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Biochar

REVIEW **Open Access**

Unravelling the role of biochar-microbe-soil tripartite interaction in regulating soil carbon and nitrogen budget: a panacea to soil sustainability

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Abstract

Global food requirements necessitating enhanced crop productivity have negative consequences such as soil degradation due to acidification and nutrient leaching escalated by excessive application of chemical fertilizers and consequently increasing greenhouse gas emission. This has sought sustainable organic approaches like soil amendment with biochar to mitigate the adverse consequences of these effects, ensuring balanced ecosystem functioning. Reconciling various studies, this review provides a better understanding of the belowground mechanisms decoding multifaceted traits associated with plant and biochar-microbe-soil tripartite interaction, including microbe-mediated regulation of C and N stoichiometry, soil enzyme functioning, regulation of greenhouse gases, soil respiration rate and alteration in abundance of microbial functional genes. Furthermore, this review exclusively gives holistic insights into specific microbes induced by biochar treatment and their role in altering soil C and N dynamics. It attempts to spur in-depth, long-term studies tackling challenges in sustainable agriculture and mitigate environmental issues to achieve C neutrality and N retention, envisaging a healthy soil ecosystem.

Highlights

- Biochar application can alter C and N stoichiometry in plant and soil.
- Biochar properties determine the proliferation of specific soil microbes.
- Soil microbial functional genes and enzymes are altered by biochar application.
- Biochar reduces greenhouse gas emission by modulating soil microbial functions.

Keywords Soil degradation, Biochar, N dynamics, Sustainable agriculture, C neutrality, Soil microbiota

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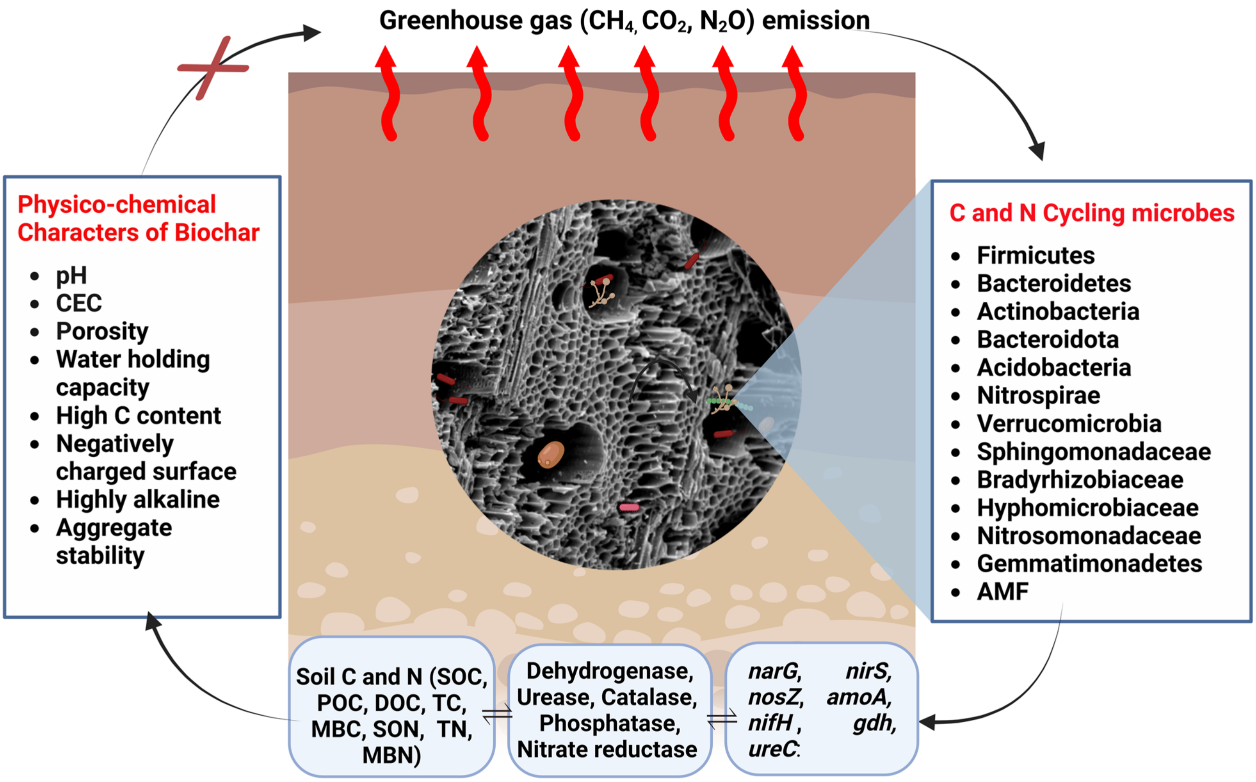
Graphical Abstract



1 Introduction

Excessive fertiliser usage has steered major environmental issues such as soil degradation resulting from acidification, nutrient leaching, structural damage, reduction in beneficial soil microbiota and led to a rise in greenhouse gas (GHG) emission (Hartmann and Six 2022). Biochar, an anaerobically produced pyrogenic solid derived from various feedstocks, has gained significant attention as an environmentally sustainable source, with advantageous properties enhancing soil functions and positively influencing soil microbial community (Ren et al. 2022). High carbon (C) content, porous structure, negatively charged surface and highly alkaline nature adorn biochar with the ability to modify the physico-chemical characteristics of soil, lowering its bulk density, raising pH, along with improvement in nutrient availability, retention, water holding capacity, cation exchange capacity (CEC) and aggregate stability (Liu et al. 2015; Hossain et al. 2020; Kang et al. 2022). Furthermore, multitude of studies have demonstrated its potential in reducing GHG emission (Lévesque et al. 2020; Lyu et al. 2022; Xia et al. 2024) and its significant role in enhancing crop production by facilitating biochar-microbe-soil interaction in the long-term (Liao et al. 2019; Xie et al. 2021; Li et al. 2024). Soil harbours highly complex habitat hosting a diverse array of microorganisms playing a crucial role in various soil functions. Biochar amendment alters these soil functions to enhance soil enzyme activity and modifies microbial community composition (Das et al. 2023). Soil enzymes assist in releasing recalcitrant nutrients for plants and support soil microbiota with steady supply of energy sources (Pokharel et al. 2020). Furthermore, high soil pH improves crop growth by releasing phosphorus (P) bound to metals such as iron (Fe) and mitigates Al^{3+} toxicity, thereby influencing various factors that regulate the nutritional dynamics of the soil (Hajiboland et al. 2023).

Organic feedstock serves as a nutrient source in biochar and determines its porosity, making it a conducive habitat for microbial growth (Singh et al. 2022). Again, porosity and surface chemistry influence the absorption and sequestration of GHGs and contend biochar as a potential C and nitrogen (N) sink (Abhishek et al. 2022). Meanwhile the extracellular polymers and adhesion compounds produced by microorganisms enable them to proliferate and disseminate across the biochar surface and interior pores (Schommer et al. 2024). The char sphere or interface between soil and biochar particles acts as a primary site for the growth of microbial biomass. The enrichment in microbiota boosts soil aggregation, aids in the enhancement of native organic matter, and mitigates the loss of soil nutrients (Chagas et al. 2022). The positive priming effect of biochar changes the soil microbial activity and alters the abundance of microbes linked with soil C and N cycling, potentially influencing the decomposition process (Zhang et al. 2023a). Changes in soil properties, such as pH levels, as well as variations in the availability of organic matter and nutrients have effects on key functional microbial groups such as N-cycling bacteria and fungi. These effects are not direct but rather are mediated indirectly through their impact on plant growth and alter the quality and quantity of plant input to the soil (Dai et al. 2021). Root exudate also recruits specific microbes in different environmental conditions (Parasar et al. 2024), often adjoined by biochar interaction, influencing plant performance and rhizosphere functions (Sun et al. 2020a). The application of biochar serves as a readily available C source for proliferation of rhizospheric microbes such as Actinobacteria (Qiu et al. 2023). Furthermore, the ratio of bacteria to fungal abundance is impacted by the addition of biochar, as it holds the potential to affect the efficiency of microbial C consumption and enhance fungal growth (Li et al. 2018). However, proliferation or reduction in specific soil microbes has contrasting effects depending on different soil conditions, feedstock source, pyrolysis temperature, and residence time.

Biochar persuades soil enzyme function as a critical regulator of ecosystem services alternating both biotic and abiotic factors (He et al. 2021). Soil enzymes including alkaline phosphatase, dehydrogenase, urease, protease, etc., induced upon biochar application are correlated with microbial extracellular secretions. Analysing microbial functional genes involved in enzymatic activities provides a more precise and direct method for comprehending the mechanisms underlying C and N regulation. The genetic makeup of microbial populations shed light on the marker for C and N cycling and decipher the structure of bacterial communities as indicators and provide insight into how soil microorganisms respond to biochar (Lu et al. 2020). These functional genes have regulatory role in GHG emission, which in turn is directly influenced by biochar properties. For example, biochar reduces N_2O emission by attracting N_2O-reducing bacteria and increases the abundance of N-fixing (*nifH*), nitrifying (*amoA*), and denitrifying (*nirK, nirS*, and *nosZ*) genes. Hence, biochar has an intricate relationship with soil nutrients, and microbiota and also regulates soil physicochemical properties to influence GHG emission and other ecosystem services. Different studies reported increasing soil nutrient status (Alkharabsheh et al. 2021; Khan et al. 2024; Pandian et al. 2024) and microbial response (Zhu et al. 2017; Meng et al. 2023) upon biochar application, but little attempt has been made to connect the dots regarding how microbes drive the changes in biochar-soil continuum and regulate C and N dynamics. The complex interaction between biochar, soil properties and associated microbiota needs further attention. There are a number of studies emphasised in exploring the role of microbe induced by biochar in nutrient cycling (Anderson et al. 2011; Dai et al. 2021; Ibrahim et al. 2021; Cui et al. 2024). Taking into all these studies into account, critical review focusing on insights into microbial interplays associated with soil C and N regulation after biochar application is not available. In this review, we summarized the biochar-driven key soil microbiome functions in regulating soil C and N status, highlighting the interlinked complex enzymatic and functional gene activities, and discussed how it balances the trade-off through C sequestration and N retention for climate-smart sustainable agricultural practices.

2 Biochar amendment enhances soil physico-chemical properties

Biochar depending on its properties, alters the physical, chemical, and biological characteristics of the soil (Gul et al. 2015). Controlled pyrolysis condition of biochar allows retention of the nutrients and proves to be an advantageous nutrient supplement for plants. The overall nutritional content of biochar is dependent on several variables, including the feedstock quality, pyrolysis temperature, residence time and anaerobic condition created using a flux of CO_2 and N_2 during pyrolysis (Das et al. 2021). Precursors of biochar including wood, straw, litter, compost, and agricultural leftovers, play a significant role in augmenting the mineral element requirement of soil. Once introduced, nutrients in biochar can gradually seep into the soil for uptake by plants and interact with microbes in soil and act as an integral functional intermediary component in ecosystem functioning (Das et al. 2022). Significant improvement in soil quality with enhancement of C, calcium (Ca), magnesium (Mg), N, and sodium (Na) content as well as alteration in the initial microbial community and soil enzyme activity has resulted upon application of biochar. It also significantly enhances the soil CEC and nutrient retention efficacy of soil including C and N (Wang et al. 2024b). A remarkable increase in the quantity and composition of soil organic C (SOC) was documented after biochar addition (Han et al. 2020a). Inclusion of substantial amount of P and potassium (K) present in biochar granules into the soil also improves the soil nutrient stock (Tahery et al. 2022). The absorption of mineral nutrients from the biochar granules is facilitated by the electrostatic attraction between soil and biochar particles. The negatively charged hydroxyl and carboxyl groups featured on the biochar surface interact with the K^+, NH_4^+, and Mg^{2+} cations in soil. This interaction is also facilitated by the formation of hydrogen bonds in the undissociated state between the dihydrogen phosphate anions and carboxyl groups and finally disseminates into the soil for plant uptake, undergoing microbial decomposition (Kumar et al. 2022b).

The impact of biochar on physico-chemical characteristics of soil includes changes in pH, structure, porosity, aggregate stability, CEC, and bulk density, along with other mineral compositions. For instance, significant increase in pH, electrical conductivity (EC), K, Na, C, and P was found in poultry litter waste biochar amendment (Da Silva Mendes et al. 2021). Additionally, soil acidity and the CEC decreased, all of which contributed to an increase in soil fertility. Moreover, the bulk density of soil is reduced while porosity, field capacity, wilting point, and plant-available water are enhanced upon biochar application (Edeh et al. 2020). Soil type is also a determinant in the functioning of biochar, which varies in different conditions. For example, application of biochar has been demonstrated to increase water-holding capacity in sandy loam soil, while it incurred no changes in silt loam. However, a decrease in these indices was noted in clay loamy soil (Adhikari et al. 2022). Proper and target-oriented application of biochar with consideration of dependent variables and analysis of its different functionalities concerning soil properties can uplift its potential as a sustainable agricultural supplement.

3 Biochar-microbe-soil tripartite interaction mediates the biogeochemical cycle

Biochar significantly influences the proliferation, diversity, and structural composition of soil microorganisms. This effect is the result of available nutrients for the growth of soil microbiota or indirectly by modifying fundamental characteristics of the soil (Dai et al. 2021). For instance, corn residue biochar was found to improve soil nutrient availability and microbial activity in calcareous soil (Karimi et al. 2020). Similarly, chicken manure biochar of high N, P, K, and other nutrient content increased soil nutrient retention (Domingues et al. 2017). Nutrient availability to plants depends on its solubilisation, often countering its availability even if its presence in large content, such as heterocyclic N in the biochar C matrix (Haider et al. 2020). A contrary to it is K, as the majority of K in biochar is present in soluble forms and is released into the soil shortly after it is applied (Xiu et al. 2023). Biochar promotes the growth of K-solubilizing bacteria as well as relative abundance of other bacteria belonging to Acidobacteriota, Actinomycetes, Chloroflexi, Firmicutes and Proteobacteria; hence improving soil K level along with bacterial functions (Xia et al. 2022). Depending on the feedstock, biochar can be a potential N source in organic as well as inorganic forms for plants. Increase in N availability improves soil fertility and encourages mycorrhizal fungi to colonize roots and alters the microbial makeup of the soil, along with providing resistance in plants against microbial diseases (Han et al. 2020b). Maximizing the N use efficiency (NUE), biochar enables a reduction in the potential losses caused during volatilization, emission, runoff, and leaching. It stimulates microbial functioning associated with symbiotic and non-symbiotic biological N fixation and N mineralization (Ahmad et al. 2021).

Biogeochemical cycles of C, N, and P within terrestrial ecosystems are intricately linked through biochemical reactions involved in primary production, respiration, and decomposition. The ratios of C:P and N:P in the soil have a positive correlation with both the soil moisture and the levels of organic C and N in the soil, subsequently impacting plant growth and soil microbiota associated with its cycling (Wu et al. 2023b). P solubilizing microorganisms act as the main regulator in solubilizing P remaining in conjugation with Fe, Ca, or stable organic P. Direct oxidation, release of H^+, and low molecular weight organic acids as well as extracellular enzyme production like phytase, phosphatase, and C-P lyase solubilize the organophosphorus source (Rawat et al. 2023). Blanco-Vargas et al. (2022) reported biochar prepared from pine-saw dust (500 °C), aid in the growth of phosphate solubilizing bacteria and can be an effective carrier for plant application. Bacteria like *Enterobacter* sp. involved in this process were promoted upon addition of rice husk biochar and sludge biochar (Thu et al. 2024). Further, biochar has a significant impact in modulating micronutrient availability in soil. It affects germination of spore and mycelial branching and hence promotes AMF growth (Wen et al. 2022). In a study by Vahedi et al. (2022), biochar inoculated with AMF improved P, Fe, and Zn content by almost twofold as compared to the control. Tea pruning litter biochar amendment on tea plants enriched Cu, Mn, and Zn availability and improved their translocation for plant uptake (Sarmah et al. 2023). It is well established that biochar increases advantageous soil bacteria like *Pseudomonas* and *Bacillus*, which in turn solubilize zinc (Zn) by releasing gluconic acid, dissolving insoluble Zn compounds (Wu et al. 2022). Again, another study substantiated biochar-induced promotion of plant growth promoting fungal species *Aspergillus niger* (Rawat et al. 2023), aiding in solubilization of several insoluble Mn oxides (Gorain et al. 2022). However, long-term biochar amendment was found to decrease soil Zn bioavailability as biochar application increases the SOM content which in turn immobilizes Zn (Wu et al. 2018). Additionally, biochar has strong affinity for Cu, Fe, Mn, and Zn in aqueous solution, therefore, its application in Fe deficient soil inhibits the absorption of Fe by plants (Xu et al. 2022). Thus, a high dose application of biochar over long time may cause micronutrient shortage in the soil and can reduce crop productivity. Hence, qualitative assessment of biochar and its critical amount should be evaluated based on soil type considered for improvement (Liang et al. 2021).

The physico-chemical changes in the characteristics of the soil upon biochar addition play a significant role in regulating the nutrient dynamics. Several studies (Dong et al. 2016; Islam et al. 2021; Sheng et al. 2023) reported positive effect of biochar on soil aggregate stability. Biochar mediated modification in the soil structural components, and its persistence in the soil have a considerable effect on the microbiological processes, serving as substrates for the growth of microbial biofilms (Wong and Ogbonnaya 2021). Soil microorganisms in turn link soil mineral particles or aggregates and stabilize them. For example, Actinobacteria and fungal hyphae improve the cohesiveness of soil particles and aggregate these particles on the biochar surface (Gorovtsov et al. 2020). Fungal hyphae allow better access to distantly located nutrient sources with heterogeneous distribution patterns. Similarly, basidiomycetous fungi secrete adhesive exopolysaccharides through hyphae aggregating soil particles (Zheng et al. 2018). However, the ability of biochar to efficiently sorb cations under specific circumstances might have detrimental effects (Li et al. 2017). Particularly, plants cultivated on carbonate soils supplemented with biochar have been found to be Fe deficient. Hydroxide ions in the biochar surfaces combine actively to form Fe hydroxide or oxide, resulting in its less availability (Xiao et al. 2023). Fe content in soil plays a major role in altering microbial communities. Its deficiency causes reduction in the formation and functioning of arbuscules and hinders the symbiotic relationship between AMF and nutrient uptake process (Rajapitamahuni et al. 2023). Biochar as a slow-releasing nutrient reservoir in soil effectively mediates the nutritional dynamics through microbial interplays and supports plant growth with improved soil fertility and resilience.

4 Biochar properties influence soil microbial diversity and its functionality

The positive effect of biochar on soil microbial activity and diversity has been extensively reported (Han et al. 2024; Massaccesi et al. 2024). Soil amended with biochar possesses greater diversity of root-associated bacteria compared to the untreated condition, promoting plant growth and development (Idbella et al. 2024). This can be attributed to nutrients in biochar that are necessary for soil microbial proliferation and increased microbial metabolic activity (Cui et al. 2024; Yang et al. 2024a). Biochar has positive influence on abundance of bacterial families Bradyrhizobiaceae, Hyphomicrobiaceae, Micromonosporaceae, Streptomycetaceae, Streptosporangineae and Thermomonosporaceae (Anderson et al. 2011). However, the effects of biochar on soil fungal diversity are much complicated. Certain fungal taxa belonging to Glomeromycetes and Sordariomycetes are reduced by biochar amendment, while those of Tremellomycetes remain unchanged (Chen et al. 2016a). High concentration of organic compounds and mineral components in biochar, as well as its ability to increase the soil pH mediate the differing effects of biochar on soil microbial diversity (Dai et al. 2021).

Negatively charged functional groups in biochar potentially interact with hydrogen ions, attributing to a shift in the pH towards the alkaline condition. These functional groups and the chemical compounds present on biochar surfaces selectively allow colonization of microorganisms and trigger microbial responses. The sorption of cations and inorganic anions with its surface functional groups, particularly oxygen-containing groups like the carboxylate, allows biochar to store and provide nutrients to soil bacteria (Vieira Firmino et al. 2024). The low molecular weight hydrocarbons on biochar surface act as a C source for thriving of microbes (Valizadeh et al. 2022), and also function as signal molecules promoting or suppressing microbial activities (Gorovtsov et al. 2020). Biochar affects microbial composition through direct and indirect mechanisms. The porous nature of biochar varying in sizes such as micro (~ 2 nm), meso (2–50 nm), and macro (> 50 nm); provides a conducive habitat for bacteria and fungi (Hamidzadeh et al. 2023). Additionally, as alkalinity rises with biochar application, the abundance of acidophilic microorganisms, such as Acidobacteria decreases, while Actinomycetes and Gram-negative bacterial abundance increases. Again, some microorganisms like Gemmatimonadetes get impacted due to biochar effect. Gemmatimonadetes generally prefer dry soil conditions, so an increase in soil moisture content upon biochar application significantly reduces their numbers (Xu et al. 2023). Idbella et al. (2024), reported change in microbial composition upon biochar addition (10 years) with a pronounced increase in Acidobacteria contradicting previous reports of its decline in short-term experiments. Despite high SOM and respiration rate, the rise in Acidobacteria signifies achieving a steady state with presence of high SOC concentration (Cleveland et al. 2007). Similarly, abundance of Acidobacteria decreased after 10 years of amendment possibly due to a rise in soil pH over time and a decrease in availability of phenolic substrates. Phenolic substrates in biochar provide competitive advantages to Actinobacteria over others and hence with time their abundance gets impacted (Fu et al. 2022). However, in a long-term study by Nguyen et al. (2018), no significant change in soil bacterial communities was found after 9 years, while few transient changes were observed after 1–2 years of biochar application. Soil re-acidification over time, along with an increase in the oxidation of biochar surfaces during ageing can also decrease soil pH in the vicinity of biochar particles (Butterly et al. 2022). Moreover, the build-up of other organic and inorganic matters and rhizodeposits on biochar surfaces over time lessens the available space for microbial growth (Pandian et al. 2024).

The biochar produced under different pyrolysis temperatures possesses a wide range of physicochemical characteristics. Bacterial and fungal diversity were found to increase under application of biochar prepared at both high and low pyrolytic temperatures, with a more pronounced effect in slow pyrolyzed ones (Singh et al. 2022). Low-temperature pyrolyzed biochar offers more labile C sources to the soil bacteria compared to the one prepared at high temperature (Yang et al. 2022a). Increasing pyrolysis temperature decreases the H/C and O/C ratios and promotes aromaticity and nonpolar nature of biochar. This in turn elevates C/N due to the condensed aromatic C structure (Wang et al. 2024a). The effect of biochar also varies with different soil conditions. Gul et al. (2015), in a meta-analysis reported that short laboratory incubation and long duration (1–3 years) field studies comprising slow pyrolyzed biochar produced from various feedstocks consistently improve soil physico-chemical properties (e.g., pH, CEC, and aggregation) and microbial community structure in different soil conditions. Biochar when added to coarse textured soil results in less aggregation, lower microbial biomass and enzyme activity. Similarly, maize plant biochar addition in calcareous soils deficient in organic matter significantly increased bacterial and fungal respiration, cumulative microbial respiration, microbial biomass C (MBC), and substrate-induced respiration. While application into acidic soil results in pH increase causing change in the microbial communities. However, overall fungal-to-bacterial ratio decreased, which is dependent upon pyrolysis temperature, application rate, and soil texture. The proportion of oligotrophs in microbial communities of the topsoil rises as compared to copiotrophs and was found to limit their presence at all soil depths (Ma et al. 2023).

Porous structure affects the efficacy of biochar in various environmental application. Large specific surface area promotes physical adsorption and attachment of microbial cells through electrostatic and van der Waals interactions (Wong and Ogbonnaya 2021). The extent of microbial attachment on biochar surface attributes to its surface area, while its porous structure provides protection to the soil microorganisms. Higher porosity or larger pores have a greater effect on microbial biomass, as evident in aggregation of fungal hyphae in the larger pores (Jaafar et al. 2015). The boost in microbial activity induced by biochar can directly or indirectly influence the surrounding microenvironment through alteration in the soil porosity (Zhang et al. 2023b). Soil porosity increases linearly with a decrease in soil bulk density upon biochar application (Blanco-Canqui 2017). The factors influencing microbial habitat are not just dependent on physical and surface properties of biochar, but also rely on feedstock and pyrolysis conditions. These factors determine the reactivity of biochar based on the presence of different functional groups on its surface. The functional groups, nutrients in the biochar as well as aqueous and gaseous flux within and outside its pores impact microbial colonization.

Organic mineral complexes are formed within and on the surfaces of biochar. These complexes have the potential to alter the adsorption characteristics of the biochar and aid in the bacterial colonization in biochar particles. Presence of various organic chemicals such as acetone, benzene, benzo[a]pyrene, methanol, methylethylketone, methyl acetate, propionaldehyde, toluene (Gorovtsov et al. 2020), aliphatic and aromatic compounds such as ethylene, propylene, and ethane, propane, butane, acetylene, pentane, hexane (Sánchez et al. 2009) and phenols (Kolton et al. 2017), in different biochar influences microbial composition in the applied soil. Many of these compounds have harmful effects on plants and microorganisms (Ruzickova et al. 2021). For instance, biochar having a high content of phenolic compounds can result in a decrease in *Bacillus mucilaginosus* population (Sun et al. 2015). Some bacteria show a negative correlation with the aromatic C concentration, while positive correlation with the aliphatic C content in the biochar (Zhang et al. 2018). Also, polycyclic aromatic hydrocarbons (PAHs) produced during pyrolysis were found to exhibit toxicity to the bacteria *Vibrio fisheri* (Kołtowski and Oleszczuk 2015). Furthermore, impact of biochar is influenced by its prior application in the soil, showing an accelerated mineralisation after second round of application. This indicates that microbes play a significant role in the mineralization process (Luo et al. 2023). Focusing on more specific studies in relation to biochar-soil microbe interaction requires further long-term field studies and deciphering responses of these microbial communities under diverse conditions.

5 Biochar balances soil nutrient status mediated by microbes

Affordability and environmentally friendly nature makes biochar a superior soil amendment influencing the soil nutrient status. It influences plant nutrient uptake by offering the majority of essential nutrients for plants and soil microbes which can alter soil properties by triggering multiple chemical reactions and nutrient cycles (Hou et al. 2022). Feedstock materials derived from various biomasses in preparing biochar, provide different macro and micronutrients, trace minerals, and other growth factors (Karim et al. 2022). Zou et al. (2023), reported increase in macronutrient content of tea plants upon biochar treatment, along with an increase in leaf and root biomass. Amending the soil with numerous nutrients, biochar increases co-metabolism among soil microorganisms raising microbial biomass as well as activity, and encourages the breakdown of native organic compounds. For example, amending biochar prepared from maize straw to silt loam soil improved the SOC, total N (TN), and total P (TP), enhancing the soil nutrient availability. Consequently, higher relative abundances of AMF and AMF: saprotrophic fungus ratio were noted in the treatment (Luo et al. 2017). However, contrasting reports with regard to the increase or decrease in fungal population upon biochar application are evident. Biochar from lignocellulosic and herbaceous waste feedstock significantly increased fungal diversity (Singh et al. 2022). While, Ji et al. (2022), reported a reduction of the fungal population when biochar was applied to subtropical tea plantations. This might be due to an increase in P input in the soil from biochar decreasing the proportion of root colonisation by AMF, as a consequence of faster root growth than the fungal colonization rate (Richardson et al. 2011). Biochar application containing N and K for 90 years with no P input increased AMF, while balanced application of N, P, and K had ambiguous impact (Cheng et al. 2013). In a 4-year study, rice straw biochar significantly increased K and Mg content in soil due to better bacterial cooperative relationship over presence of unique functional groups on biochar surface (Nan et al. 2020). Liao et al. (2019), reported promotion in abundance of N-fixing and P-solubilizing bacteria such as *Bacillus* and *Clostridium* in the legume rhizosphere, which are crucial for N-solubilization. Remarkably, bacteria *Alicyclobacillus*, *Desulfosporosinus*, and *Geobacter* involved in Fe and sulphur oxidation were enhanced. In general, an increase in the relative abundance of several bacterial families including Acidothermaceae, Acidothermaceae, Cellulomonadaceae, Geodermatophilaceae, Microbacteriaceae, Streptosporangiaceae, and Thermomonosporaceae was found (Anderson et al. 2011). Biochar-induced changes in the abundance of soil microbiota associated with C and N cycling and their specific role have been mentioned in Table 1 and the overall functional role has been depicted in Fig. 1.

5.1 Microbes driven by biochar involved in C regulation

Biochar increases soil C pool by maximizing C sequestration and enhances both labile and stable C fractions in the soil. Its amendment alters rhizospheric bacterial diversity and influences the bacterial members that actively assimilate C derived from plants. As a result, an increase in the relative abundances of Firmicutes and Bacteroidetes members (such as *Alicyclobacillus*, *Bacillus*, *Clostridium*, *Desulfosporosinus*, and *Sporomusa*), while a reduction in plant-derived C utilisers like *Methylobacterium* and *Sphingomonas* (belonging to Proteobacteria) occurs (Liao et al. 2019). On the other hand, only a few species of Acidobacteria, Planctomycetes, and Gemmatimonadetes develop slowly in response to the biochar effect in the rhizosphere, as they are more likely to break down the organic C already present in the soil rather than the fresh input (Liu et al. 2020b). Firmicutes, being copiotrophic in nature justify their predominance in the amended soil; while oligotrophs like Acidobacteria with high C use efficiency (CUE) thrive abundantly in soil rich in high recalcitrant organic matter (Liu et al. 2020c). This increase in substrate utilization efficiency with the addition of biochar mediates changes in the microbial composition and accelerates the mineralization of SOC (Jiang et al. 2016). Chagas et al. (2022), in a global meta-analysis, showed a significant increase in TC, organic C, MBC and labile C induced by biochar, showing diverse responses for each soil C fraction. Similarly, an 8-year experiment using *Calotropis procera* biochar improved the soil C-stock by 45% and the recalcitrant C by 67% (Ghosh and Maiti 2021). The rise in labile C correlates positively with MBC except in microbial limiting conditions and thereby, increases the soil C stock (Chen et al. 2016b). The pore-filling process in biochar due to selective sorption of the aliphatic C components from natural soil organic matter (SOM), reduces the microbial accessibility of biochar labile organic C (Herath et al. 2014). In long term, as a result of sorption of aliphatic C, the proportion of resistant C components in the soil increases and hence raising the residual C pool (Ramesh et al. 2019). Moreover, the addition of biochar to all types of soil resulted in an increase in the pooled abundance of phospholipid fatty acids (PLFAs) of Actinobacteria and Gram-negative bacteria, while the maximum PLFA level of Gram-positive bacteria detected at 1% biochar application (Jiang et al. 2016). Gram-positive bacteria utilise more recalcitrant C sources derived from SOM while Gram-negative bacteria utilise more labile C sources which are usually plant derived. This might account for

Table 1 Application of biochar in different soil condition changes relative abundance of soil microorganisms to regulate C and N balance

Sl No	Biochar feedstock	Pyrolysis condition	Application rate	Treated Soil	Microbe triggered	Role in C and N dynamic	References
1	Apple wood chip	500 °C for 5 h	2% w/w	Plinthosol	Proteobacteria (*Methylobacterium*, *Sphingomonas*) ↓; Firmicutes and Bacteroidetes (*Alicyclobacillus, Bacillus, Clostridium, Desulfosporosinus, Flavisolibacter, Geobacter, Sporomusa*) ↑	N fixation ↑, plant-derived C assimilation ↑	Liao et al. (2019)
2	Maize straw	400 °C	30 t ha^{-1}	Silt loam soil of the semi-arid area	AMF/saprotrophic fungi ↑	SOC and TN ↑	Luo et al. (2017)
3	Maize and wheat straw	450 °C 2 h	20 t ha^{-1}	Loamy aqufluvent	Fungi/ bacteria ↑	SOC mineralization rate ↓	Liu et al. (2020c)
4	Oak wood	550 °C	20%	Silt loam	PLFAs of Actinobacteria and Gram-negative bacteria↑	C/N ↑	Jiang et al. (2016)
5	Wheat straw	350–550 °C	40 t ha^{-1}	Sandy loam	Actinobacteria and Chloroflexi ↑ Glomeromycota (Glomeromycetes) and Ascomycota (Sordariomycetes) ↓	SOC, DOC, and TN ↑	Chen et al. (2016a)
6	Corn straw	400 °C for 4 h	6 and 12 t ha^{-1}	Sandy loam	Gram-positive bacteria, Fungi ↑	SOC and TN ↑	Li et al. (2019b)
7	Grass	400 °C	30 mg g^{-1}	Utisol	Actinobacteria and Firmicutes ↑ (initially), Sordariomycetes and Tremellomycetes ↑ (later)	DOC ↑	Yu et al. (2018b)
8	Wheat and eucalypt shoots	450 °C for 40 min	0.6 g of into 12 g soil	Aridic arenosol	Gram-positive bacteria ↑	Mineralisation of native SOC↑, fungal uptakes of C ↑	Farrell et al. (2013)
9	Forest logging residues	500 °C for 40 min	20 g kg^{-1}	Sandy loam calcareous soil	Actinobacteria, Proteobacteria, and Ascomycota ↑	SOC, TC, TN, and Available N ↑	Yan et al. (2021)
10	Wheat straw	350–550 °C	40 t ha^{-1}	Sandy loam	Actinobacteria and Chloroflexi	Degrade recalcitrant carbon, (SOC, TN, and DOC)↑, MBC and MBN ↑	Chen et al. (2016a)
11	Peanut shell	500 °C	0% 1%, 2%, and 4%	Wheat growing top soil	Actinobacteriota↓, Acidobacteria↑	POC and SOC↑; DOC↓	Qiu et al. (2023)
12	Maize	500 and 600 °C for 30 min	20 g kg^{-1}	Loamy clay	Bacilli, Acidobacteria, Thermoleophilia, Clostridia and Acidimicrobiia ↓; Gemmatimonadetes, Bacteroidia, Alphaproteobacteria and Gammaproteobacteria ↑	Mineralize soil recalcitrant C, SOC↑,	Ling et al. (2022)

Table 1 (continued)

Sl No	Biochar feedstock	Pyrolysis condition	Application rate	Treated Soil	Microbe triggered	Role in C and N dynamic	References
13	Maize straw	450 °C for 90 min	2.625 t ha^{-1}	Haplic luvisols	Gram-positive bacteria, Actinomycetes PLFA, Fungal PLFA ↑	POC ↑, SOC, DOC and MAOC, MBC ↑	Sun et al. (2022b)
14	Swine manure and straw	700 °C	5% w/w	Loamy clay	Actinobacteria, Proteobacteria↑	Recalcitrant organic C, mineralization of SOC↑	Fu et al. (2022)
15	Maize straw	400 °C for 2 h	1% and 3%	Meadow soils	Proteobacteria, Chloroflexi and Bacteroidota ↑; Actinobacteriota and Gemmatimonadota↓ Nitrosomonadaceae *Nitrospira*, Rhizobiaceae, *Lysobacter*, Xanthomonadales,↑ Myxococcota and Nitrospirota ↓	TOC, Soluble inorganic C (only in 3%), TON ↑	Zhao et al. (2023)
16	Bamboo residue	500 °C for 2 h	3% and 6%	Inceptisols	Acidobacteria, Actinobacteria, Proteobacteria, Firmicutes, Nitrospirae ↑	NH_4^+-N, NO_3^--N and TN ↑	Chen et al. (2021)
17	Rice straw	350 °C for 30 min	7.2 t ha^{-1}	Typical stagnic anthrosols and Pup-orthic-entisol	*Nitrosospira* (↓in paddy soil, ↑ in purple soil), *Mycobacterium* and *Bradyrhizobium* ↑	Available N, NH_3 volatilization ↑; reduce emission of N_2O↓	Yan et al. (2019)
18	Corn straw	400–500 °C for 4 h	0.5%, 1.0%, 2.0%, and 4.0%	Farmland soil	Proteobacteria, Actinobacteria, Chloroflexi, Acidobacteria, and Bacteroidetes ↑	TN and NH_4^+-N, MBN↑	Hu et al. (2023)
19	Monterey Pine	–	15 and 30 t ha^{-1}	Silt-loam soil	*Bradyrhizobiaceae* and *Hyphomicrobiaceae* ↑	N fixation ↑	Anderson et al. (2011)
20	Organic grain husk and paper fibre sludge	450–500 °C for 20 min	3, 15 and 30 Mg ha^{-1}	Acidic sandy soil	*Azospirillum brasilense*, *Arthrobacter crystallopoietes*, Sphingomonadaceae, Rhodospirillaceae, Bradyrhizobiaceae ↑	N fixation ↑	Kari et al. (2021)
21	Corn stover	500 °C for 60 min	1.5% w/w	Soybean experimental field soil	*Burkholderia* and *Bradyrhizobium* ↑; *Sphingomonas* and *Ottowia* ↓	TN and plant N uptake ↑	Gou et al. (2023)
22	Corn straw	300 and 600 °C for 2 h	0.5%, 1%, and 2% w/w	Calcareous purple soil	*Bradyrhizobium, Skermanella, Azotobacter* ↑; *Desulfovibrio* and *Klebsiella* ↓	TN, NH_4^+, NO_3^-, MBN, and DON↑	Zhao et al. (2021a)

Table 1 (continued)

Sl No	Biochar feedstock	Pyrolysis condition	Application rate	Treated Soil	Microbe triggered	Role in C and N dynamic	References
23	Corn straw	500 °C	5 t ha^{-1}	Cd-contaminated rice field	Proteobacteria (Euryarchaeota, Desulfobacterales) and Bacteroidetes (Sphingomonadales) ↓	SOC, C:N ratio, N fixation ↑	Jiang et al. (2023)
24	Corn stover	350–550 °C	20, 40, and 60 t ha^{-1}	Meadow soil with sandy loam texture	*Nitrospira* ↓, *Bradyrhizobium*↑	TN, available N, $NH_4{}^+$-N, $NO_3{}^-$-N ↑	Cui et al. (2024)
25	Eucalypt green waste	650–750 °C 3 min	2.5, 5 and 10% *w/w*	Black clay loam, red loam and brown sandy loam	Proteobacteria, Actinobacteria, Acidobacteria and Verrucomicrobia↑ *Nitrospira, Rhizobium, Azospirillum, Bradyrhizobium* spp., *Azosprillum* spp., *Rhizobium* spp., *Frankia* spp. and *Herbaspirillum* spp ↑	TC ↑ $NH_4{}^+$, $NO_3{}^-$, and TN ↑	Abujabhah et al. (2018)
26	Corn stalk	450 °C	3%	Weakly alkaline chernozem	*Ilumatobacter, Luteolibacter, Lysobacter, Arthrobacter, Mesorhizobium* ↑; *Gemmatimonas*↓	Organic matter, alkali-hydrolyzable N, N availability↑	Wu et al. (2024b)
27	Rice straw and waste wood particles	600 °C for 90 min	4 and 8 t ha^{-1}	Silt loam	*Bacillus*, *Geobacter*, *Sideroxydans* ↓; *Thiobacillus*, *Thermomonas*, Spicellomyces and *Crustoderma*↑	TC and TN ↑	Yin et al. (2021)

Here, ↑ indicates increase and ↓ indicates decrease

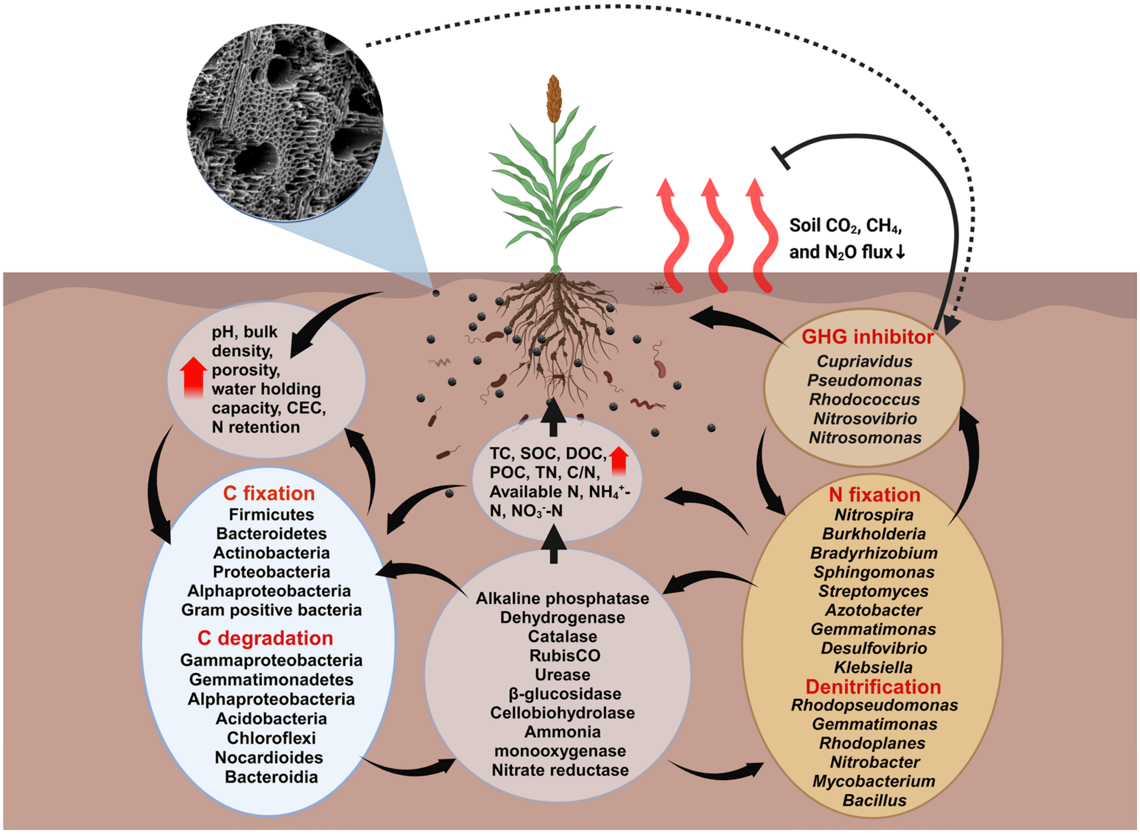


Fig. 1 Biochar induced changes in soil physico-chemical properties and corresponding alteration in the soil microbes involved in regulating soil C and N dynamics. The shift in soil microbial abundance modulates soil properties through various enzyme production and also reduces GHG emission. Here ↑ indicates increase while ↓ indicates decrease (created with BioRender.com)

the higher abundance of Gram-positive bacterial groups in the high dosage biochar treated soil, as these bacteria can use more recalcitrant biochar or SOM substrate (Bhattacharyya et al. 2022). Maize straw biochar application for 3 years to sandy loam soil follow a similar trend and showed enrichment of Actinobacteria, Gram-positive bacteria and some fungi (Li et al. 2019b).

The saprotrophic characteristics of fungi confer them advantages over bacteria in degrading semi-recalcitrant materials like wood and lignin and turn out to be the primary users of biochar C (Gujre et al. 2021). Once the labile-C compounds in biochar are utilized, saprophytic fungi switch to recalcitrant C and hence, result in a microbial succession shift from bacterial (Actinobacteria and Firmicutes in the initial phase) to fungal communities, including families like Sordariomycetes and Tremellomycetes dominating in the later phase over time (Yu et al. 2018b). Farrell et al. (2013) demonstrated rapid release of C from eucalypt and wheat shoot biochar mediated by microbes, which is respired catabolically and gets incorporated into microbial PLFAs. Also, the microbial community utilising the biochar C was found to vary with time, predominantly fungal uptake of C occurs as the biochar ages. The primary reason for the high C stability of biochar and SOC compared to pristine feedstock can be attributed to the elevated pH of the soil. Increase in pH prevents the disruption of the structure and functions of the heterotrophic soil microbial community, promoting the growth of Actinobacteria, Proteobacteria, and Ascomycota (Yan et al. 2021). Additionally, certain Ascomycota can break down and mineralize the aromatic C in biochar, which assimilates to contribute MBC, indicating that biochar acts as a C source for soil bacteria (Zhang et al. 2021b). However, high-throughput sequencing revealed a reduction in the relative abundance of Actinobacteriota upon high biochar application, while increase in Acidobacteria was evident. In consequence, particulate organic carbon (POC) and SOC showed a positive correlation with the biochar application rate; while a decline in dissolved organic carbon (DOC) and water-soluble organic carbon (WSOC) was found. Qiu et al. (2023) examined these variations in soil labile organic C and found that it is more dependent on time after application rather than the rate of application.

Significant changes in the active microbial community structure of both bacteria and fungi play a indispensable role in regulating SOC as well as DOM and pH of the soil. For instance, biochar amendment comprising mainly recalcitrant C compounds was found to be potentially degraded by Actinobacteria and Chloroflexi (Chen et al. 2016a). Lower relative abundance of Firmicutes comprising class *Bacilli* and *Clostrida* along with reduction in Acidobacteria, Acidimicrobia and Thermoleophilia upon biochar amendment signify their lesser influence on SOC mineralization. The shift in the microbial community supporting the dominance of Alphaproteobacteria, Bacteroidia, Gammaproteobacteria and Gemmatimonadetes contribute to the SOM mineralization process, coinciding with the rise in soil pH and recalcitrant C components. This shift was further aided by a decrease in persistent DOM components (such as condensed aromatics and tannin), while an increase in labile DOM components (such as carbohydrates, unsaturated hydrocarbons, lipids, and amino sugar) occurs (Lévesque et al. 2020; Wu et al. 2021b; Ling et al. 2022). However, Firmicutes' microbial biomass and necromass help in C transformation to boost MBC (Yang et al. 2022b). Similarly, biochar increased MBC content along with increase the SOC, DOC and MAOC (mineral-associated organic C) content. In contrast to bacterial necromass C being unaffected by biochar application, fungal-derived necromass C content was found to be significantly high. Biochar increases fungal activity and turnover, which supports a stable soil C pool and increases POC concentrations strengthening the SOC sink (Sun et al. 2022b). Negative priming of native SOC can be induced by biochar with increases in CUE and stabilize the microbial necromass. But higher biochar application rate results in lower mineralization of SOC as most biochar particles contribute to free particulate organic matter (POM) fraction (Kalu et al. 2024).

Abundant labile C sources, nutrients and accessible cations aid bacterial sustenance in early stages of application, while decline in its availability as the biochar ages corresponds to lesser availability of labile C and nutrient sources (Xiao et al. 2022). SOC within biochar is prominently mineralised by Actinobacteria, facilitated by its hyphal structure reaching deeply located source and decomposing it. For instance, genus *Nocardioides* belonging to order Actinomycetales in biochar amended soil plays a key role in rhizodeposition and SOC mineralization in *Zea mays* planted soil (Fu et al. 2022). Similarly, another filamentous bacterium *Streptomyces* of the same order promoted the mineralization of pine wood biochar assisted by a higher O/C ratio (Zeba et al. 2022). The oxidation of biochar surfaces during the ageing process adds oxygenated functional groups such as carboxylic and ester groups, this stabilises the native SOC by physically shielding soil aggregates (Li and Tasnady 2023). Maize straw biochar increases the abundance of Proteobacteria, Chloroflexi, and Bacteroidota, while decreasing Actinobacteriota, Gemmatimonadota, Myxococcota, and Nitrospirota. This microbial alteration corresponds to increasing DOC initially, while insignificant increase in the later stage as hydrolysis of biochar-adsorbed carbonate occurs on its surface. Biochar amendment increases the soil permeability and aids in the inherent properties of microbes involved in C regulation like Chloroflexi fixing CO_2 in the presence of light. Also, Sphingomonadaceae members being accustomed to using a variety of C sources, play an essential role in C cycling. Pyrogenic C input provides labile C compounds associated with biochar and stimulates their abundance (Fu et al. 2021).

In a 10-year experiment, an increase in the relative abundance of oligotrophic bacteria compared to copiotrophic bacteria over time was found. In the short phase, enhanced soil respiration contributes more labile C which gets depleted within months. While, in the long term greater availability of non-labile C significantly increases SOC concentration, stabilised through microbial C pump mechanism and biochar-induced organo-mineral interactions (Singh and Cowie 2014; Idbella et al. 2024). Guo et al. (2024), elucidated that increasing humin (a stable and resistant component of SOC) content induced by 7-year biochar application results in enhanced native SOC content due to stabilization of soil organic–inorganic complexes. On the contrary, a reduction in native SOC content over 8 years (Sun et al. 2020b) and 11 years of biochar application was found (Ding et al. 2023). Long-term biochar ageing may accelerate the breakdown of root C inputs supporting microbial proliferation, increasing CO_2 emission, and lowering CUE. Decreases in labile organic C components, such as sulphuric acid-hydrolyzed organic C and hot water dissolvable organic C, may be linked to this increase in CO_2 emission, while reduction in the SOC pool. Meng et al. (2024) in a meta-analysis concluded that biochar prepared at low temperature (≤ 400 °C) with a lower application rate (< 25 t ha^{-1}) for a long time (> 3 years) benefits soil C sequestration and GHG emission reduction process. Biochar, although considered as a promising C sequestration agent, long-term field experiments are limited to assess the comprehensive effects of biochar application on the different forms of soil C and associated microbial community. To confirm the mechanisms of biochar mediated key functioning in C mineralization, further validation is required. Comprehending feasibility, safety, and effectiveness poses biochar as a global C sink and a masterstroke to achieve C neutrality.

5.2 Biochar regulates N dynamics through microbes

Biochar has the potential to improve soil fertility through the retention of N. Many studies have elucidated the positive role of biochar in decreasing soil bulk density and remarkable increase in NO_3^- accumulation preventing its leaching (Borchard et al. 2019; Chen et al. 2020; Haider et al. 2020). Its amendment significantly increases the activities of nitrite reductase, urease, and N-acetylglucosaminidase in soil, indicating an accelerated microbe-mediated N cycling (Chen et al. 2021). Nitrite reductase involved in the denitrification process, catalyses the reduction of NO_2^- to NO, while urease catalyses the hydrolysis of urea and contributes to the soil ammonium–N (NH_4^+–N) content (Pan et al. 2023). N-acetylglucosaminidase is involved in the breakdown of organic N, sufficing the initial need for N for soil microbe proliferation and concurrently improving immobilization of leachable N to maintain the soil N pool (Chen et al. 2018). Primarily, leaching out of organic and NH_4^+–N has been found to reduce remarkably upon biochar amendment. Following application, the number of active sites and functional groups increases, allowing improved sorption and availability of NO_3^- and NH_4^+ in the soil solution for plant uptake. Hematimatin et al. (2024), in a long-term study (7 years) emphasized microbial role in reduced nitrification rate via activating heterotrophs for NH_4^+ utilization. Moreover, enriched microbes can increase N mineralisation/nitrification of NO_3^-, NH_4^+ or available N present in the biochar. H. Sun et al. (2018), reported more effective decrease in N leaching when applied twice than a single application of biochar. Alteration in the soil properties induced by biochar regulates the abundance of nitrifying and denitrifying microbes in soil, particularly those that reduce the flux of N_2O such as *Mycobacterium* and *Bradyrhizobium*, eventually boosting crop yields. High C: N ratio imparted by biochar raises the microbial biomass and the N-fixing activity of the microorganisms (Yan et al. 2019) and with increase in biochar amendment rate, the microbial biomass N (MBN) proportionately improves (Hu et al. 2023). These organisms change the dynamics of soil N by producing NH_4^+ that can be adsorbed to the biochar or enhance the denitrification of N_2O to N_2 (Ahmad et al. 2021). Liming effect of biochar converts NH_4^+ in the soil solution to NH_3, consequently making it accessible for ammonia monooxygenase catalysis (Ji et al. 2020). AOB and AOA populations increased by biochar boost the momentum of biochemical processes (Hu et al. 2022) and hence, benefit soil net nitrification making the soil environment more conducive to nitrifier activity. However, Liu et al. (2024a, b), indicated more prominent role of AOB in soil nitrification rather than AOA, with a significant increase in AOB following biochar addition. Neutral-to-alkaline pH and nutrient-rich environment favour presence of higher ammonia monooxygenase gene containing AOB than AOA, shifting the soil condition more favourable towards proliferation of AOB. Biochar from peanut shells hindered nitrification due to presence of phenolic compounds, which decreases the abundance of AOB (Wang et al. 2015).

Biochar significantly reduces NH_4^+–N loss in soils amended with it. This can be attributed to carboxyl and ketone functional groups retaining NH_4^+ through hydrogen bonding and electrostatic interaction. Additionally, reduction in the soil ammonia volatilization retains ammonium ions by enhancing the CEC of the soil, and thereby, reduces cumulative NH_4^+–N loss (Gupta et al. 2024). Breakdown of biochar derives certain PAHs and ethylene, which are metabolized by species of *Mycobacterium*, known for their ability as NO_3^- reducers (Assil et al. 2021). The presence of biochar induces proliferation of some Mycobacteriaceae members participating in dissimilatory NO_3^- reduction and NO_3^- ammonification to counteract the loss of NH_4^+ and hence cause a shift in the N cycle. Biochar promotes mycobacterial nitrate reduction to NH_4^+ in tandem with N fixation while reducing the abundance of microbiota converting NH_4^+ to nitrite (NO_2^-) (Anderson et al. 2011). Similarly, *Arthrobacter* although aerobic in nature, certain species of it have the ability to utilize NO_3^- as an electron acceptor in anaerobic metabolism. These species convert NO_3^- into ammonia and can endure extremely high concentrations of NO_3^- (Pandey et al. 2020). Fox et al. (2016), reported notable rise in *Arthrobacter* species abundances following treatment with *Miscanthus* biochar. Furthermore, *Arthrobacter crystallopoietes* alongwith *Azospirillum brasilense*, enhanced N fixation and released available P under acidic soil conditions treated with biochar. Bacterial families Rhodospirillaceae and Bradyrhizobiaceae metabolize a wide range of C compounds available in biochar, being copiotrophic in nature and plays significant role in N_2 fixation and respiratory NO_3^- reduction (Kari et al. 2021). Bradyrhizobiaceae members including *Bradyrhizobium, Nitrobacter, Rhodoblastus*, *Rhodopseudomonas* and Hyphomicrobiaceae members *Rhodoplanes* and *Starkeya* are involved in denitrification of NO_3^- to N_2. *Bradyrhizobium* has both N fixing and denitrification abilities due to the presence of *nosZ* gene, which reduces N_2O to N_2 (Mania et al. 2020). *Nitrobacter* converts NO_2^- to NO_3^- through oxidation. *Rhodopseudomonas*, *Rhodoplanes* and *Rhodoblastus* contribute to the denitrification pathway by removing excess redox and alleviating toxicity from certain nitrogen oxide intermediates (Zhu et al. 2018) and also result in decrease in methane flux when coupled with NH_4^+ adsorption to biochar (Anderson et al. 2011).

N fixation can also be accelerated by boron and molybdenum derived from biochar (Ghazimahalleh et al. 2022). For instance, papermill waste biochar application increased biological N_2 fixation and improved yield of Faba bean, due to promotion of boron and molybdenum uptake by the plant with reduced soil acidity (Van Zwieten et al. 2015). The proportional increase in N-fixing microorganisms *Burkholderia* and *Bradyrhizobium* upon biochar use was clearly evident. However, the abundance of *Sphingomonas* and *Ottowia* associated with nitrification and denitrification respectively, was found to be reduced (Gou et al. 2023). *Sphingomonas* plays a critical role in converting nitrite-nitrogen (NO_2^-–N) to nitrate-nitrogen (NO_3^-–N) during the nitrification process. Reduction in this nitrifying and denitrifying bacteria contributes to retention of soil N and reduces its leaching and N_2O emission (Hu et al. 2023). Furthermore, the addition of biochar lead to rapid consumption of DOC, which enhances the proliferation of N-fixing diazotrophs like *Streptomyces, Azotobacter Bradyrhizobium* and *Skermanella,* while reducing *Desulfovibrio* and *Klebsiella* abundance (Zhao et al. 2021a). Also, an increase in pH and molybdenum availability was promoted due to the presence of sulphur in the biochar, which positively correlated with the abundance of the diazotrophs. However, toxic PAHs and presence of other contaminants in biochar can inhibit biological N fixation (BNF). Jiang et al. (2023) reported reduced N fixation and limited primary NUE in cadmium-contaminated paddy soil upon biochar amendment. Though an increase in BNF in the vegetative stage was found, later stages were marked by a sharp reduction in it. Soil diazotrophic bacterial communities with reduced abundances of Euryarchaeota, Desulfobacterales (Proteobacteria) and Sphingomonadales (Bacteroidetes) during the tillering stage were evident.

Promotion of the relative abundance of nitrifying bacteria like *Nitrospira* and Nitrosomonadaceae, Rhizobiaceae, Lysobacter, and Xanthomonadales members, enhances TOC, NO_3^--N, and TON content (Zhao et al. 2023). These *Rhizobiaceae* and *Xanthomonadales* members are mostly aerobic in nature, indicating that biochar improves soil aeration and contributes to BNF (Zhang et al. 2024a). Cui et al. (2024), contrary to the earlier report, found reduction in *Nitrospira,* irrespective of the increase in soil TN. A high application rate may incur such decrease in abundance of *Nitrospira,* as generally lower biochar concentration promotes an initial rise in its abundance. Increase in TN was attributed mainly due to rise in diazotroph like *Bradyrhizobium.* Also, a strong positive correlation with the abundance of Actinobacteria, *Frankia* spp., *Rhizobium, Azospirillum,* and methane oxidizing bacteria such as *Methylocaldum, Methylomicrobium,* and *Methylopila* with increasing biochar application was observed in different soil condition (Abujabhah et al. 2018). Wu et al. (2024b) found a correlation between NO_3^- levels altered by biochar and the relative abundance of specific microbe, positively correlated with abundance of *Gemmatimonadetes* while negatively impacting *Ilumatobacter*. Amendment of biochar led to a reduction in the relative abundance of Gemmatimonas, while it increased the relative abundance of Arthrobacter, Ilumatobacter, Luteolibacter, Lysobacter, and Mesorhizobium. Furthermore, phyla Anaerolineae, Deltaproteobacteria, Gemmatimonadetes, and Verrucomicrobiae were reduced, while the relative abundance of Alphaproteobacteria, Gammaproteobacteria, Bacteroidia, and Acidimicrobiia were increased. Functional genes that support N fixation, mineralization, denitrification processes and dissimilatory/assimilatory nitrate reduction are found in *Gemmatimonas* species. In soil treated with biochar, the bacterium *Gemmatimonas* impacts nitrate accumulation as it is involved in different N conversion pathways (Wu et al. 2024b). By facilitating the conversion of N_2O to N by reducing bacteria, biochar reduces N_2O emission. In the process, the relative abundances of N cycling bacteria like Bacteroidetes, Gemmatimonadetes, Nitrospirae, Proteobacteria and Robobacteria increases. Nitrospirae has high nitrification activity, and Gemmatimonadetes are essential to assimilative and dissimilative N processes, while Bacteroidetes and Proteobacteria have a positive correlation with the soil NH_4^+-N content (Liao et al. 2021). Similarly, N-rich biochar drastically increased TC, and TP, while decreasing N:P and C:P ratio with an increase in the abundance and diversity of soil microbiota. Relative abundance of the *Bacillus*, *Geobacter*, and *Sideroxydans* were decreased upon N-enriched biochar application, whereas that of *Thiobacillus*, *Thermomonas*, Spicellomyces and *Crustoderma* were increased. Nguyen et al. (2018) in a 9-year long study found increase in *Bradyrhizobium*, and *Bacillus* involved in N_2 fixation and denitrification respectively. Fungal genera *Westerdykella*, *Synchytrium*, *Russula*, and *Orbilia* showed a positive correlation with TC in the soil, whereas *Trapelia*, *Leptosphaerulina*, and *Tremella* were positively correlated with TN (Yin et al. 2021). Hence, biochar induced changes in the abundance of soil nitrifying and denitrifying microbes manage soil N status and microbial function associated with it.

5.3 Effect of biochar and fertilizer combined application in soil C and N regulation

The combined application of biochar and exogenous fertilizer has inconsistent effects in regulating soil C and N status. Fertilizer influences biochar effect on the microbial diversity/abundance and C and N cycling related enzymes (Ibrahim et al. 2020). The application of NPK fertilizer combined with biochar significantly impacts the composition and functions of the microbial community, which in turn mediates the SOM cycle. Soil microorganisms start mining N from the SOM to make up for high C: N ratio upon biochar application, speeding up the C and N cycling (Tian et al. 2016). Wu et al. (2021a) reported a significant increase in soil CO_2 emission rates after straw and manure addition, while the emission dropped when it was co-applied with biochar. Biochar raises soil organic and inorganic C content, reduces imbalance in soil C and N stoichiometry (Wang et al. 2021**),** and leads to a reduction in CO_2 emission from biotic and abiotic processes (Fernández et al. 2014). For example, Oladele et al. (2019), emphasized this reduction in CO_2 flux and microbial metabolic quotient (qCO_2) with increasing biochar application rate. Biochar and N fertilizer combination increased the fungal: bacterial ratio and shifted toward a more fungal-dominated population. On the other hand, Song et al. (2020) concluded that the primary parameters influencing microbial community structure are available K, TN, pH and total dissolved N; and rejected the notion of rapid fungal growth upon combined amendment. Moderate application of biochar with N fertilizer (5 years) yielded high microbial biomass, microbial quotient, and enzyme activity associated with C and N cycling. While application of biochar alone comparatively reduced MBC content due to the high C: N ratio (Meng et al. 2023). Combined application increased total microbial biomass, however Yu et al. (2018a) reported no significant change in the microbial community structure in such conditions. High pH induced by biochar promotes Gram-negative bacterial activity to increase soil labile C content and enhances N retention. These effects on MBC and MBN pools are dependent on the amounts of biochar used, the application rates of fertilizer as well as the depth and type of the soil (Oladele et al. 2019).

Urea, the most extensively used fertilizer when co-applied with biochar influenced N mineralization rate and enhanced N retention. For example, rice-residue biochar and poultry manure biochar in combination with urea lowered N mineralization (up to 45%) (Dey and Mavi 2021). Generally, when biochar is applied in combination with urea, biochar of higher CEC reduces the rate of nitrification and ammonification, whereas biochar containing higher ash content reduces N_2O emission (Li et al. 2021). Li et al. (2022), in a field experiment (5 years) found an increase in diversity and abundance of N-fixing and P-solubilizing bacteria such as *Bradyrhizobium*, *Haliangium* and *Sphingomonas* upon co-application of NPK fertilizer and biochar. Likewise, biochar and organic fertilizer amendment improved maize production, plant N absorption, and reduced average TN losses (Yan et al. 2023). Application of biochar (4%) was found to raise the rate of N fertilizer retention reducing leaching losses in yellow soil (Zhang et al. 2021c). Ali et al. (2020), reported considerable improvement in soil pH, total N, soil microbial C, and soil microbial N, along with increase in rice grain production. The phyla Acidobacteria, Actinobacteria, Proteobacteria, and Verrucomicrobia were found to be enhanced, while the relative abundance of soil fungi belonging to the Ascomycota, Basidiomycota, Chytridiomycota, and Rozellomycota was reduced. The increase in rice productivity was mainly promoted by soil bacteria such as Acidobacteria, Actinobacteria, Bacteroidetes, Planctomycetes, and Proteobacteria (Ali et al. 2022). *Prosopis juliflora* biochar amendment with fertilizer considerably increased soil NO_3^- concentration and raised maize grain production (Kamau et al. 2019). Moreover, biochar-based microbial fertilizer was found to effectively prevent N and P leaching, and improved soil nutrient status with enhancement of bacterial abundance regulating soil C and N metabolism (Wang et al. 2023b). For instance, the combined application of biochar and N fertilizer effectively increased total N and total inorganic N (Xia et al. 2023). A meta-analysis revealed 25.3% increase in crop productivity including an additional boost of 10% when biochar was applied in combination with either inorganic or organic fertilizers in acidic soil (Bai et al. 2022). Similarly, Dangi et al. (2020), reported higher rate of increase in TC and TN in a period of 2 years in co-application than fertilizer applied alone. When biochar with organic fertilizer was used, *Rhodanobacter* and *Azospirillum* were found in greater relative abundances and contributed to minimizing the N_2O emission (Shi et al. 2019). Biochar's ability to adsorb N immobilizes surplus N in fertilizer attributed to lower emission of N_2O. A high biochar to N fertilizer ratio suppresses N_2O emission, while the reverse ratio promotes emission (Feng and Zhu 2017). In acidic soil, aged biochar encourages fungal growth (lacking N_2O reductase gene) and results in N_2O production (Zhong et al. 2022; He et al. 2022). It is pertinent to mention that the effectiveness of reduction in N_2O emission can also be impacted by the nitrification or denitrification inhibitors when applied with biochar. Negative correlation between the abundance of the *amoA*-AOB and *amoA*-AOA genes and NO_3^--N content is influenced by addition of biochar and N fertilizer. It impacts autotrophic nitrification rate by significantly lowering the abundance of the *amoA*-AOB gene (Yao et al. 2022). For instance, biochar and N fertilizer application (8-year duration), increased AOB abundance, while decreasing the abundance of AOA. Biochar alone or in combination with fertilizer increased the soil nitrification rate, but single N fertilizer application decreased the soil nitrification rate and resulted in ammonia oxidation (Sun

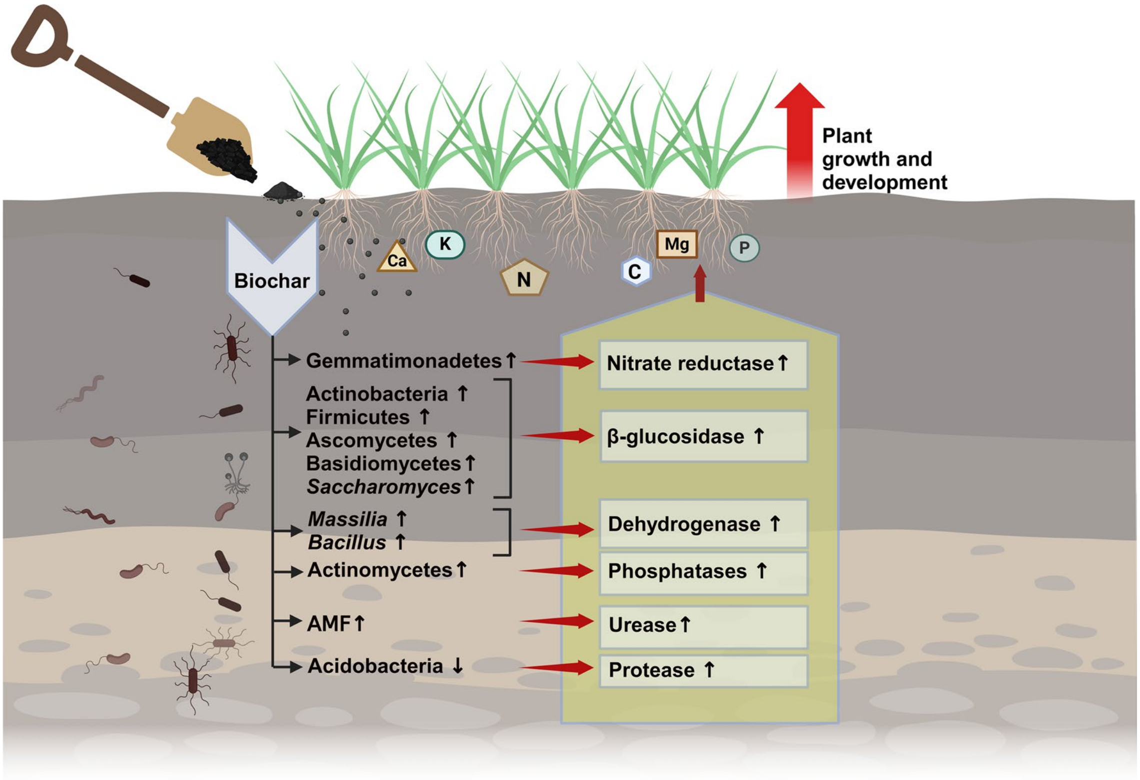


Fig. 2 Biochar amendment impacts the abundance of soil microbes which upregulate/downregulate soil enzymes responsible for plant nutrient availability (this depiction is derived from some specific studies, which may not be consistent in varying conditions). Here ↑ indicates an increase, while ↓ indicates a decrease in soil microorganisms and enzymes (created with BioRender.com)

et al. 2024). A specific proportion of fertilizer should be co-applied with biochar for effective soil functionalities. This can promote C and N use efficiency by reducing nutrient losses and ensure high crop productivity.

6 Biochar impacts microbial enzymatic functionalities and soil respiration to balance C and N

Range of biogeochemical activities in the soil are facilitated/catalysed by the extracellular as well as intracellular enzymes released by soil microorganisms (Zuccarini et al. 2023). These soil enzymes are important indicators of soil quality as they reflect soil microbial activity and biogeochemical cycling of nutrients (Meena et al. 2024). Biochar from different feedstock directly affects the abundance of microbial communities and soil properties by influencing the enzymatic activities of the soil (Fig. 2). Biochar impact on soil enzyme activities varies as the optimal range for a certain enzyme differs with a shift in soil pH (Das et al. 2023). For instance, the shift towards alkaline pH induced by biochar directs optimal activity of protease by promoting the growth of protease-producing microorganisms, while a significant decrease in acid phosphatase activity due to rising soil pH can be seen (Peng et al. 2024). The impact on reactions of biochar and the target substrate can also be influenced by the sorption of trace elements, which are necessary for many enzymatic processes. Biochar engages in organic matter decomposition through direct extracellular electron transfer (DEET) and direct interspecific electron transfer (DIET) between soil organic matter and microbial cells (Zhu et al. 2017). This forms the basis for an increase in dehydrogenase activity upon biochar application, as it shuttles electrons onto the substrate (Triphenyltetrazolium chloride) (Yang et al. 2024b). Microbial co-metabolism involving enzyme production causes SOC mineralization and with C availability microbial activity boosts in the soil (Wu et al. 2023a).

Biochar properties and type of soil in which it is applied influence soil enzyme activities. An increase in MBC, as well as the activities of alkaline phosphatase, dehydrogenase, and urease, were evident, with a more prominent effect of biochar in fine-textured soil such as clay, clay loam, and silt clay having low pH (<6.5) (Pokharel et al. 2020). Significant reductions in bulk density and increase in the activities of soil urease, sucrase, catalase, and β-glucosidase along with enhanced soil respiration rate were observed on biochar addition. However, with ageing time of biochar, the respiration rate and enzyme activities decrease (Wang et al. 2022). Furthermore, high application rate can reduce the soil bulk density, while increasing the soil respiration rate due to increasing oxygen flux and water content along with an increase in microbial activity in the biochar-soil system. This can lead to long-term CO_2 emission (Guo et al. 2024). Some extracellular enzymes involved in the soil C cycle, including β-glucosidase, β-D-cellobiosidase, β-xylosidase, and α-glucosidase were found to be more active in biochar-treated soil (Palansooriya et al. 2019). These enzymes directly or indirectly regulate the soil respiration process (Becker and Holz 2021). Recalcitrant or complex forms of C require specific enzymes like arylesterase for its decomposition. Such complex C impacts extracellular enzymes such as β-glucosidase and cellulase involved in the C cycle by either decreasing or remaining unchanged in its activity, hence slowing the C mineralization process to boost soil C stock. Idbella et al. (2024), in 10 years of biochar amendment, found an increase in arylesterase activity while a reduction in cellulase activity was evident. However, β-glucosidase activity was found to be unchanged over time. This can be attributed to elicitation of cellulose decomposing and phosphate mineralising bacteria (like *Pseudomonadaceae* members) in the long term, mostly due to the influx of labile C compounds supplemented by the biochar. Other microbes like Actinobacteria, Firmicutes, fungi belonging to Ascomycetes, Basidiomycetes and some yeast species of *Saccharomyces* genus secretes β-glucosidases which decompose soil cellulose (Tahir et al. 2024). Similarly, Actinomycetes produce phosphatases, contributing to soil phosphorus cycling (Neemisha and Sharma 2022).

Li et al. (2018) while applying biochar in a bamboo plantation reported reduced activities of β-glucosidase and cellobiohydrolase, while the aromatic C content and RubisCO enzyme activity were significantly boosted. As a result, decline in soil heterotrophic respiration occurs with alteration in SOC recalcitrancy and microbial activity. Similarly, soil respiration rate reduced on higher application (40 t ha^{-1}) of biochar due to rise in the recalcitrant C and lowering of the labile C pool. On the other hand, it raised the temperature sensitivity of soil respiration (upto 35 °C) by promoting the activities of enzymes and microbial abundance (Chen et al. 2016a). Reduced β-glucosidase, β-glucosaminidase, and phosphatase activity can be accredited to the adsorption potential of enzymes on biochar surfaces which render them inactive for enzymatic activities. For example, a reduction in the soil enzyme activity of β-glucosidase and phosphatase was found upon adding pine biochar (Foster et al. 2018). β-glucosidase activity is also influenced by soil composition, showing higher activity in lighter granulometric than heavier granulometric composition (Wei et al. 2020).

Biochar changes several essential biological properties that are mostly responsible for regulating soil microbiota and enzyme activities associated with the N cycle. Enhancement of Verrucomicrobia, Cyanobacteria, Glucosylbacteria, *Nitrospira* and decreased soil urease activity controls of amino acid N, whereas Bacteroidetes, Gemmatimonadetes, Acidobacteria, and Proteobacteria are primarily responsible for controlling acid-hydrolysable ammonium N content. Enriched Gemmatimonadetes leads to enhancement in soil nitrate reductase activity control hydrolysable N, whereas enriched Acidobacteria and reduction in soil protease mediates amino sugar N level (Wang et al. 2024a). This suggests a direct relationship between the generation of acid-hydrolysable N fraction and their activities with specific soil microbiota. Different biochar has been demonstrated to elevate the dehydrogenase activities in amended soil under different conditions. The higher levels of dehydrogenase activity in soil treated with biochar are often caused by the high volatile matter content of the utilized biochar and the presence of labile organic matter (Rathour et al. 2022). Sakin et al. (2021) reported a significant increase in dehydrogenase activity upon use of almond shell biochar. Similarly, corn cob biochar increased dehydrogenase and urease enzyme activities in weathered tropical sandy loamy soil, with an increase in the abundance of AMF (Amoakwah et al. 2022). An increase in dehydrogenase activity upon biochar amendment boosts bacteria of the genus *Massilia* and *Bacillus* which in turn degrades lignin and chitin by secreting the extracellular enzymes (Akumuntu et al. 2024). Hence, different enzyme activities are interlinked. Dehydrogenase is often impeded by low soil moisture content which lowers intracellular water potential and thereby decreases hydration and dehydrogenase activity (Korav et al. 2024). This phenomenon may also be attributed to increased SOM content in the amended soils. Soil dehydrogenase enzyme fastens up the breakdown of SOM, as substantiated by soil respiration and CO_2 effluxes from the rhizosphere (Ansari et al. 2024), confirming the notion that dehydrogenase enzyme is positively correlated with SOM content. However, Mierzwa-Hersztek et al. (2020), reported reduced dehydrogenase activity upon biochar treatment, probably due to the unavailability of microbe available C. Increasing pyrolysis temperature as well as residence duration irrespective of its feedstock, upon application results in declined dehydrogenase activity and soil respiration rate (Beheshti et al. 2018). Biochar feedstock material was found to be a primary factor in regulating the enzyme activity responses (Wojewódzki et al. 2022). Moreover, enhancement of sucrase, catalase, urease (Meng et al. 2023) and peroxidase (Liu et al. 2024b) enzyme activities were reported in the biochar amended topsoil layers (after 5 years). The possible mechanisms behind the increase of catalase and peroxidase activity following biochar amendment are the response of microbial communities to oxidative stress. The presence of persistent free radicals on biochar surface induces antioxidant protection enzymes to counter oxidative stress (Kumari et al. 2024). However, biochar prepared at a high pyrolysis temperature contains high free radical content which can have toxic effects on microbial communities and subsequently decrease the enzymatic activity (Yang et al. 2023). In response to this, an increase in soil nitrogenase while decrease in ammonia monooxygenase and nitrate reductase were reported (Gou et al. 2023). Further research is needed to understand the mechanisms via which biochar regulates soil enzyme activity and the processes engaged in this relationship.

7 Biochar regulates GHG emission by recruiting soil microbes

Biochar amendment influences GHG (mostly CO_2, CH_4, and N_2O) emission from paddy fields and wetlands (Lyu et al. 2022). Numerous meta-analyses have shown the effect of biochar addition on GHG emission and their impact on C and N cycles, eventually affects crop performance (Jia et al. 2023; Li et al. 2024; Xia et al. 2024). Discrepancy between soil C fixation and atmospheric C release contributes to a steady rise in atmospheric CO_2. Acidification increases the number of heterotrophic microbes, particularly Proteobacteria and Acidobacteria, which are responsible for high CO_2 emission (Hamamoto et al. 2022). Biochar treatment decreases their abundance due to increasing pH and higher nutrient incorporation into the soil (Han et al. 2024). Longer persistency of biochar than its biomass source accounts for half of the reduction in emission and removal of CO_2. Biochar has the potential to reduce emissions by 3.4–6.3 Pg CO_2e globally, with half of the reduction caused by the removal of CO_2 (Lehmann et al. 2021). Soil to which biochar has been amended also plays an important role in altering microbial abundance and thereby regulating GHG emission. In ferralsol, biochar led to increased CO_2 emission mostly because of increased biochar decomposition promoting proliferation of copiotrophic bacteria, but in alkaline phaeozems, negative priming effect of SOC resulted a decrease in total CO_2 emission (Slavich et al. 2013). Enrichment of copiotrophic bacteria such as Bacteroidetes, Gemmatimonadetes, while decrease in oligotrophs such as Acidobacteria plays dominant role in high emission of CO_2. However, a greater prevalence of oligotrophic bacteria in phaeozems caused by the lower bioavailability of SOC due to the adsorption of biochar resulted in reduced CO_2 emission (Sheng and Zhu 2018). Biochar reduces CH_4 emissions from soil, especially from acidic soils and paddy fields. However, adding biochar to neutral or alkaline soil can potentially weaken the CH_4 retention capacity of the soil (Jeffery et al. 2016). Additionally, biochar can adsorb cations such as Fe^{3+}, Al^{3+}, or NH_4^+ from paddy soils. Reduction in these cations makes it compete with CH_4 for methanotrophs' oxidation sites (Wang et al. 2023a). The amount of CH_4 emission from soil is significantly influenced by the choice of feedstock for biochar (Ippolito et al. 2020). Biochar prepared from feedstock with low C: N ratio such as dung or straw increases the amount of C available for methanogenesis, which in turn enhances CH_4 production. However, feedstock such as cellulose and wood contain lignin and its durability preserves the pore structure during pyrolysis and reduces CH_4 emissions (Ji et al. 2018). Lin et al. (2022), investigated the combined effect of biochar and biogas residue and reported reduction in CO_2 and CH_4 emission by enhancing *pmoA* and *acsB* (acetyl-coA synthase complex β subunit) gene expression. Similarly, bamboo biochar decreased the abundance of methyl coenzyme-M reductase and thereby reduced CH_4 emission (Yan et al. 2022). Moreover, biochar reduces C loss in composting by suppressing the activity of CO_2 emitting microorganisms.

Biochar amendment influences both nitrifying and denitrifying bacteria and impacts N_2O emission. Previous studies have documented both increases (Chen et al. 2024; Sanchez-Garcia et al. 2014) and reductions (Wang et al. 2019; Shen et al. 2024) in N_2O emissions, having conflicting effects on biochar addition. Significant reduction in soil gross nitrification and denitrification rate, NH_4^+–N, NO_3^-–N, water-soluble organic N content and activities of urease and protease directly or indirectly reduce soil N_2O emissions (Song et al. 2019). Direct immobilization induced by biochar, adsorption of inorganic N and promotion of denitrifiers belonging to the genera *Cupriavidus*, *Pseudomonas* and *Rhodococcus* causes inhibitory effect on N_2O emission during nitrification (Liu et al. 2021). While a significant reduction in soil net N mineralization and nitrification can remarkably decrease cumulative N_2O emission (Cheng et al. 2024). Decrease in the relative abundance of *Nitrosovibrio* and *Nitrosomonas* with increasing biochar application rate can also contribute to this reduction (Cole et al. 2019), due to the oxidation of NH_4^+ by it or decrease in the NH_4^+ pool through adsorption to biochar surface functional groups. Another crucial factor responsible for this mechanism is the soil exchangeable NH_4^+–N and NO_3^-–N concentrations. In the presence of biochar, soil exchangeable NH_4^+–N content gets converted to NO_3^-–N and results in reduction of N_2O emissions during the nitrification process (Zhou et al. 2023). Soil NO_3^-–N content and abundance of *nosZ* gene further promote the reduction of N_2O via denitrification process. Promotion of *nosZ* harbouring microbes implies induction of denitrification which reduces N_2O to N_2 (Fudjoe et al. 2023). Low pH in soil usually decreases denitrification rate by lowering N_2O reductase activity and hence, limits the expression of the *nosZ* gene. Therefore, biochar-induced increase in pH aids in the denitrification process. Although biochar promotes oxygen circulation through reduction in the bulk density of soil, the aerobic condition usually hinders denitrification activity. However, some autotrophic nitrifying bacteria using O_2 and NO_2^- as electron acceptors can perform denitrification (Song et al. 2021). Again, nitrification and denitrification processes may proceed simultaneously and comparative increase in the nitrification rate can suffice the substrate for initiating denitrification process (Lin et al. 2009). The exact mechanisms behind these belowground complex intricacies are not yet deciphered totally as multitude of factors may simultaneously influence their role and need further comprehensive studies.

Applied dose and duration of biochar application determine its effectiveness in regulating soil N_2O emissions. For instance, Liu et al. (2020a), investigated the inhibitory effect of biochar on N_2O emissions in wheat and maize, varying across different parameters. A comparative study using pristine biochar application and aged ones showed that incorporation of pristine biochar increased NH_3 emission while aged biochar led to decrease in the emission. This decrease in case of aged biochar can be explained by the presence of greater concentration of oxygen functional groups, showing improved ammonia monooxygenase activity and increased NH_4^+/NH_3 adsorption capability in soil. Biochar induced accumulation of NH_3 oxidation products (NH_2OH) encourages nitrification-derived N_2O emissions (Chen et al. 2024). However, Duan et al. (2018), reported a rise in soil N_2O emissions due to accelerated nitrification and denitrification by aged biochar. Moreover, reactive oxygen species and persistent free radicals derived from biochar often impede its ability to decrease soil N_2O emissions by blocking expression of *nosZ* (Wu et al. 2023c). Further, He et al. (2018), found reduction in N_2O, NO and NH_3 emission upon combined application of urease and nitrification inhibitors along with biochar. Biochar application has turned out to be a sustainable approach to reduce GHG emissions. However, it is difficult to anticipate the effect of biochar on $CH_{4,}$ CO_2, N_2O, NO, and NH_3 emission in different soil types, land use systems, application rate, duration and other environmental variables and hence proper multifaceted studies concerning its impact in soil functionalities is the need of the hour.

8 Biochar effect on functional microbial gene expression mediates soil enzyme activities and GHG emission

Biochar has a prominent role in influencing rhizosphere microbial gene expression related to C and N cycling. Hewitt et al. (2023) reported alteration of gene expression in rhizosphere inhabiting bacteria and fungi upon biochar amendment. Several plant-beneficial bacteria belonging to the family Micromonosporaceae, Pseudomonadaceae, Rhizobiaceae, and Sphingomonadaceae exhibited higher gene expression in response to biochar treatment. An increase in microbes comprising ribulose-1,5-diphosphate carboxylase/oxygenase (*RuBisCO*) gene promotes CO_2 fixation by preventing its emission from tricarboxylic acid cycle. In this process, pyruvate dehydrogenase (*PDH*), isocitrate dehydrogenase (*IDH*), and alpha-ketoglutarate dehydrogenase (*A_KGD*) are inhibited to enrich C fixing microbiota, while CO_2 emitting bacteria like *Luteimonas* and *Proteobacteria* were reduced (Yan et al. 2022). On the contrary, Lu et al. (2020), reported a reduction in the abundance of C fixing gene *CarbFix* after biochar application. Higher relative abundance of this gene belonging to Alphaproteobacteria, while significant decrease in Actinobacteria and Acidobacteria was observed. Biochar made from wheat straw reduced the abundance of fungal gene *cbh*I (cellobiohydrolase I), by modulating fungal community structure and also resulted increase in the soil aromatic C content (Li et al. 2018). Similarly, biochar reduced the abundance of soil C sequestration genes *cbbL* (RuBisCO form I) and *cbbM* (RuBisCO form II), primarily influenced by the moisture content of the soil (Zhang et al. 2024b). Moreover, high porosity of biochar increases the pace of oxygen transfer, limiting the capacity of methanogens to adapt to that condition (Zhao et al. 2021b) and likewise, prevents CH_4 emission by stimulating its oxidation through the abundance of the *pmoA* (particulate methane monooxygenase) gene (Wu et al. 2019). On a similar note, Ye et al. (2023) reported reduction in CO_2 and CH_4 emission regulated by *cdh, acsB* and *pmoA* genes.

Biochar amended soils differ in abundance of genes responsible for N cycling. An important aspect of the presence of these functional genes in Actinobacteria and Alphaproteobacteria signifies their indispensable role in regulating the N cycle (Lu et al. 2020). Applying biochar enhances the N fixing bacteria, *N*-acetyl-glucosaminidase activity, and influences the expression of soil denitrification {nitrate (*narG*), nitrite (*nirK*, *nirS*), and nitrous oxide (*nosZ*)}, nitrification (*amoA*: ammonia monooxygenase), N fixation (*nifH*: nitrogenase) and ammonification (*gdh*:

glutamate dehydrogenase and *ureC*: urease) genes (Ren et al. 2020; Zhang et al. 2021a). Amendment of biochar yielded a considerable increase in AOA as well as *nirK*, *nirS*, and *nosZ* genes (Xiao et al. 2019). Abundance of these genes are significantly impacted by soil moisture content, available P, available K, TN, TOC, NO_3^-, NH_4^+, pH, and C: N ratio. Although an initial increase in abundance of *amoA* and *nos*Z genes was marked, consistent reductions in these genes were documented till maturity upon excessive biochar application in wheat-cultivated soil. Contradictorily, in maize-cultivated soil, biochar dramatically enhanced the expression of *nosZ* and *nirS* genes in the topsoil. This explains the different effects of biochar based on its application rate and soil depth and thereby impacts crop yield (Xie et al. 2021). Yu et al. (2019) confirmed disparity in results of biochar application, charosphere showing higher abundance of bacterial *amoA* gene, while transition from AOB to AOA occurs as distance increases from charosphere. Moreover, increase in ratio of *nosZ*/(*nirS* + *nirK*) gene with increasing distance from charosphere depicts the functional asymmetry, primarily influenced by dropping pH and a rise in C availability at farther away from the biochar. Whereas, high (*nirS* + *nirK*)/*nosZ* ratio results increase in N_2O emission. However, nitrification inhibitors in biochar can block nitrification genes and decrease the expression of *amoA* gene and thereby reduce N_2O emission (Shen et al. 2024). Zhang et al. (2021a), reported biochar induced increase in *narG* and *nirS*/*K* abundance as compared to *nosZ,* promoting N_2O emission.

Biochar amendment enhances BNF by boosting the abundance of *nifH* genes. Low pyrolyzed biochar amendment in soil deficient in N significantly modulates *Azotobacter* abundance, *nifH* gene expression and nitrogenase activity, concurrently increasing the TN content (Zhao et al. 2021a). Biochar-enriched topsoil reveals the presence of *narG* and *nosZ gene* (Harter et al. 2016). *Mycobacterium* and *Bradyrhizobium* containing these genes participate in NO_3^- reduction in the presence of biochar and convert N_2O to N_2, accounting for decreases in N_2O emissions (Yang et al. 2024c). However, Li et al. (2019a), reported the pivotal role of biochar on the *narG* gene abundance, implying its effectiveness when applied in addition to compost. Amendment of 2% biochar resulted substantial rise in the relative abundance of denitrifier carrying *nirK* gene such as *Rhodococcus* and *nosZ* containing *Cupriavidus* and *Pseudomonas* (Liu et al. 2021). Again, biochar when co-applied with mineral fertilizers, nirK-containing bacteria (*Rhizobium* and Alphaproteobacteria) and *amoA* gene containing AOB increased, while the relative abundance of AOA reduced, along with reduction in the copy number of *nirS* and *nosZ* genes (Huang et al. 2019). Rise in the relative abundance of *Dechloromonas, Nitrosomonas*, *Nitrospira*, *Pseudomonas*, and *Thauera* regulates nitrification and denitrification process to reduce N_2O emissions with considerable increase in the *amoA*, *hao*, *nirS*, and *nosZ* gene abundance. This resulted in the promotion of NH_2OH oxidation during the nitrification process, as well as the facilitation of denitrification to remove NO_2^-–N, thereby reducing N_2O emission (Liang et al. 2020). Hence, enzyme activities, and GHG emissions are intermediated by presence of microbial functional genes signifying enhancement or reduction in specific soil microbes and influencing the C and N status of the biochar-amended soil (Fig. 3).

9 Assessment of sustainability and potential negative impact of biochar on soil health and crop productivity

Biochar amendment improves soil fertility and crop productivity by uplifting nutrient use efficiency and ameliorating beneficial properties of plant-soil system. However, potential benefits of biochar can mostly be noted in soil deficient in nutrients or acidic soil, while reports of negative or no impact have also been reported in certain cases when applied in SOM/nutrient-rich soil (Hossain et al. 2020; Brtnicky et al. 2021). Limwikran et al. (2019), reported the unreliable nature of biochar with regard to sorption and release of nutrient elements, often insensitive to soil properties. High biochar amendment in clay soil decreased water content availability, while it increased erosion and particulate matter emissions in sandy soil. Furthermore, precipitation of nutrients with increase in pH due to biochar application may aggravate soil salinity stress with reduction in soil fertility (Brtnicky et al. 2021). Also, higher application rates as well as some inherent properties of biochar (like pH) may inhibit plant growth and development (Godlewska et al. 2021). For example, biochar application of more than 50 t ha^{-1} in salt-stressed soil suppressed crop growth due to lower N availability and increased salt content (Wu et al. 2024a). While lower amendment promoted exchangeable Ca^{2+}/Mg^{2+} to replace Na^+ in highly saline soil and hence potentially tackles salt stress (Li et al. 2023). Overuse of biochar can impede water and nutrient flow by clogging soil pores and absorbing vital plant essential nutrients. Absorption of important cations has a detrimental effect on the soil CEC and limits plant development (Kumar et al. 2022a). Further, negative effects of excessive biochar application on soil MBC can be found due to high C/N ratio inducing soil microbial N immobilization and thereby decreasing microbial activities (Dey and Mavi 2021). Increasing soil pH with application may induce micronutrient (Cu, Fe, Zn) deficiency in the crops due to its immobilization and adsorption on the biochar

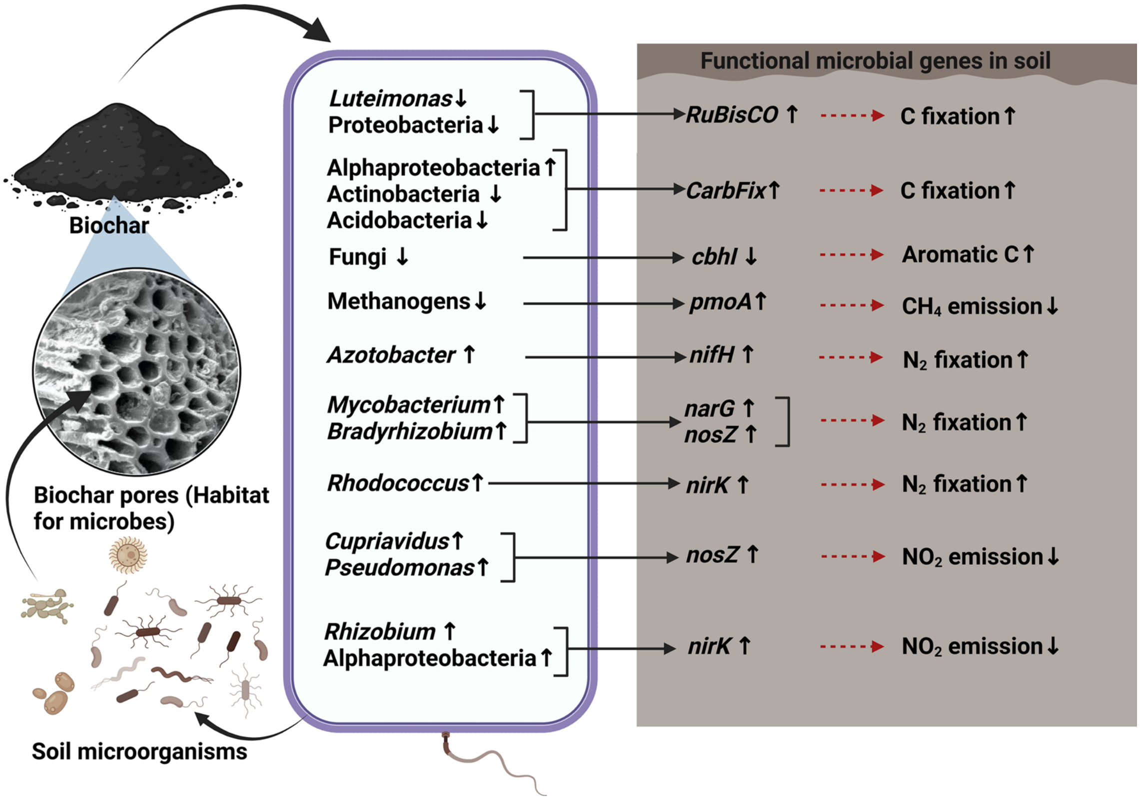


Fig. 3 Changes in microbial functional gene in biochar amended soil portraying the enhancement of specific microbes. Here ↑ indicates increase in the microbial abundance while ↓ indicates decrease in it (created with BioRender.com)

surface (Rodríguez-Vila et al. 2022). Rise in pH decreases *N*-acyl-homoserine lactone (AHL) due to its hydrolysis, which acts as a signalling compound in bacterial cell-to-cell communication thereby hampering the belowground microbial communication. Moreover, presence of certain contaminants like dioxins, furans, PAHs, environmentally persistent free radicals (EPFR), heavy metals (Pb, Cd, Cr, Ni, Zn), and other toxic compounds can have detrimental effects on plants as well as microbial communities in the applied soil (Hussain et al. 2017; Cheema et al. 2024). EPFRs present in biochar can trigger neurotoxic effects in *Caenorhabditis elegans*, inhibiting its function in soil biochemical processes (Lieke et al. 2018). Again, sewage sludge biochar containing PAH like naphthalene resulted in a decline in the radical and shoot length of *Lepidium sativum* (Zielińska and Oleszczuk 2015). Pyrolysis by-products such as phenol, polyphenols and ethylene have antimicrobial properties and may reduce microbial development as evident in AMF (Sun et al. 2022a). Furthermore, ecological services pertaining to other soil biotas including microarthropods, and earthworms are also hindered. Gasified biochars prepared from grape marc (10–50%) increased trace metal content and had a toxic effect on soil arthropod *Folsomia candida* (Conti et al. 2018). Moreover, biochar may reduce the relative proportion of active SOC pool and thus may lower the soil quality if not applied appropriately.

Biochar amendment has been shown to enhance GHG emission in some cases. It exhibits a potential risk of an increase in N_2O emissions induced by nitrification from low-pH soils (Liu et al. 2024a) and may result in soil CO_2 emissions due to the priming effect (Qadeer et al. 2017). An increase in soil nitrification rate synchronously increases N_2O emission. This is evident from increased soil N_2O emission in upland soils owing to its low pH and precipitation conditions, favouring higher nitrification rate. Hence, the conventional use of biochar as a reducer of soil GHG emissions gets compromised. However, GHG fluxes may be influenced by the co-application of biochar and chemical fertilisers/manure, subliming the individual effect of biochar when applied alone (Li et al. 2024). Additionally, the possibility of long retention of pesticide, insecticide or herbicide sorbed by biochar may result in its inactivity upon weed or pest control (Alkharabsheh et al. 2021). Thus, a negative influence on soil biochemical processes and further repercussions in soil health are directly reflected in crop productivity. Although biochar usually improves crop production and aids in its sustenance under biotic or abiotic stress conditions, reports of crop loss and other negative effects of biochar have also been demonstrated in some cases (Murtaza et al. 2021; Khan et al. 2024). For instance, high application of biochar (120 t ha^{-1}) was found to reduce red clover production and resulted in crop loss due to N immobilization (Mia et al. 2014).

Biochar functions as an effective soil conditioner to sustain nutrients in soil and promotes sustainable agricultural nutrient management. Being a C-negative technique, it effectively transforms feedstock like crop residues into nutrient-rich soil supplements and also has a multi-functional role like pollutant remover in soil and water systems (Murtaza et al. 2024). Sustainability assessments of biochar amendment include economic, environmental, social, and technical aspects associated with the large-scale production of biochar (Zhu et al. 2022). Long-term studies figuring out its limitations, specifying the proportionate application dose and assessing the potential ecological threats needs further studies. Controlled pyrolysis of feedstock can reduce GHG emissions promoting a sustainable production process (Zhang et al. 2020). Tracing biochar's long-term effects in soil can prevent potential ecotoxicological impacts associated with it and can ensure sustainable soil applications (Kamali et al. 2022).

10 Conclusion and future perspectives

Biochar as a sustainable soil supplement has perceived global attention possessing the ability to counteract climate change. Liming potential allows it to alleviate soil degradation effects such as acidity through the restoration of the ecological functions, aid in sequestering persistent C compounds in the applied soil and enhances soil physico-chemical properties by increasing plant C uptake and henceforth, boosts agricultural productivity. Biochar-induced improvement in soil ecological function includes increase in microbial and soil enzyme activities, alteration in functional microbial gene abundance, regulation of soil C and N status and shifts in soil microbial community structure and composition to mitigate GHG emission. As a high labile C and mineral nutrients source, biochar with its porous structure provides a suitable habitat for microbial colonization and protects from deleterious effects of various organic and inorganic toxicants. Biochar-microbe-soil tripartite interactions form the basis for regulating the C and N biogeochemical cycle through multifaceted traits involved in this crosstalk. The inherent properties of biochar attributed to feedstock source and pyrolysis condition, soil condition where it is applied determine its ability of priming, impact on the native C and N pool, directly or indirectly stimulate soil microbiota influencing soil enzyme activities and respiration rate. This review comprehensively examines biochar's effect on microbially mediated C and N cycling and fate of associated soil enzyme functioning, microbial functional genes and GHG emission. The increase in soil C and N mineralization and fixation is accompanied by the corresponding increase in the abundance of relevant genes and enzyme activities. Some components in biochar as well as pH and EC of the biochar may turn out to be toxic and negatively impact the soil and microbial diversity. However, the impact is predominantly influenced by the characteristics of the biochar, particularly feedstock type and the pyrolysis temperature and contaminants level.

The intricate relationship between soil microbiome driven by biochar, soil C and N dynamics and crop productivity holds the key function in an agroecosystem. Response of native soil microbial communities, their function and diversity upon biochar application and mechanism pertaining to their successful colonization needs further exploration. Developing cost-effective, and highly efficient strategies for biochar preparation, proper guidelines integrating dose requirements specific to crops, nutrient management, and assessing CUE and NUE can evaluate its holistic impact. Long-term studies comprising biochar's effect on the environment and its consequences on human health should be taken intertwining researchers, academics, farmers, and biochar-producing industries. The review intends to better understand the prospects of biochar towards sustainable, resource-efficient agriculture and caters insight into soil-biochar-microbial complexities to achieve global C neutrality and balance soil nutrient budget for enhanced agricultural productivity.

Abbreviations

GHG	Greenhouse gas
CUE	Carbon use efficiency
NUE	Nitrogen use efficiency
CEC	Cation exchange capacity.
BNF	Biological nitrogen fixation
MBC	Microbial biomass carbon
PLFA	Phospholipid fatty acid

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Availability of data and materials

Data sharing is not applicable to this article as no datasets were generated or analyzed during the current study.

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