such as substrate sorption, colour quenching, and changes in assay pH (Garbuz et al. 2022; Liao et al. 2022; Pokharel et al. 2020; Sharma et al. 2025).

Pyrolysis temperature is one of the most consistently identified moderators of enzymatic responses. Low-temperature biochars are more often associated with increases in enzymes involved in C, N, and P acquisition, whereas high-temperature biochars tend to show weaker or non-significant effects (Jin et al. 2024; Liao et al. 2022; Tomczyk et al. 2020; Zhang et al. 2019). This difference reflects the contrasting surface chemistry of the two material types: low-temperature biochars retain a larger fraction of labile organic compounds and oxygen-containing functional groups, which can act as substrates or co-factors stimulating microbial and enzymatic activity (Keiluweit et al. 2010; Liao et al. 2022; Tomczyk et al. 2020). High-temperature biochars, by contrast, have more carbonised and recalcitrant surfaces that interact more weakly with extracellular enzymes and may adsorb enzymes or substrates, potentially reducing apparent activities in assays or in the soil solution (Bailey et al. 2011; Paz-Ferreiro et al. 2012). Consequently, when the goal is to stimulate soil enzymatic activity in the short term, medium- to low-temperature biochars are more likely to elicit measurable increases in potential activities, although trade-offs exist with respect to carbon stability, sorption capacity, and liming intensity (Tomczyk et al. 2020; Wang et al. 2020).

Feedstock type is a second important moderator. Biochars produced from nutrient-rich feedstocks (manures, sewage sludge, and organic wastes) are generally associated with stronger enzymatic responses than wood-derived or otherwise nutrient-poor materials, reflecting the higher nutrient and ash inputs and greater availability of reactive organic fractions (Holatko et al. 2025; Zhang et al. 2019). In practice, feedstock and pyrolysis temperature interact: their combined effects on labile C content, nutrient supply, and surface chemistry jointly determine the magnitude and direction of enzymatic responses in a given soil context. Because P availability in P-rich feedstocks generally declines with increasing pyrolysis temperature, sewage-sludge biochars intended for nutrient recovery are often produced at relatively low to moderate temperatures (Rathnayake et al. 2023). Table 3 summarises these response patterns across the main soil enzyme classes.

Enzymatic responses also vary over time following biochar addition. In many studies, dehydrogenase and urease activities increase shortly after application, then stabilise or decline slightly as the biochar ages in soil. This pattern has been attributed to shifts in sorption-desorption equilibria and progressive microbial adjustment to the amended habitat (Bailey et al. 2011; Jones et al. 2012; Li et al. 2018; Zimmerman 2010). Responses of other hydrolases, such as β-glucosidase and arylsulfatase, tend to be more variable across soils and experimental conditions (Paz-Ferreiro et al. 2012; Zhang et al. 2019).

Application rate and soil properties introduce further non-linearity: very high application rates may fail to provide additional enzymatic benefits and can occasionally reduce activities through excessive sorption or nutrient imbalances (Garbuz et al. 2022; Liao et al. 2022; Pokharel et al. 2020). Stronger responses are consistently reported in acidic or coarse-textured soils and in the rhizosphere, where biochar alleviates limiting conditions and creates favourable microhabitats for microbial activity (Ali et al. 2025; Fan et al. 2023; Kolton et al. 2017; Pei et al. 2020). In contaminated settings, biochar can sorb contaminants and thereby reduce their bioavailable fraction, which may stimulate enzyme activities involved in their degradation, although outcomes depend strongly on contaminant type, biochar sorption properties, and the broader soil context (Haider et al. 2022; Sanchez-Hernandez et al. 2019; Sigmund et al. 2018; Singh et al. 2024). Taken together, biochar most reliably enhances soil enzymatic functioning when it alleviates dominant baseline constraints, particularly in degraded soils where microbial activities are initially depressed (Bolan et al. 2024; Palansooriya et al. 2019a, b; Sharma et al. 2025).

5 Linking Structure and Function: From Microbiome Shifts to Functional Outcomes

Biochar-induced changes in microbial community composition can co-occur with functional shifts, but isolating specifically microbial contributions remains challenging. Biochar simultaneously modifies several abiotic conditions that regulate process rates, including pH, nutrient availability, moisture, and microhabitat structure (Dai et al. 2021; Lehmann et al. 2011; Palansooriya et al. 2019a, b; Xu et al. 2021). Community composition and process rates can be partially decoupled through functional redundancy and co-varying abiotic drivers, so the relationship between taxonomic shifts and ecosystem-level outcomes is rarely linear (Allison and Martiny 2008; Eisenhauer et al. 2023; Graham et al. 2016; Louca et al. 2018; Philippot et al. 2013). An additional mechanism that has received increasing attention concerns the redox-active and, in some biochars, electrically conductive character of the material. Quinone-like surface moieties and other redox-active functional groups may participate in electron-transfer processes, while sufficiently

Table 3 Typical patterns in the responses of major soil enzyme classes to biochar amendments across feedstock types

Enzyme group (examples)	Overall mean response (meta-analyses where available)	Feedstock pattern (typical)	Key moderators/ boundary conditions	Key reference(s)
C-cycling hydrolases (β-glucosidase, α-glucosidase, cellulase)	More variable than N and P enzymes. Low-T: ~+4% (C enzymes); High-T: near-zero (often n.s.).	Nutrient-rich biochars tend to stimulate C hydrolases more than high-T woody biochars, which often have low to neutral effect on early C-hydrolase activity.	Pyrolysis temperature (labile C preservation); baseline SOC/substrate supply; sorption of enzymes/substrates; time/ageing.	Zhang et al. (2019); Liao et al. (2022); Dotaniya et al. (2024); Wojewódzki et al. (2022)
N-cycling enzymes (urease; other N-acquiring hydrolases)	Positive on average. Urease: +23.1% (global); N enzymes: ~+14% overall. Low-T: ~+23%; High-T: ~+6% (often n.s.).	Manure/sludge biochars generally show stronger increases than wood-derived biochars due to higher nutrient/ash inputs; woody biochars often smaller/neutral unless soils are strongly N-limited/acidic.	Application rate (non-linear; saturation at high rates), soil pH/texture; plant presence (rhizosphere) often amplifies responses; short-term transients at very high application rates.	Pokharel et al. (2020); Zhang et al. (2019); Liao et al. (2022); Holatko et al. (2025)
P-cycling enzymes (acid/alkaline phosphatase; phosphomonoesterase)	Positive on average. Alkaline phosphatase: +25.4% (global); P enzymes: ~+11% overall. Low-T: ~+12%; High-T: ~+1% (often n.s.).	Nutrient-rich biochars (manure/sludge/wastes) often stimulate phosphatases more strongly via nutrient inputs and pH correction, particularly in acidic or contaminated soils.	Soil pH (liming), P status and metal/toxic constraints; enzyme/substrate sorption on highly sorptive chars; time since application.	Pokharel et al. (2020); Zhang et al. (2019); Liao et al. (2022); Paz-Ferreiro et al. (2012)
S-cycling enzymes (arylsulfatase)	Often positive but context-dependent; increases reported especially when biochar alleviates toxicity/acidification. No global meta-analytic estimate available; values based on individual studies.	More frequent stimulation with nutrient-rich feedstocks (e.g., sewage sludge) than with high-T woody biochars; woody biochars can be neutral unless other constraints are alleviated.	Soil S demand and organic matter; co-limitation by pH/moisture; biochar surface interactions; rhizosphere effects.	Paz-Ferreiro et al. (2012); Zhang et al. (2019)
Oxidoreductase proxy (dehydrogenase)	Positive on average. Dehydrogenase: +19.8% (global). Low-T: ~+22%; High-T: ~+0.5% (often n.s.).	Strong stimulation often observed for low-T manure/sludge biochars; for high-T woody biochars commonly weak/neutral.	Pyrolysis temperature and labile fractions; application rate; baseline microbial activity (stronger in degraded soils); temporal dynamics during ageing.	Pokharel et al. (2020); Liao et al. (2022); Paz-Ferreiro et al. (2012); Gascó et al. (2016)

Low-T low pyrolysis temperature (≤500 °C), *High-T* high pyrolysis temperature (≥500 °C), *n.s.* non-significant, *SOC* soil organic carbon

carbonised biochars can, under some conditions, facilitate extracellular electron exchange or modify the redox microenvironment experienced by microorganisms (Hagemann et al. 2025; Kappler et al. 2014; Klüpfel et al. 2014). These mechanisms have been proposed as potentially relevant to denitrification and other redox-sensitive processes, but the available evidence does not yet support broad generalisation across biochar types and soils. Rather, any contribution of electron-transfer-related mechanisms should be interpreted together with co-varying controls such as pH, mineral N availability, moisture regime, oxygen status, and biochar ageing. Accordingly, redox-active and conductive properties should be viewed as possible modifiers of response windows rather than as stand-alone predictors of microbial or biogeochemical outcomes.

A clear illustration of structure-function decoupling comes from studies of N cycling. Even a pronounced increase in nitrifying bacteria quantified at the DNA level may not translate into higher nitrification rates if soil pH remains sub-optimal or inorganic N is limiting. Under these conditions, community abundance and process rate become uncoupled (Borchard et al. 2019; Cayuela et al. 2014; Harter et al. 2014; Liu et al. 2018; Philippot et al. 2013). In contaminated soils, coupling is more readily observed but depends on the mechanism of action: biochar may facilitate the recovery of degradative microbial activity primarily by reducing contaminant bioavailability through sorption, thereby relieving toxicity pressure on degrading communities rather than directly stimulating their activity. Where this occurs, faster apparent dissipation and lower plant uptake have been reported, but outcomes remain strongly dependent on contaminant chemistry, biochar ageing, sorptive behaviour, and site conditions (Haider et al. 2022; Li et al. 2025; Mukherjee et al. 2022; Shi et al. 2024; Singh et al. 2024; Sun et al. 2020; Xiang et al. 2022).

Taken together, these examples illustrate that biochar-induced microbial shifts can co-occur with measurable functional responses, but the strength and direction of this

coupling remain strongly dependent on soil conditions, biochar traits, and management context. Structure-function links tend to be most apparent when constraint relief co-occurs with rhizosphere feedbacks; partial decoupling is more common when abiotic limitations or functional redundancy dominate. Representative examples of biochar-driven microbial shifts linked to functional responses and ecosystem-level outcomes are summarised in Table 4.

Understanding these relationships therefore requires approaches that go beyond co-occurrence patterns. Recent studies advocate complementing amplicon sequencing-based community data with functional multi-omics

Table 4 Representative examples of biochar-driven microbial taxonomic shifts linked to functional responses (enzyme activities and/or soil process rates) and ecosystem-level outcomes. Examples are illustrative and do not imply universal causality; mechanistic confirmation requires targeted controls and direct process or disease measurements

Scenario / system	Biochar intervention	Microbial shift (taxa / guilds / genes)	Functional response (enzymes / processes)	Ecosystem-level outcome / interpretation	Key references
Cotton-cropping and paddy soils (bulk/rhizosphere)	Biochar amendment (field context; soil type varies)	↑ *Pseudomonas* (PGPR/antagonists); ↓ *Nitrospira* (nitrifiers)	Inferredreduced nitrification potential and/or altered pathogen pressure (requires confirmation with direct rate measurements and/or disease assessments)	Potentially improved crop performance; possible reduction in nitrate losses under some conditions	Bhatt et al., 2024; G. Han et al., 2017; Kolton et al., 2017; Yin et al., 2020
Crop-residue return / biochar-straw systems (incl. paddy soils)	Biochar co-applied with straw residues	Selection for decomposer communities (copiotrophic bacteria) under higher pH / improved C/N balance	C-degrading enzymes; enhanced activity along multiple residue decomposition pathways (hydrolytic and oxidative)	Faster straw decomposition and nutrient release to crops	Y. Qi et al., 2021; Xia et al., 2024; S. Zhang et al., 2025
Cambisol and Luvisol (contrasting biochars)	Bone-derived biochar (P-, Ca-rich) vs wood-derived biochar	Bone-derived: stimulation of P-cycling microorganisms; Wood-derived: stimulation of general copiotrophs	Bone-derived: ↑ phosphatase-related activity; Wood-derived: ↑ C- and N-degrading hydrolases	Biochar-specific nutrient inputs create distinct "hotspots" (P availability vs labile C habitat effects)	Holatko et al., 2025; Kracmarova-Farren et al., 2024; Ghorbani et al., 2025; Grafe et al., 2021; Kruse et al., 2022; Tang et al., 2019
Organic-pollutant / pesticide-contaminated soils	Biochar amendment (often acting as sorbent + habitat/carrier for degraders)	↑ pesticide-degrading bacteria and associated catabolic genes; reduced toxicity via sorption	↑ pollutant dissipation rates; recovery/stimulation of microbial metabolism and enzyme activities	In some systems, faster remediation and lower contaminant assimilation by plants	Haider et al., 2022; Mukherjee et al., 2022; Shi et al., 2024; S. Li et al., 2025; R. P. Singh et al., 2024; Sun et al., 2020; Xiang et al., 2022; S. Qi et al., 2024; Wu et al., 2025
N cycling and greenhouse-gas regulation	Biochar amendment across contrasting soils; context strongly dependent (pH, N availability, moisture)	Shifts in nitrifiers/denitrifiers and shifts in the abundance of functional marker genes (e.g., *amoA*, *nirK/nirS, nosZ*), quantified at DNA level, may occur without corresponding changes in transcriptional activity or process rates	Changes in nitrification/denitrification rates and N_2O emissions can be decoupled from community shifts under limiting conditions	N_2O mitigation is possible but depends on boundary conditions and co-limiting factors	Borchard et al., 2019; Cayuela et al., 2014; Harter et al., 2014; Q. Liu et al., 2018; Philippot et al., 2013
Rhizosphere carbon use and plant-growth related functions	Biochar in vegetated systems (field and greenhouse studies)	Enhanced bacterial utilisation of plant-derived C; shifts in rhizosphere community structure	Coupled changes in C-cycle functional activity (respiration/enzyme profiles) and nutrient mobilisation	Improved rhizosphere functioning potentially supporting plant growth	Kolton et al., 2017

C/N carbon-to-nitrogen ratio, *DOC* dissolved organic carbon, *N_2O* nitrous oxide, *PGPR* plant growth-promoting rhizobacteria, *POPs* persistent organic pollutants

approaches, including metagenomics, metatranscriptomics, and metabolomics, alongside direct measurements of enzyme activities and ecosystem-level process rates, to assess when and how community shifts translate into functional outcomes (Graham et al. 2016; Jansson and Hofmockel 2019; Louca et al. 2018; Naylor et al. 2020). Robust microbiome-to-function links, however, require causal support rather than correlation alone. Suitable approaches include isotope tracers, expression-level data, and manipulative experiments that disentangle biochar-driven physicochemical changes from biotic mechanisms. Such integration may inform the development of fit-for-purpose biochars and management packages, but should be interpreted as context-dependent unless mechanistic attribution has been explicitly demonstrated.

6 Environmental Implications

The interactions between biochar, soil microbial communities, and extracellular enzymes can have broader environmental relevance; however, the following domains are discussed here only insofar as they can be plausibly linked to the microbial and biochemical responses reviewed above. These include: (i) carbon sequestration and greenhouse-gas-related outcomes, (ii) soil fertility and plant productivity, (iii) biological control of soil-borne pathogens, and (iv) bioremediation of contaminated soils.

One motivation for biochar use is its recognised contribution to long-term carbon storage and climate-change mitigation in terrestrial systems (IPCC 2019). The magnitude and permanence of this effect depend on biochar properties and environmental context (Schmidt et al. 2019, 2025; Woolf et al. 2010, 2021). Climate-related benefits beyond biochar carbon storage depend on how biochar interacts with microbial decomposition, root activity, and greenhouse-gas-related processes (Fidel et al. 2019; L. Wang et al. 2023a, b). Evidence on soil CO_2 responses remains difficult to interpret because measured efflux integrates microbial mineralisation, root respiration, and plant-soil feedbacks, and both biotic and abiotic processes can contribute to short-term CO_2 release after biochar addition (Blanco-Canqui et al., 2021; He et al. 2017; Jones et al. 2011). Across studies, average CO_2 responses are generally small and strongly context-dependent, reinforcing the need to interpret them in relation to soil conditions, plant presence, and biochar properties (Fidel et al. 2019; Zhang et al. 2020).

Responses in methane dynamics are often non-significant in upland soils, whereas in hydromorphic systems such as rice paddies, lower CH_4 emissions are more frequently reported, possibly reflecting biochar-induced structural and redox shifts that constrain methanogenesis. These contrasting patterns are consistent with the response-window framework: CH_4-related outcomes depend on the interaction between baseline soil moisture regime, oxygen status, and biochar properties, rather than representing a universal effect of biochar amendment (Bu et al. 2022; Cong et al. 2018; Han et al. 2016; Jeffery et al. 2016; Ji et al. 2018; Nan et al. 2021).

For N_2O, emission reductions are reported more frequently than for CH_4, but the mechanisms are multifactorial and should not be interpreted as direct consequences of microbial community shifts alone (Cayuela et al. 2013, 2014; Kaur et al. 2023; Zhang et al. 2023). Proposed mechanisms include liming-driven changes in denitrification pathways and enhanced completion of denitrification to N_2 (Cayuela et al. 2013, 2014; Harter et al. 2016a, b), altered pore structure and water-filled pore space, and changes in mineral N availability (Hüppi et al. 2015; Kammann et al. 2017). Gas entrapment of N_2O within the biochar pore network has also been proposed as a contributing factor (Kaur et al. 2023; Rittl et al. 2021; Davys et al. 2023). Redox-active surface moieties and shifts in denitrifier communities may also contribute, but they probably operate together with broader physicochemical controls such as pH, mineral N availability, oxygen status, and soil moisture (Pascual et al. 2020; Yang et al. 2022; Yuan et al. 2019; Zhang et al. 2024).

Stronger N_2O mitigation is most often observed in fertilised, N-rich, initially acidic, or structurally constrained soils, whereas effects are generally smaller or more inconsistent in well-drained systems with limited mineral N. Biochar carbonisation is another important moderator. In particular, Cayuela et al. (2015) identified the molar H: C_{org} ratio as a key predictor of N_2O mitigation efficacy: biochars with H: $C_{org} < 0.3$ reduced N_2O emissions more strongly than less condensed materials with H: $C_{org} > 0.5$. This indicates that pyrolysis temperature alone should not be treated as a stand-alone predictor of N_2O mitigation. Structural and surface-chemical properties linked to carbonisation may therefore be more informative moderators.

Biochar application can result in agronomic benefits through pH effects, improved nutrient retention, altered sorption-desorption equilibria, and biochar nutrient release, especially in highly weathered or nutrient-poor soils (Ding et al. 2016, 2022; Pokharel et al. 2020). These benefits should not be extrapolated to already fertile systems, where responses are typically smaller or absent (Alkharabsheh et al. 2021; Bekchanova et al. 2024; Conte et al. 2021; Liu et al. 2025). In addition to these direct physicochemical pathways, biochar may stimulate microbial activity and accelerate mineralisation of native soil organic matter, a process known as positive priming (Rasul et al. 2022). When positive priming occurs, nutrient recycling and short-term mineral nutrient availability may increase. However, priming

responses are bidirectional, and their magnitude depends strongly on biochar type, soil organic matter status, nutrient availability, and observation time (Rasul et al. 2022).

Disease suppression represents a further environmental implication of biochar's effects on soil biota. Across published studies, biochar amendment has been associated with lower disease severity and greater plant biomass, although outcomes vary substantially with pathosystem, biochar type, application rate, and management, and should be interpreted as recurring tendencies rather than universal causal effects (Bonanomi et al. 2015; Iacomino et al. 2022; Yang et al. 2022). Proposed mechanisms include reduced activity of pathogen-derived toxins or enzymes, enrichment of antagonistic rhizosphere populations, and induction of plant systemic defence responses (Bhatt et al. 2024; Graber et al. 2014; Iacomino et al. 2022; Jaiswal et al. 2014, 2018). Studies in pepper and tomato systems have linked biochar-mediated suppression to rhizosphere microbiota shifts and defence pathway induction, though the relative importance of these mechanisms is pathosystem-specific (Elad et al. 2010; Graber et al. 2014; Jaiswal et al. 2017, 2020; Jin et al. 2022). Evidence that biochar-mediated disease suppression translates into reduced pesticide need or lower pesticide use at farm scale remains limited and context-dependent (Bonanomi et al. 2015; Graber et al. 2014; Iacomino et al. 2022; Lehmann et al. 2011; Vijay et al. 2021).

In contaminated soils, biochar can reduce the mobility or bioavailable fraction of many contaminants through sorption, surface interactions, and changes in soil chemistry (Ahmad et al. 2014; Beesley et al. 2010, 2011; Q. Chen et al. 2022a, b; Siedt et al. 2021). This effect is particularly well documented for hydrophobic organic compounds and, in some systems, for selected inorganic contaminants. This reduction in bioavailability may create conditions more favourable to biological recovery, but the extent of any microbially mediated transformation of contaminants remains contaminant- and site-specific. Where enhanced biodegradation is reported, it should therefore often be interpreted as a secondary consequence of reduced toxic pressure and improved habitat conditions, rather than as evidence of direct stimulation of degrader activity by biochar itself. For inorganic contaminants in particular, reduced plant uptake or lower bioavailable fractions should not be interpreted as evidence of uniform sorptive affinity across all biochars (Bao et al. 2020; Beesley et al. 2011; Puga et al. 2015; Singh et al. 2024).

Taken together, biochar application can result in environmental co-benefits in some systems, but these outcomes remain strongly context-dependent and should not be generalised across soils, climates, and management regimes (Cayuela et al. 2014; Jeffery et al. 2011; Kaur et al. 2023; Rittl et al. 2021; Schmidt et al. 2021). Integrated approaches combining biochar with compost or microbial inoculants may further enhance soil functioning in selected systems, though evidence remains limited and system-specific (Agegnehu et al. 2017; Bolan et al. 2023; Xiang et al. 2022).

7 Knowledge Gaps and Future Research Directions

Despite the considerable progress achieved in recent years, several knowledge gaps remain regarding the effects of biochar on the soil microbiome. The pronounced heterogeneity of reported responses indicates that generalisable predictive models are not yet available. Outcomes depend on multiple concomitant factors, including biochar properties, soil type, climate, agronomic management, and plant presence, whereas individual studies often capture only a narrow portion of this overall picture (Li et al. 2020). Although recent meta-analyses have identified recurring tendencies, variability around these averages remains high and many comparisons show weak, null, or context-specific effects (Li et al. 2020; Pokharel et al. 2020; Sharma et al. 2025; Wang et al. 2023a, b). The main research priority is therefore not simply to refine global mean effects. Rather, future work should define more rigorously the boundary conditions under which biochar alters microbial communities and functions in desirable ways. These boundary conditions include soil pH and texture, feedstock and pyrolysis conditions, water regime, plant presence, application rate, and experimental duration.

A major reason why this remains difficult is the dual heterogeneity of both the biochar materials tested and the methods used to assess microbial responses. At a minimum, future studies should report feedstock, pyrolysis temperature and residence time, post-pyrolysis treatment, particle size, pH, EC, ash content, elemental composition, molar H:C_{org} ratio, nutrient content, and relevant contaminants such as PAHs and trace metals. Soil metadata should include baseline and post-application pH, EC, texture, SOC, mineral N, available P, moisture, and temperature, because these variables are needed to interpret microbial and enzymatic responses. Standardisation is also required for biological endpoints: microbial biomass methods should be clearly specified; amplicon studies should report primer sets, sequencing depth, quality-filtering procedures, negative controls, and raw-read deposition; and enzyme assays should report substrate, buffer, incubation time, temperature, assay pH, and controls for substrate or product sorption by biochar (Alteio et al. 2021; Kerner et al. 2023; Li et al. 2020; Tammeorg et al. 2017).

Beyond measurement heterogeneity, a distinct experimental-design gap remains largely unaddressed: most

published studies lack controls that isolate biochar-specific effects from co-varying changes in soil chemistry. Future mechanistic studies should therefore include, as appropriate, pH-matched controls for alkaline biochars, nutrient-matched controls for nutrient-rich biochars, and EC- or salt-matched controls for high-ash or high-EC materials. Such controls are needed to determine whether changes in community composition, microbial biomass, enzyme activity, or greenhouse-gas-related processes reflect biochar-mediated habitat effects, or non-specific responses to liming, fertilisation, or salinity.

A further major gap is the scarcity of long-term, open-field studies and coordinated multi-site trials. Most available evidence derives from short-term incubations or pot experiments, whereas multi-year field networks across contrasting soils and climates are needed to capture ageing effects, delayed microbiome responses, persistence of benefits, and late-arising trade-offs such as salinity increases or progressive saturation of sorption capacity (Da Silva Mendes et al. 2021; Idbella et al. 2024; Lehmann et al. 2011; Schmidt et al. 2021; Sharma et al. 2025; Song et al. 2024). Such trials should include repeated sampling before application, shortly after application, during the first growing season, and across subsequent years. Monitoring should combine microbial endpoints with soil physicochemical variables, biochar ageing indicators, plant responses, greenhouse-gas fluxes where relevant, and risk indicators such as salinity, nutrient imbalance, contaminant mobilisation, or delayed pathogen responses. Without harmonised long-term field validation, response-window models will remain useful interpretative frameworks but will have limited predictive value for agronomic or environmental decision-making.

A related priority is the development of fit-for-purpose biochars designed in relation to specific soil constraints, desired agronomic or environmental functions, and management goals, rather than treated as a single amendment category (Gryta et al. 2023). Applications targeting specific outcomes, such as improved N availability, N_2O mitigation, pathogen suppression, or the recovery of enzyme activity in degraded soils, require a more targeted approach. Future studies should move beyond generic comparisons among feedstocks and pyrolysis temperatures and identify which biochar traits are most relevant to each outcome. In this context, microbial community responses should be interpreted as potential mediators rather than endpoints in themselves.

In acidic and nutrient-poor soils, for example, biochars produced at low to intermediate pyrolysis temperatures and derived from ash-rich or nutrient-rich feedstocks may be more effective at improving pH, nutrient retention, and habitat quality for soil biota than highly carbonised, nutrient-poor materials (Biederman and Stanley Harpole 2013; Joseph et al. 2015; Lehmann and Joseph 2015). Post-pyrolysis modifications may offer additional ways to enhance targeted agronomic or biological functions. These include nutrient-enriched coatings and inoculation with beneficial microbial strains, although the available evidence remains preliminary and strongly context-dependent (Chen et al. 2023; Gryta et al. 2023).

An emerging research avenue is the integration of biochar with complementary agronomic practices. Initial evidence suggests that biochar-compost mixtures can outperform either component alone, likely because compost supplies active microbial communities and labile substrates while biochar provides protected microhabitats and moderates inhibitory conditions (Agegnehu et al. 2016, 2017). Biochar is also increasingly explored as a carrier for beneficial microbial inoculants because its porous structure can enhance inoculant survival and rhizosphere colonisation (Bolan et al. 2023; Egamberdieva et al. 2018). Candidate inoculants include arbuscular mycorrhizal fungi, N-fixing bacteria, and phosphate-solubilising bacteria. Pilot studies with pre-inoculated biochars have reported improvements in enzyme activities, soil fertility, disease incidence, and plant performance compared with either component applied separately, although evidence remains limited and strongly system-specific (Chen et al. 2023; Liu et al. 2023).

These considerations also reinforce the need to evaluate biochar effects across the wider soil biotic network rather than restricting assessment to bacteria and fungi alone. Biochar may alter trophic interactions within the soil food web; one still incompletely tested hypothesis is that biochar pores can provide partial refuges for bacteria from predation by protists and nematodes, thereby weakening top-down control and partially decoupling increases in microbial biomass from functional activity (the so-called shelter effect). At present, however, direct experimental evidence for this mechanism remains limited (Asiloglu 2022; Asiloglu et al. 2021; Liu et al. 2020). Future studies should therefore include explicit measurements of protists, nematodes, and other soil biota to obtain a more complete picture of how biochar-induced changes in resources and habitat structure propagate through the food web (Asiloglu 2022). Advanced meta-omics approaches, including metagenomics and metatranscriptomics that explicitly capture eukaryotic taxa, combined with ecological network analyses, will be useful for identifying predator–prey links, trophic interactions, and keystone taxa in biochar-amended soils (Hewitt et al. 2023; Sharuddin et al. 2022; Siles et al. 2021). However, functional predictions or network-inferred interactions should be treated as hypothesis-generating rather than as direct evidence of process rates. Predicted changes in N-, C-, or P-cycling potential should therefore be validated, where possible, with targeted functional genes or transcripts, enzyme activities, nutrient transformation rates,

greenhouse-gas fluxes, isotopic tracing, or plant performance indicators. Multifactorial experiments manipulating the presence or absence of specific predators, symbionts, or functional groups will be important for moving from correlative patterns towards mechanistic understanding.

8 Conclusions

This critical synthesis demonstrates that biochar can impact soil microbial communities and modulate enzymatic functioning under appropriate conditions, often co-occurring with measurable changes in ecosystem processes including nutrient cycling, carbon stabilisation, and pathogen suppression. Attributing these outcomes to microbial drivers alone, however, remains challenging. Biochar simultaneously modifies several key abiotic constraints, such as pH, nutrient availability, moisture, and microhabitat structure, all of which independently regulate process rates. Across studies, the most consistently reported response is an increase in microbial biomass carbon, followed by compositional restructuring of bacterial communities; α-diversity responses are smaller, more variable, and more context-dependent. Agronomic co-benefits are frequently reported and reflect the interplay of abiotic and biotic mechanisms. These benefits include improved N and P availability, reduced nutrient losses, and, in some systems, yield gains. Disentangling their relative contributions requires targeted manipulative approaches that go beyond the correlative designs used in most available studies. Similarly, reductions in N_2O emissions and, under suitable moisture regimes, in CH_4 fluxes represent examples of context-dependent structure–function coupling that cannot be attributed solely to biochar-induced shifts in microbial community composition.

The variability of these responses does not undermine biochar's potential. Rather, it reframes the central question. The key issue is not simply whether biochar works, but under which soil conditions, biochar types, and management contexts it works reliably. This review synthesises those conditions as "response windows": that is, combinations of baseline soil constraints, biochar functional traits, and application context that jointly determine the likelihood and direction of microbial and functional outcomes. Benefits are most consistently observed when biochar alleviates a dominant constraint in soils where its properties are well matched to the site's limiting factors. The most common constraints include acidity, low resource availability, and poor water retention. Conversely, very high application rates or high-EC biochars in weakly buffered systems define a risk window where trade-offs become more probable, warranting careful monitoring of soil salinity, pH, and plant-available nutrient balance. Between these two extremes, the framework also recognises intermediate domains, including minimal, moderate, and inconsistent response windows, where microbial and enzymatic outcomes remain weak, variable, or only partially coupled to measurable soil functional changes. It is important to note that adverse biological outcomes have not been reliably demonstrated in temperate agricultural soils when biochar is applied at agronomically realistic rates and meets established quality standards, such as those defined by the European Biochar Certificate and the International Biochar Initiative (European Biochar Certificate, n.d.; IBI, n.d.). These realistic rates are generally below 5 t ha^{-1} yr^{-1} and, in practice, are often around 1 t ha^{-1} yr^{-1}. Risk windows are therefore primarily associated with excessive application rates or poorly characterised materials in weakly buffered soils.

Without this foundation, the response-window framework proposed here will remain an organising concept supported by pattern recognition rather than a mechanistically grounded predictive tool. Developing that mechanistic basis is the most important frontier for advancing soil biochar science. This will require causal experimentation, multi-omics integration, and coordinated field networks.

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Declarations

Competing interests The authors declare that they have no known competing financial interests or personal relationships that could have influenced the work reported in this paper.

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