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How does biochar reduce N_2O emission from soil? - a review of mechanisms

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ABSTRACT

Agricultural soils are a major source of nitrous oxide (N_2O), a potent greenhouse gas. Biochar application has emerged as a promising mitigation strategy, but our understanding of the mechanisms behind its effects and the interplay between biochar properties, soil conditions, and microbial processes is still incomplete. This review synthesizes recent advances of our understanding of how biochar influences nitrogen transformations and N_2O production, consumption and transport in soils and sediments. Biochar properties, governed by feedstock type and pyrolysis conditions, determine its surface area, porosity, functional groups, pH, and aromaticity, which in turn influence nitrogen cycling pathways involving both production and consumption of N_2O. Mechanistically, biochar reduces N_2O emissions primarily by altering the environmental conditions that regulate N_2O production and consumption pathways rather than by directly suppressing a single microbial process. The most consistently supported mechanisms include increases in soil pH promoting N_2O reduction to N_2, changes in oxygen diffusion and redox conditions affecting the balance between nitrification and denitrification, modulation of carbon and nitrogen substrate availability, and electron transfer-mediated enhancement of denitrification. Despite substantial experimental evidence, knowledge gaps remain regarding the relative importance of mechanisms under specific soil contexts, the roles of critical alternative pathways (e.g., co-denitrification, chemodenitrification), and the electrochemical properties of biochar. Future research should integrate isotopic tracers, imaging, microsensors, light-based techniques and molecular tools, systematically characterize the electron donating and accepting capacity (EDC/EAC), and conduct cross-comparisons across diverse biochars to identify traits that consistently reduce N_2O emissions. A mechanistic framework linking biochar properties to soil processes is essential to guide the design and targeted application of biochar for effective greenhouse gas mitigation in agriculture.

1. Introduction

The climate change that is taking place as a consequence of anthropogenic emissions of greenhouse gases poses serious threats to humans and ecosystems. Nitrous oxide (N_2O) is a greenhouse gas with a global warming potential 273 times that of carbon dioxide over a 100-year timescale (EPA, 2023). Global anthropogenic N_2O emissions, estimated at 7.3 Tg N yr^{-1} in 2020, have shown a significant increasing trend over the 1980-2020 period of 0.043-0.085 Tg N yr^{-1} ($P < 0.05$) (Legg, 2021; Tian et al., 2024).

The amount of nitrogen fixed by human activities (210 Tg N yr^{-1}) is now larger than by natural processes (203 Tg N yr^{-1}), which means that human activities have doubled the global cycling of nitrogen over the last century (Fowler et al., 2013). This additional input of nitrogen has greatly enhanced emissions of N_2O. The proportion of N_2O emissions caused by human activities are as high as 36%, among which agricultural emissions are the most important source, accounting for 56% of the anthropogenic emission (Ussiri and Lal, 2012). As global concerns regarding the environmental impact of N_2O continue to grow, finding effective ways to mitigate emissions has become a pressing issue.

A diverse range of agronomic strategies has been developed to mitigate N_2O emissions, including soil management (e.g., crop residue removal, cover cropping, diversified rotations, and reduced tillage), fertilization practices (e.g., organic amendments, increased application frequency, and deep placement), specialized technologies (e.g., slow-release fertilizers, and chemical N-cycle inhibitors) and biochar application (Grados et al., 2022). While these approaches vary in efficacy, the application of biochar and nitrification inhibitors has demonstrated the most successful in reducing N_2O emissions (Grados et al., 2022). Biochar is a carbonaceous material formed by pyrolysis of biomass, such as crop residues and other agricultural waste types, wastewater sludge, or forestry residues. Biochar is known for its ability to sequester carbon in soils, improve soil health and fertility, and more recently suppressing N_2O emissions (Agegnehu et al., 2017). Meta-analyses have indicated that the application of biochar can result in reduction of N_2O emission from soils ranging from 10.5% to 54.8% (Borchard et al., 2019; Cayuela et al., 2014; Kaur et al., 2023; Li et al., 2024). However, the effectiveness of biochar for N_2O emission reductions has displayed substantial variation depending on the dosage and properties of biochar, soils types and climates (Liu et al., 2018). Therefore, a mechanistic understanding is

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required to identify which biochar properties are critically linked to N_2O reductions, and how these properties interact with environmental factors that regulates N_2O production and consumption.

Nitrous oxide is formed by a suite of different biotic and abiotic processes in soils (Butterbach-Bahl et al., 2013). The main processes are nitrification and denitrification, other process may also contribute and the relative importance of these varies with the soil physical, chemical, and biological conditions that are all potentially affected by the addition of biochar. However, the difficulties in predicting mitigation outcomes arise from the complexity these interactions.

This review aims to establishing a mechanistic framework to disentangle these complexities. We first explore the key processes of the nitrogen cycle that contribute to emissions of N_2O to identify factors affecting the contribution to the N_2O production and consumption. We then examine the specific biochar properties capable of influencing these factors, and finally, we discuss how biochar functions within the soil context to affect these processes. Such knowledge is essential for the future customization and strategic application of biochar in climate mitigation.

2. N_2O production and consumption pathways

Microbial nitrification and denitrification account for the majority of N_2O emissions in natural and agricultural soils, with account for approximately 70% of global N_2O emissions (Butterbach-Bahl et al., 2013). Other sources include co-denitrification and abiotic chemodenitrification, but these pathways remain poorly characterized under natural conditions. Moreover, N_2O is consumed in soils by reduction to N_2, the least step in the denitrification pathway. Hence, emissions represent the net outcome of production and consumption. The processes involved are affected by physical and chemical soil properties and conditions, which in turn depend on the soil management practices and climatic conditions. The following sections will present the known nitrogen pathways, summarized in Fig. 1, for N_2O production and emphasize the key drivers involved that may potentially be influenced by biochar. Additional biotic pathways (e.g., DNRA and ANAMMOX) leading to competition for shared substrates but not directly involved in N_2O production are included in Fig. 1.

2.1. *Nitrification*

Nitrification-derived N_2O emissions originate from the biological oxidation of ammonia (NH_3) in equilibrium with ammonium (NH_4^+) or reduced organic nitrogen compounds to nitrite (NO_2^-) and nitrate (NO_3^-), mediated by both autotrophic and heterotrophic microorganisms. Although classically described as an aerobic process, nitrification can yield N_2O via both oxidative reactions and interactions with reductive N transformations, particularly under oxygen-limited conditions.

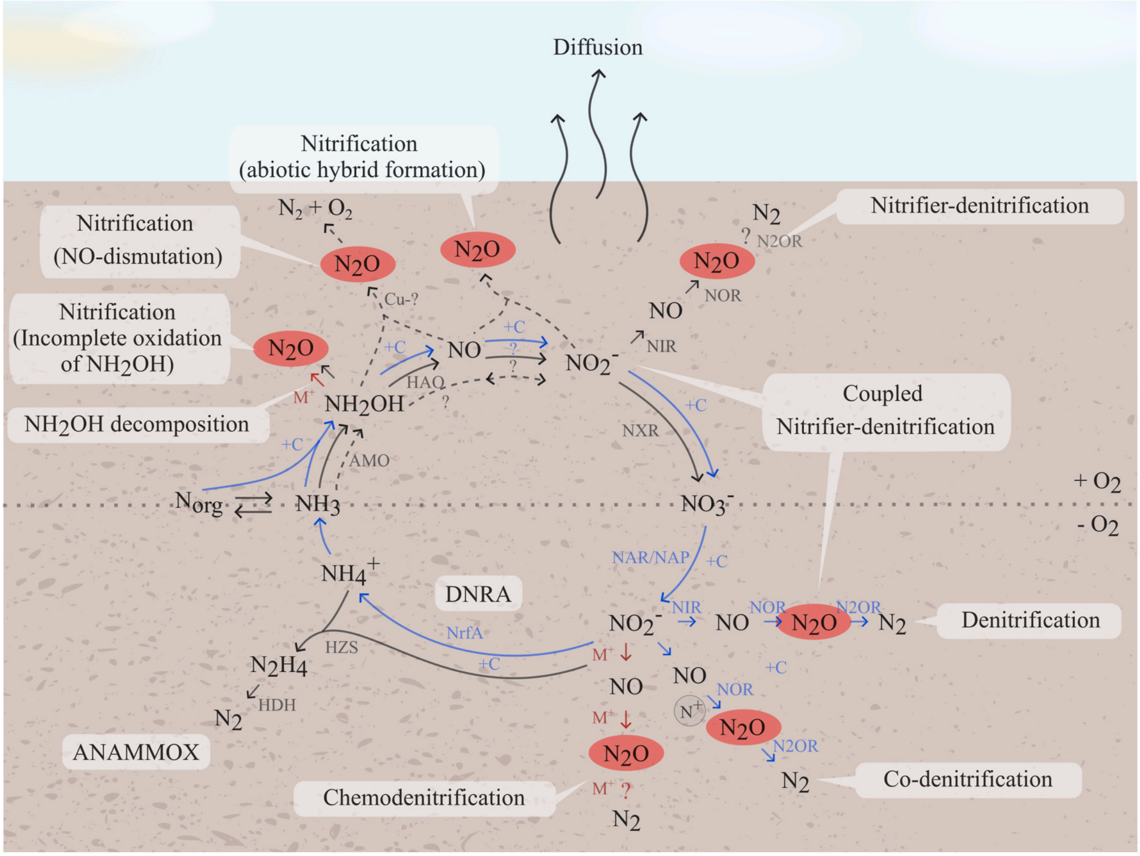

Fig. 1. N_2O production and consumption pathways in soil. Oxygen regime [aerobiosis ($+O_2$) and anaerobiosis ($-O_2$)], organic matter (OM), organic nitrogen (N_{org}), Fe^{II}, Mn^{IV}, and Cu^{II} metal ions (M^+), organic carbon consumption (+C), ammonia (NH_3), ammonium (NH_4^+), nitrite (NO_2^-), nitrate (NO_3^-), hydroxylamine (NH_2OH), hydrazine (N_2H_4), dinitrogen (N_2), nitric oxide (NO), inorganic and monomeric organic N compounds ($N^+ = NH_4^+$, NH_2OH, amino acids, aniline or azides). Pathways and corresponding enzymes: nitrification [ammonia monooxygenase (AMO), hydroxylamine dehydrogenase (HAO), and nitrite oxidoreductase/nitrite oxidase (NXR)], dissimilatory nitrate reduction to ammonium (DNRA) [pentaphene cytochrome *c* nitrite reductase (NrfA)], anaerobic ammonia oxidation (ANAMMOX) [hydrazine synthase (HZS) and hydrazine dehydrogenase (HDH)], and denitrification/co-denitrification [nitrate reductase and periplasmic nitrate reductase (NAR/NAP), nitrite reductase (NIR), nitric oxide reductase (NOR), and nitrous oxide reductase (N_2OR)]. Autotrophic pathways are represented as black arrows: AOB mediated as black arrow only and AOA mediated as dashed black arrow. Heterotrophically mediated pathways are in blue, and chemically mediated reductive reactions are in red. The question marks indicate that either the process's occurrence is unknown or the enzyme responsible is unidentified.

2.1.1. *Autotrophic nitrification*

Autotrophic nitrification is the chemolithoautotrophic oxidation of NH_3 to NO_3^- via NO_2^-, typically partitioned between ammonia-oxidizing bacteria and archaea (AOB and AOA) and nitrite-oxidizing bacteria (NOB), although complete ammonia oxidizers (COMAMMOX *Nitrospira*) perform both steps within a single organism (Fig. 1). In nitrification, N_2O is a byproduct during the oxidation of NH_3 to NO_3^-. This oxidation is initiated by copper-containing ammonia monooxygenase (AMO) producing hydroxylamine (NH_2OH). In AOB, NH_2OH is further oxidized by hydroxylamine dehydrogenase (HAO), yielding nitric oxide (NO) as a key intermediate, which is subsequently converted to NO_2^- via abiotic or yet unidentified enzymatic mechanism (Prosser et al., 2020). In contrast, AOA lack a canonical HAO and likely oxidize NH_2OH via alternative, potentially a copper-containing unknown enzyme (Prosser et al., 2020). Nitrous oxide is formed through several pathways during ammonia oxidation. In AOB, N_2O arises from incomplete oxidation of NH_2OH and reactions involving NO as an intermediate (Caranto et al., 2016), whereas in AOA it is attributed to NO dismutation and/or abiotic hybrid reactions involving metabolic intermediates such as NO, NH_2OH, and NO_2^- (Hernández-Magaña and Kraft, 2024; Prosser et al., 2020; Stieglmeier et al., 2014). Consistent with these mechanistic differences, AOB typically exhibit higher N_2O yields than AOA, reflecting both metabolic pathways and higher cell-specific yields (i.e. the amount of N_2O produced per unit of NH_3 oxidized) (Hink et al., 2018; Tzanakakis et al., 2019), while COMAMMOX organisms show lower yields comparable to AOA, consistent with their limited genetic capacity for enzymatic N_2O production and/or intracellular retention of N intermediates, preventing secondary reactions in the extracellular soil matrix (Kits et al., 2019).

In addition to these pathways, which are tightly linked to the rate of NH_3 oxidation, ammonia oxidizers also produce N_2O from the reduction of their NO_2^- product in what is known as nitrifier-denitrification. This pathway is best characterized in autotrophic AOB and is typically expressed under oxygen-limited conditions. Here, AOB reduce NO_2^- via NO to N_2O in enzymes homologous to those in canonical denitrification (Section 2.2), including nitrite reductase (encoded by *nirK*) and nitric oxide reductase (encoded by *norB*). As AOB generally lack the *nosZ* gene encoding nitrous oxide reductase (N_2OR) this pathway is associated with high N_2O yields (Chen et al., 2020; Prosser et al., 2020). In contrast, AOA generally lack both *norB* and *nosZ* preventing them from reducing NO to N_2O (Prosser et al., 2020). However, in AOA possessing a *nirK*, NO_2^- may still be the source of N_2O via subsequent conversion of NO through the alternative pathways described above, but again at lower yields than in AOB (Hernández-Magaña and Kraft, 2024; Wan et al., 2023). Similarly, COMAMMOX organisms appear to lack key genes required for enzymatic N_2O production via nitrifier-denitrification, consistent with their low observed N_2O yields (Kits et al., 2019).

Nitrifier-denitrification is strongly controlled by O_2 availability, being favored at 0.1 - 0.5% O_2 (Zhu et al., 2013) yet it is suppressed under strictly anoxic environments ($<0.1\%$ O_2) along with ammonia oxidation (Bollmann and Conrad, 1998; Zhu et al., 2013; Wrage-Monnig et al., 2018). Substrate availability further regulates this pathway: elevated NH_4^+ concentrations stimulate ammonia-oxidation and NO_2^- accumulation, thereby enhancing its activity (Qin et al., 2023). In contrast, the role of organic carbon remains less clear; while low organic carbon availability has been proposed to favor nitrifier-denitrification by enhancing autotrophic nitrification, the influence of carbon quantity and quality remains insufficiently understood (Wrage-Monnig et al., 2018).

The multiple pathways of N_2O formation make the relative contributions of ammonia oxidizers to N_2O emissions strongly context-dependent. AOB with higher N_2O yields tend to dominate in NH_4^+-rich environments (e.g., fertilized agricultural soils) (Hink et al., 2018; Prosser and Nicol, 2012). In contrast, AOA are more competitive in NH_4^+-poor and acidic soils where inorganic nitrogen is primary supplied via mineralization (Hink et al., 2018; Prosser and Nicol, 2012). Across systems, N_2O production from ammonia oxidation is enhanced under conditions of low oxygen availability, where nitrifier-denitrification in particular can yield disproportionally high N_2O relative to other N pathways and may account for a substantial fraction of ecosystem emissions, particularly in fertilized systems ($>50\%$ in some cases) (Opdyke et al., 2009). This is particularly relevant in NH_4^+ rich agricultural soils, where AOB dominance and high respiratory demand promote this pathway (Robertson and Groffman, 2007).

2.1.2. *Heterotrophic nitrification*

Heterotrophic nitrification encompasses the oxidation of NH_3 and reduced organic N compounds to NO_2^- and NO_3^- by heterotrophic microorganisms that rely on organic substrates for energy and carbon, rather than chemolithotrophic NH_3 oxidation though underlying pathways are poorly understood (Martikainen, 2022; Myrold, 2021; Pulikova et al., 2025). While some heterotrophic bacteria possess AMO-like enzyme, these are structurally distinct from those found in autotrophic ammonia oxidizers, and many heterotrophs, particularly fungi, appear to oxidize N substrates via alternative pathways involving enzymes such pyruvic oxime dioxygenase, nitroalkane oxidase, and nitronate, although their quantitative contributions to soil N transformations remains uncertain (Martikainen, 2022; Pulikova et al., 2025).

N_2O production from heterotrophic nitrification has been attributed to the conversion of intermediates such as NH_2OH and NO through abiotic decomposition or oxidation of NH_2OH catalyzed by HAO (Zhang et al., 2015; Zhao et al., 2019). Moreover, several heterotrophic bacteria and fungi appear capable of coupling heterotrophic nitrification and aerobic denitrification, supported by the presence of genes such as *nirK* and *norB* (Stein, 2011; Aldossari and Ishii, 2021; Chen et al., 2015).

The specific N_2O production per cell in heterotrophic nitrifiers is much higher than that in autotrophic nitrifiers (Anderson et al., 1993), but environmental drivers of heterotrophic nitrification remain difficult to constrain. Although early studies suggest a dominant role in acid soils ($pH < 6.0$) (Verstraete and Focht, 1977), where the process may be a significant source of N_2O, more recent studies indicates an occurrence across a broad pH range (2.4 - 8.7) (Zhang et al., 2023b). Conveyed by heterotrophs, the process is expected to respond to labile organic carbon availability, and environments with high organic inputs or elevated C/N ratio are often favorable (Zhang et al., 2023b). However, a review of global data reported only a weak positive correlation between the gross rates and soil C/N ratio ($r = 0.13$, $p = 0.09$) (Zhu et al., 2015), highlighting substantial context dependency.

In conclusion, the primary controls on N_2O production from nitrification in soils include pH and availability of substrates, NH_3/NH_4^+ and oxygen, and NO_2^- in the case of nitrifier-denitrification. These are in turn affected by the availability of organic matter as a source of NH_3 and sink for oxygen, and on a higher level by management practices that regulate NH_4^+ availability, oxygen diffusion and microbial activity.

2.2. *Denitrification*

Denitrification is the stepwise reduction of NO_3^- and NO_2^- to N_2 via NO and N_2O (Fig. 1, bottom right), carried out by facultative anaerobic microorganisms under oxygen-limited conditions (Firestone, 1982). In soils, this process is predominantly mediated by heterotrophic bacteria (Firestone, 1982), although autotrophic denitrification exists with, e.g., hydrogen, sulfide, or elemental sulfur as the electron donors (Ma et al., 2020; Satoh, 1977). Hereafter, *denitrification* refers to the heterotrophic pathway.

Denitrification is catalyzed by metalloenzymes, NAR/NAP (Mo and Fe), NIR (Cu or Fe), NOR (Fe), and N_2OR (Cu), that control pathway rates and product stoichiometry. N_2O is an obligatory intermediate and can either accumulate or be further reduced to N_2 under strict anaerobic conditions, such that denitrification can function as both a source and sink of N_2O (Liu et al., 2019; Xiang et al., 2023). The final reduction step is catalyzed by the enzyme N_2OR, whose presence and activity are widely used as molecular target of N_2O reduction potential across soils and other environments (Wang et al., 2017). Notably, two phylogenetically distinct clade of *nosZ* have been identified with clade I belonging to Proteobacteria, and a more diverse clade II being widespread across bacterial phyla with about half of the organisms of this group lacking other denitrification genes (e.g., *nar*, *nir*, and *nor*), thereby they are only participating in N_2O reduction and not the other steps of denitrification and sometimes referred to as non-denitrifying N_2O reducers (Jones et al., 2014; Orellana et al., 2014). In many environments, *nosZ* clade II organism can outnumber clade I, suggesting that the ratio of clade I and II in soil might impact N_2O emissions (Jones et al., 2014; Orellana et al., 2014).

Environmental factors strongly regulate both the activity and completeness of denitrification. Oxygen availability is a primary driver, with anoxia inducing expression of denitrification genes and oxic conditions suppressing their activity, although legacy effects of prior redox conditions can modulate microbial communities and their responses (Kellermann et al., 2022; Sennett et al., 2024). Soil pH exerts an additional control, particularly on N_2O reduction: acidic conditions ($pH < 6$) impair N_2OR assembly and function, promoting N_2O accumulation (Bakken et al., 2012). This sensitivity arises because the N_2OR assembly occurs in the periplasm (i.e. space between the inner and outer membrane of bacteria cell wall), where pH is strongly influenced by external acidity (Bakken and Frostegård, 2017). However, once properly assembled, N_2OR function at low pH (Liu et al., 2014). Carbon availability further constrains denitrification, as organic substrates provide the electrons required for reduction; low C/(NO_2^- or NO_3^-) are therefore associated with incomplete reduction and elevated N_2O emissions (Surey et al., 2020). In addition, the availability of essential trace metals such as copper (required for nitrite and N_2O reductase) and molybdenum (required for nitrate reductase) can limit enzyme functionality and shift gaseous N outputs (Black et al., 2016; Giannopoulos et al., 2020; Schwarz et al., 2009). Collectively, these factors determine whether denitrification acts as a source or sink of N_2O.

Two other but less recognized biological sources of N_2O are co-denitrification and coupled nitrification-denitrification. In co-denitrification during the N–N bond formation requiring two molecules of NO, an alternative N substrate can be used (e.g., NH_4^+, NH_2OH, or organic N), producing "hybrid" N_2O (Fig. S1) (Spott and Florian Stange, 2011; Tanimoto et al., 1992). This pathway can be significant in N-rich environments amended with urine (e.g. pasture soils) or urea fertilized soils and expands the range of substrate contributions to N_2O formation beyond classical denitrification (Rex et al., 2019).

Coupled nitrification-denitrification emerges in environments with fluctuating oxygen availability, where nitrification and denitrification can co-occur across redox gradients (Butterbach-Bahl et al., 2013). Such conditions are widespread in soils, sediments, and biofilms, where limited gas diffusion, variable moisture, and high microbial respiration generate microscale heterogeneity (Gao et al., 2023). Under these conditions, nitrification-derived NO_2^- and NO_3^- can be rapidly consumed by denitrifiers, linking the two processes and enhancing N_2O production. Denitrifying fungi may represent a significant contribution to N_2O emissions in this context, as many lack *nosZ* and therefore terminate denitrification at N_2O (Aldossari and Ishii, 2021). While coupled nitrification-denitrification is not unique pathway as such, it is frequently discussed separately from nitrification and denitrification because of analytical implications resulting from tight coupling of the two. The relative contribution of coupled nitrification–denitrification to N_2O emissions remains highly uncertain, posing a challenge for source attribution and mitigation (Wrage-Monnig et al., 2018).

2.3. *Abiotic chemodenitrification*

In addition to microbial mediated pathways, abiotic chemodenitrification can represent a significant and often overlooked source of N_2O (Fig. 1). This process involves reactions between reactive N intermediates (e.g. NO_2^-, NO, NH_2OH) and reduced soil constituents, including Fe(II) and Mn(II), and organic matter, as well as the abiotic decomposition of NH_2OH (Carlson et al., 2013; Rue et al., 2018; Wei et al., 2017; Zhu-Barker et al., 2015).

Nitrite is the central precursor for most chemodenitrification reactions. Although typically transient, NO_2^- can accumulate under the right conditions of stoichiometric imbalance (e.g., production exceeding consumption), such as high NH_4^+ availability combined with limited oxidation to NO_3^- (e.g., under low O_2 or high organic matter, or alkaline pH) (Giguere et al., 2018; Shen et al., 2003; Van Cleemput and Samater, 1995). The best-characterized pathway involves the reduction of NO_2^- coupled to the oxidation of Fe(II) (Jones et al., 2015; Otte et al., 2019). This reaction is favored in moderately reducing environments that sustain Fe(II), such as soils with high soil moisture and organic carbon content (Cui et al., 2021; Wang et al., 2020; Zhu et al., 2014).

In contrast to biological denitrification, chemodenitrification lacks a mechanism for N_2O reduction, therefore N_2O is often the dominant gaseous product (Robinson et al., 2021; Moraghan and Buresh, 1977). Reaction kinetics are strongly influenced by mineral surfaces and microsite conditions, for instance Fe(II) sorbed onto mineral surfaces or dead microbial biomass is often a more effective reductant than dissolved Fe(II) (Dhakal et al., 2021; Picardal, 2012). Although frequently associated with acid environments, Fe(II)-mediated chemodenitrification produces substantial N_2O even at circumneutral pH (6.5 and 7.0) (Kampschreur et al., 2011; Wang et al., 2026) and may account for up to ~75% of total N_2O emissions in agricultural soils, as favored by low O_2 availability or NO_2^- concentration (Venterea, 2007).

3. Critical biochar properties potentially affecting N transformation processes

Biochar properties vary greatly depending on feedstock and pyrolysis conditions, and interact with soil characteristics, including microbial composition, as well as climatic factors to influence N transformations. A detailed examination of biochar production processes and resulting material properties is beyond the scope of this review, and readers are referred to previous syntheses (Xiao et al., 2016; Li et al., 2019; Lehmann and Joseph, 2024) and Fig. 2. In this section, critical biochar properties leading to shifts in soil and, consequently, affecting N_2O production and consumption are reviewed.

3.1. *Physical properties*

3.1.1. *Particle size*

Soil aggregation and porosity are intrinsically connected to biochar's particle size, influencing aeration, water retention and hydraulic conductivity (Case et al., 2012; Laghari et al., 2016; Lim et al., 2016). In general, finer biochar particles (<1 mm) are more effective at increasing the water holding capacity of the soil (Li et al., 2019). However, these fine particles can simultaneously decrease soil saturated hydraulic conductivity, particularly in sandy soils, by clogging larger conductive pores and slowing water infiltration (Bruun et al., 2023; Dikinya et al., 2008). Meaning that dissolved nutrients, gases, contaminants, and ions face greater resistance and slower transport though the soil matrix increasing the chances of reaction and/or physical entrapment (Esmaeelnejad et al., 2017). Conversely, larger biochar particles (>1 mm) can be more effective at increasing soil macroporosity and aeration, which are critical factors controlling the oxygen status and thus the balance between nitrification and denitrification pathways (de Jesus Duarte et al., 2019; Zhu et al., 2025).

3.1.2. *Specific surface area and porosity*

Specific surface area (SSA) and porosity are fundamental properties of biochar, as they govern the abundance of its active sites. These characteristics play a critical role in enhancing functions such as cation exchange capacity (CEC), water holding capacity (WHC), and

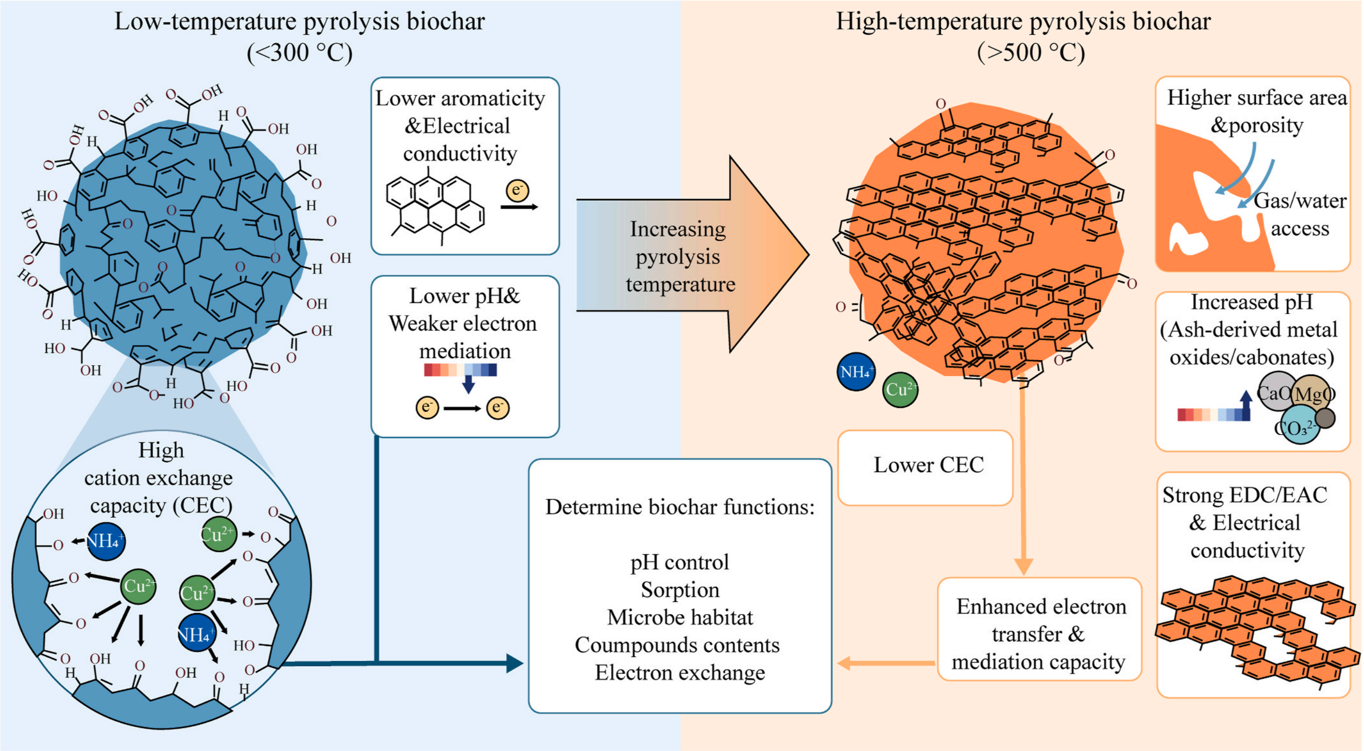

Fig. 2. Effects of pyrolysis temperature on key biochar properties. CEC, EAC, EDC stands for cation exchange capacity, electron accepting capacity and electron donating capacity of biochar.

adsorption behavior. Biochars derived from woody feedstocks and produced at higher pyrolysis temperatures generally exhibit greater SSA and pore development compared to those produced from crop residues or manure under similar pyrolysis conditions (Li et al., 2019). This difference is largely attributed to variations in lignin, cellulose, and salts content, as well as the thermal stability of the feedstock components during pyrolysis (Yang et al., 2007). Micropores (<2-5 nm) in biochar demonstrate high adsorptive capacity for small molecules (e.g., gases and solutes) (Lehmann and Joseph, 2024). These pores have also been associated with a higher abundance of facultative bacterial genera (Yang et al., 2022). In contrast, larger pores (>5 nm) contribute less to adsorption but enhance air diffusion, which can support aerobic bacteria genera (Yang et al., 2022). Macropore further improve soil structure by facilitating root penetration and promoting rapid water movement (Lehmann and Joseph, 2024).

Collectively, these physical properties can influence soil redox conditions, act as an indicator for surface reactivity in biochar (i.e., SSA) and modulate microbial community, with potential implications for nitrogen cycling in soil, including N_2O production and its emissions from the soil.

3.2. Chemical and electrochemical properties

3.2.1. Alkalinity and liming capacity

Most biochars are alkaline due to the presence of metal oxides in the ash, and their pH generally increases with pyrolysis temperature (Yuan et al., 2011; Lehmann, 2007; Li et al., 2019b; Tomczyk et al., 2020). However, the magnitude of soil pH changes following biochar application is highly variable and depends strongly on soil buffering capacity and initial acidity. Substantial increases are typically observed in acid soils (ΔpH up to ~3.29), whereas neutral to alkaline soils often show little response (−0.6 to +1.34) (Yao et al., 2025). Biochar's liming values can range from as low as 2.75 g $CaCO_3$-eq kg^{-1} (coconut shell) to as high as 245 g $CaCO_3$-eq kg^{-1} (sewage sludge 400 °C) (Klanmohammadi et al., 2015; Singh et al., 2017), and their effect at realistic application rates (e.g., ~10 t ha^{-1}) is often modest, resulting in pH increases of <0.5 units in a medium buffer loamy soil with sewage sludge biochar (**Text S1**).

However, biochar-induced pH changes are spatially heterogeneous and occur primarily at the microscale, often within a few millimeters of biochar particles (<4.5 mm radius), but reaching pH values exceeding 8.5 (Zhu et al., 2022; Chen et al., 2024). Therefore, greater pH effects of biochar would be expected in proximity to biochar particles, granules or pellets. These localized shifts are highly relevant for nitrogen cycling, substantially influencing nitrogen transformation pathways (Chintala et al., 2014; Dai et al., 2017).

3.2.2. Aromaticity and electron conduction

Condensed aromatic structures containing conjugated π-electron systems are primarily responsible for the electron conduction properties in biochar. These delocalized electron networks enable electron transport across the carbon matrix, allowing electrons move to redox-active sites (Xu et al., 2019; Yang et al., 2021; Dorner et al., 2022; Wan et al., 2020; Wang et al., 2012). As pyrolysis temperature increases, biochar undergoes graphitization increasing electrical conductivity (Fig. 3) (Guizani et al., 2017; Sun et al., 2017). This internal conductivity enables the biochar particle to serve as a solid-phase conduit for direct interspecies electron transfer which may support microbial processes involved in nitrogen cycling, including denitrification (Gao et al., 2023; Pascual et al., 2020).

3.2.3. Surface functional groups and redox-active structures

3.2.3.1. *Surface chemistry and nutrient interactions.* Biochar surfaces are enriched with a variety of functional groups, predominantly oxygen-containing moieties such as carboxyl (-COOH), hydroxyl (-OH), and carbonyl (C=O). These functional groups play a central role in soil interactions by providing active binding sites that enhances CEC, promote nutrient retention, and immobilize contaminants (Chacón et al., 2017, 2020). In addition to carbon and oxygen, biochar surfaces may contain

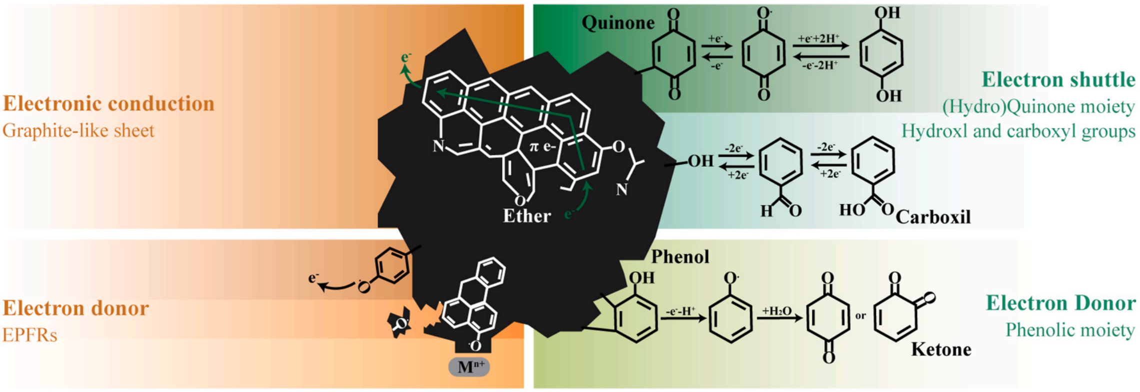

Fig. 3. Aromaticity and functional groups related to electron exchange in biochar.

heteroatom functional groups involving nitrogen (e.g., amines, pyridinic-N), sulfur (e.g., thiophenes), and phosphorus (e.g., phosphate esters), depending on feedstock and pyrolysis conditions (Leng et al., 2020, 2022; Liu et al., 2021a; Yuan et al., 2021). Low temperature biochars typically retain a higher density of oxygen-containing groups, resulting in greater surface polarity and higher CEC (Domingues et al., 2020; Munera-Echeverri et al., 2018). In contrast, high-temperature biochars exhibit reduced surface functionality due to thermal degradation of these groups (Domingues et al., 2020; Munera-Echeverri et al., 2018). Feedstock type also plays a key role, with nutrient rich materials such as manure and grasses generally producing biochars with higher ash content and greater functional group abundance compared to woody feedstocks (Ippolito et al., 2020). Through these surface interaction sites, biochar can retain essential cations such as NH_4^+, calcium (Ca^{2+}), magnesium (Mg^{2+}), and trace metals (e.g., Cu^{2+}), as well as immobilize pollutants including Cd^{2+} and Hg^{2+}. These interacting sites can evolve over time due to oxidation and microbial interaction increasing moieties and elevating sorption capacities in biochar surface (Ghaffar et al., 2015; Mia et al., 2017). Although biochar typically exhibits limited anion exchange capacity, NO_3^- and NO_2^- may be retained via physical entrapment within pore structure and/or through interactions with mineral phase such as Fe- and Al-oxides, particularly under acid to neutral pH conditions (pH < 8) (Kammann et al., 2017; Haider et al., 2016).

3.2.3.2. Redox-active functional groups and electron exchange capacity. Beyond sorption processes, surface functional groups also contribute to the redox activity of biochar. This behavior is commonly described in terms of electron donating capacity (EDC) and electron accepting capacity (EAC) (Fig. 3) (Prévoteau et al., 2016). These redox properties are primarily associated with oxygen-containing functional groups embedded within or attached to the aromatic carbon matrix, particularly quinone/hydroquinone systems, as well as phenolic moieties (Jerigová et al., 2022; Qin et al., 2018; Zhang et al., 2023a). Such groups can undergo reversible redox cycling, enabling biochar to act as an electron mediator in soil environments. Biochar can facilitate electron shuttling between microbial cells or between microbes and electron acceptors/donors in the soil matrix (Van der Zee and Cervantes, 2009). While conductivity governs electron transport across the biochar structure, EDC and EAC determine the capacity of biochar to participate in reversible redox reaction.

In addition to reversible redox-active functional groups, biochar may also contain environmentally persistent free radicals (EPFRs), which represent another class of redox-active species. These radicals are typically stabilized organic structures, such as semiquinone-type moieties, associated with the aromatic carbon matrix (Chen et al., 2025). Although more persistent than transient radical species, EPFRs are not permanently stable and their lifetimes in soil can range from days to months, depending on environmental conditions (Odinga et al., 2020; Pan et al., 2019). EPFRs may participate in redox reactions by transiently donating or accepting electrons, potentially contributing to electron transfer processes at the biochar surface. EPFRs may participate in redox reactions. However, under optimized production conditions, biochar is expected to contain only low concentrations of EPFRs (EBC, 2022).

3.2.4. Dissolved organic matter and other components

The degree of aromatic condensation in biochar does not only governs its electrochemical properties but also strongly influences its dissolved organic matter (DOM) availability in soil systems. As pyrolysis temperatures increases (>500 °C), the formation of highly condensed aromatic structures reduces the amount of DOM and labile dissolved organic carbon (DOC), resulting in a more recalcitrant carbon pool with limited accessibility to microorganism (Gross et al., 2024; Azeem et al., 2023). This dissolved and reactive fraction of biochar consists of polar organic compounds with phenolic, polycyclic aromatic (-OH and –COOH) groups, and heterocyclic molecules (Azeem et al., 2023). In contrast, low-temperature (400-500 °C) biochar typically contain a greater proportion of labile organic compounds, which can be readily mineralized and stimulate microbial activity (Gross et al., 2024; Jones et al., 2011). Sawdust and manure-based biochars yield higher levels of dissolved organic matter (DOM) than straw, bone, or sludge-derived feedstocks (Azeem et al., 2023). Biochar only contains small amounts of inorganic N (NH_4^+ and NO_3^-) but its overall contribution as an N source is typically minor due to low total N (~0.4 - 1.9% total N) and limited bioavailability (**Text S3**) (Mukherjee and Zimmerman, 2013; Zhang et al., 2017).

The limited release of biovailable DOM and DOC from highly carbonized biochars may contrain heterotrophic activity and reduce competition for electron donors, indirectly influencing redox processes such as heterotrophic nitrification and denitrification.

4. Biochar-induced shifts in N_2O production pathways

Building on the nitrogen transformation pathways outlined in Section 2 and the key biochar properties described in Section 3, it is evident that N_2O production in soils can be influenced by biochar through multiple interacting mechanisms. These include pH regulation, changes in the availability of carbon, nitrogen, and redox-active metals, as well as electrochemical processes such as electron conduction and redox mediation. Through these physicochemical properties, biochar can modify fundamental environmental controls governing nitrogen transformations, thereby altering the relative contributions of microbial and abiotic N_2O production pathways. Fig. 4 summarizes the mechanisms through which biochar properties can affect nitrogen transformations and resulting N_2O emissions from soil.

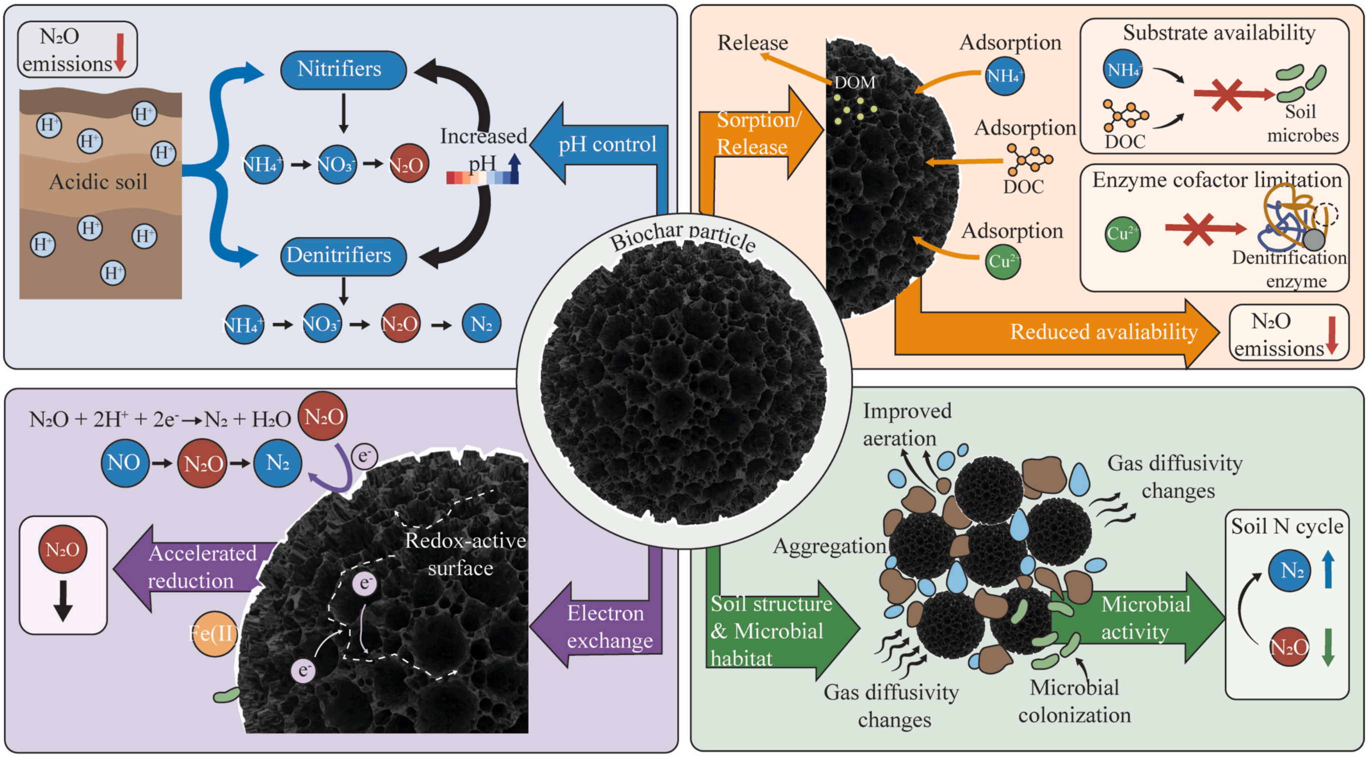

Fig. 4. Mechanisms through which biochar properties can affect N_2O emission.

4.1. pH regulation

Biochar-induced pH changes represent one of the most consistently observed mechanisms influencing N_2O emissions, particularly in acid soils (Ji et al., 2020). Through its liming capacity (Section 3.2.1), biochar can increase soil pH at both bulk and microsite scale, thereby directly affecting microbial processes involved in N transformations. Among these, autotrophic nitrification by AOB predominantly occurs in soils with pH 6.0-8.5 and is strongly inhibited under acid conditions (pH 5.0), where AOA and heterotrophic nitrifiers tend to dominate (Gao et al., 2023; Zhang et al., 2012; Sahrawat, 2008). Consequently, biochar-induced increases in soil pH alleviates acidity constraints, potentially restoring AOB activity and associated N_2O production, which is generally higher than that of AOA dominated systems (Hink et al., 2018; Tzanakakis et al., 2019; Zhang et al., 2022). Denitrification is especially sensitive to pH (ideal range: pH 7 – 8.5), as the activity and assembly of N_2OR are strongly inhibited under acid conditions ($pH < 6$) (Bakken et al., 2012; Obia et al., 2015; van Groenigen et al., 2015; Pan et al., 2022). Consequently, low pH soils tend to accumulate N_2O due to incomplete denitrification (Obia et al., 2015; Čuhel et al., 2010). By increasing pH, biochar promotes an environment favorable for the synthesis and functionality of N_2OR, enhancing the reduction of N_2O to N_2 and thereby decreasing net emissions (Ji et al., 2020). Heterotrophic nitrification, often associated with acid environments and high N_2O yields, may be suppressed as pH increases with biochar, further contributing to emission reduction (Cheng et al., 2020).

Beyond biological pathways, pH also influences abiotic N_2O formation via chemodenitrification. The reduction of NO_2^- by Fe(II) is highly pH-dependent, with acid conditions favoring near-complete conversion to N_2O (Wang et al., 2026). As pH increases toward neutral conditions, N_2O yields decline, and under alkaline conditions (e.g., pH ~8.5), electron transfer pathways may shift toward the formation of NH_4^+ rather than N_2O, substantially reducing N_2O emissions (Wang et al., 2026). Thus, biochar-induced increases in soil pH may suppress abiotic N_2O production.

The effects of pH on N_2O emissions are multifaceted, influencing substrate availability, microbial activity, enzyme functionality, and abiotic reaction pathways. However, isolating the specific contribution of pH remains challenging, as biochar-induced pH changes are often accompanied by concurrent shifts in other soil properties (Cayuela et al., 2014; Hüppi et al., 2015). Therefore, pH alone is not always a reliable predictor of N_2O mitigation.

4.2. Carbon availability and microbial competition

By altering both the quantity and quality of carbon available in soil for microorganisms, biochar influences N_2O emissions. Estimates from a pine sawdust biochar (500 °C) with released range of 0.57-12.0 g kg^{-1} of DOM suggest that typical application rates (~10 t ha^{-1}) can introduce DOM inputs (~60 t ha^{-1}) that exceeds native DOC pools in soil (**Text S2**), this is roughly three times larger than the typical stock of DOC in agricultural soil pore water (~19 kg ha^{-1}), thereby stimulating microbial activity shortly after application (Ji et al., 2024). Low temperature and freshly applied biochar typically release labile carbon that can stimulate microbial activity (Jones et al., 2011), whereas high temperature or aged biochars provide more recalcitrant carbon potentially suppressing heterotrophic activity (Guo et al., 2026). Although biochar can release small amounts of nitrogen, the dominant effect of biochar on N_2O emissions arises from its regulation of N substrate availability rather than direct N inputs (Khater et al., 2024; Sika and Hardie, 2014).

Biochar can alter microbial community composition. Highly aromatic biochars exert a selection pressure that shifts soil microbial community toward specialized taxa (Biswal and Balasubramanian, 2025), potentially reshaping both carbon turnover and nitrogen cycling. For example, isotopic incubation studies involving rice straw biochar revealed an increased prevalence of *Actinobacteria*, a group particularly effective at decomposing complex organic compounds (Zhu et al., 2019). The impact on N_2O however remeins unknown.

Changes in carbon availability may additionally alter competition among microbial N transformation pathways. In systems containing microorganisms capable of dissimilatory nitrate reduction to ammonium (DNRA), such as paddy soils, elevated carbon availability may also shift competition away from denitrification (see SI). Because DNRA conserves nitrogen in the system and does not produce N_2O, biochar mediated shifts in carbon availability can indirectly alter nitrogen partitioning among competing pathways, with important consequences for N_2O emissions (Yuan et al., 2022; Wei et al., 2022).

4.3. Sorption

Biochar regulates N_2O emissions by altering the availability, spatial distribution, and temporal dynamics of key substrates and cofactors involved in nitrogen cycling.

4.3.1. Dissolved organic carbon

A central mechanism is the sorption of soil DOC, which directly affects heterotrophic nitrification and denitrification. Adsorption of DOC onto biochar surfaces can reduce its bioavailability, creating a stoichiometric imbalance between carbon and NO_3^- (Dippold et al., 2014; Lammirato et al., 2011; Eykelbosh et al., 2015). Under such electron-limited conditions, denitrifiers may be unable to fully reduce N_2O to N_2 (Surey et al., 2020). Conversely, in systems where biochar releases labile carbon, this limitation may be alleviated, enhancing electron supply to N_2OR and promoting complete denitrification. Thus, biochar acts as both a sink and source of carbon, with contrasting effects on N_2O emissions depending on carbon availability and structural interaction.

4.3.2. N substrates

Biochar shows sorption potential for NH_4^+, whereas sorption of anions such as NO_3^- and NO_2^- is less consistent, thereby directly influencing substrate availability for different N_2O producing pathways (Liu et al., 2021b; Liu et al., 2018). These effects may be especially important for AOB driven nitrifier-denitrification, which depends on NO_2^- produced from NH_4^+ under low O_2 conditions. Reduced NH_4^+ availability may therefore indirectly constrain NO_2^- formation, limiting substrates for both nitrifier-denitrification and denitrification, as well as abiotic chemodenitrification.

4.3.3. Enzymes and microbial signaling compounds

Beyond substrates, biochar also interacts with enzymes and microbial signaling compounds, introducing and additional level of control over pathways expression. Sorption of extracellular enzymes (e.g., urease and protease) may stabilize their structure and prolong activity (Yin et al., 2023), sustaining processes such as urea hydrolysis and maintaining NH_4^+ supply for nitrification (Zhang et al., 2019, 2021). This is attributed to surface interactions that stabilize enzymes, protecting them from biodegradation while maintaining their catalytic sites active (Elzobair et al., 2016; Foster et al., 2016). This could indirectly support AOB/AOA activity and associated N_2O production (Guo et al., 2026). At the same time, microorganisms work together to drive elemental cycling through signaling, and biochar is able to absorb and enhance the hydrolysis of signaling molecules, thereby disrupting microbial communication and altering the composition of microbial communities (Aziz et al., 2023; Masiello et al., 2013).

Biochar may also interfere with microbial quorum sensing by sorbing signaling molecules (e.g., N-(3-oxododecanoyl)-L-homoserine lactone mediated cell-cell communication between gram-negative bacteria) (Masiello et al., 2013), potentially altering denitrifier activity and N_2O reduction efficiency.

4.3.4. Metal co-factors

A potential but unresolved mechanism involves the regulation of trace metal availability, particularly Cu and Fe, which are essential cofactors for enzymes in nitrification and denitrification (Section 2) (Glass and Orphan, 2012). Biochar treatments can modify the partitioning of Cu from the easily exchangeable phase to the less bioavailable organic-bound fraction (Park et al., 2011). The determining factor for metal sequestration is not the total sorption capacity, but the relative affinity (distribution coefficient, K_d) of the biochar compared to the soil matrix. Our estimations suggest that while biochar may represent less than 0.3% of the total soil mass, its high distribution coefficient ($K_d \approx 10^5$ L kg^{-1}) allows it to contribute approximately 36% of the total Cu-binding potential in the soil system (**Text S4**). This reduction in bioavailability has significant implications for enzymatic N transformation (Hilber et al., 2017; Mierzwa-Hersztek et al., 2018). Copper is required for both *nirK* and *nosZ*, and its availability can directly constrain N_2O reduction (Black et al., 2016; Gui et al., 2017). Due to its high sorption affinity for cations, biochar may immobilize Cu, potentially limiting N_2OR activity and creating a bottleneck in the final step of denitrification, leading to the increased N_2O accumulation (Kambo and Dutta, 2015; Zhao et al., 2013). However, direct evidence linking biochar-induced Cu limitation to increased or decreased N_2O emissions in soils remains scarce. Similarly to Cu, interaction with Fe(II) may influence chemodenitrification, as biochar can modify Fe speciation and availability, thereby affecting abiotic N_2O production under conditions of NO_2^- accumulation (Wang et al., 2026).

4.3.5. N_2O

Direct sorption of N_2O itself has also been hypothesized to affect N_2O emissions (He et al., 2019). However, it appears to play a negligible role in emission mitigation as estimated from sorption capacities based on Langmuir isotherms indicating that biochar can retain only a minute fraction (<0.01%) of annual N_2O emissions at typical application rates **(Text S5)** (Cornelissen et al., 2013). However, transient retention of N_2O within biochar micropores could increase residence and promote microbial reduction of N_2O to N_2.

4.4. Electron transfer-mediated processes

As discussed in Section 3.2.2 and 3.2.3, the intrinsic electrochemical properties of biochar enable it to serve as a solid-phase electron mediator (Qin et al., 2018; Zhang et al., 2023a). Specifically, biochar can enhance biotransformations, such as denitrification and ANAMMOX, through Direct Interspecies Electron Transfer (DIET) and Mediated Interspecific Electron Transfer (MIET) (Rotaru et al., 2021; Kayoumu et al., 2025).

The most significant functional consequence of this electrochemical activity is the potential acceleration of the terminal step of denitrification (Cayuela et al., 2013; Harter et al., 2014). Rather than directly lowering the activation energy of the periplasmic N_2OR enzyme, which remains physically separated from the biochar surface, biochar is hypothesized to function as an extracellular electron buffer or conduit. In this role, biochar facilitates the delivery of electrons from donors (e.g., organic carbon, Fe(II)) to the microbial cell. This external electron supply may bypass internal electron bottlenecks where enzymes like nitrate reductase typically outcompete N_2OR for the internal quinone pool (Yuan et al., 2017). Recent evidence highlights extracellular polymeric substances (EPS) as a critical biological bridge in this process; redox-active proteins (e.g., cytochrome *c*) within the EPS potentially facilitate the interfacial electron exchange between the biochar surface and the cell membrane (Li et al., 2016; Zhao et al., 2021).

Studies using model denitrifying strains, such as *Paracoccus denitrificans*, have demonstrated a strong, direct correlation between the EDC and electrical conductivity of biochar and the rate of N_2O reduction (Pascual et al., 2020). However, because most biochar studies do not simultaneously quantify N_2 emissions and EDC values, it remains difficult to definitively assess biochar-induced changes in the $N_2O/(N_2 + N_2O)$ ratio. Consequently, further research is required to isolate this proposed electron-exchange mechanism from indirect effects such as soil aeration or pH-induced enzymatic stabilization. Furthermore, the aging process increases oxygen-containing functional groups on the biochar's surface, which raises its polarity and promotes π-π* interactions (Zhang et al., 2025). Consequently, these alterations modify the biochar's redox activity, ultimately enhancing its electron transfer capabilities. However, their ultimate impact on N_2O emissions remains unclear. Because most studies rely on chemical oxidation to simulate aging, and different aging techniques yield different results and tend to overpredict biochar decomposition, further research using biochar aged under natural conditions is critical to clarifying these electron transfer-mediated effects over time (Zhang et al., 2025; Chen et al., 2022).

4.5. Environmental redox conditions and oxygen dynamics

Oxygen dynamics in soil are controlled by water - air balance and pore connectivity. Because oxygen diffuses far more slowly in water than in air, aerobic activity declines as soils approach saturation, suppressing nitrification and promoting reductive processes such as denitrification, nitrifier-denitrification, and chemodenitrification, often increasing N_2O emissions.

Biochar modifies soil diffusion by altering porosity, pore size distribution, tortuosity, and air permeability and these changes direct impact N_2O emissions (Keller et al., 2019). Larger biochar larger particles (>1 mm) generally enhance microporosity and consequently aeration, but increased water retention and microbial respiration, especially with labile carbon, can locally deplete oxygen and create anaerobic microsites (Keiluweit et al., 2018; Hyun and Yoo, 2023; Groffman et al., 1988). These hotspots, often associated with particulate organic matter, may sustain denitrification even when bulk soil remains oxic (Keiluweit et al., 2018). These biochar mediated effects are often transient, because labile carbon pool declines with biochar aging (Guo et al., 2026). Biochar application adds further complexity, as carbon release varies with biochar type, and the availability and effects of its labile fractions, as well as associated changes in soil structure, are still to be elucidated. A critical unresolved question is whether biochar-derived carbon behaves differently from native organic matter in regulating heterotrophic activity and the formation of anoxic microsites in soil.

4.6. Inhibitory compounds and persistent radicals

Biochar may contain inhibitory compounds such as polycyclic aromatic hydrocarbons (PAHs), EPFFS, dioxins, perfluorochemicals (PFCs) and heavy metals (Xiang et al., 2021). These compounds have been proposed to affect N_2O emissions by suppressing microbial pathways, particularly AOB/AOA and nitrifier-denitrification (Cayuela et al., 2014a; Zhao et al., 2023). Among these, PAHs are the most studied. At high concentrations (>10-50 mg kg^{-1} soil), they can inhibit nitrification and alter denitrifier community composition, potentially affecting the balance between *nosZ* containing organisms (Maliszewska-Kordybach et al., 2007; Guo et al., 2013). However, PAH concentrations in properly produced biochar are typically several orders of magnitude lower (≈0.06 mg kg after amendment), far below toxicity thresholds. For instance, even at concentrations of up to 20 mg PAHs kg^{-1} soil, no notable inhibitory response on N_2O emissions was observed for any of the PAHs tested (Angst and Sohi, 2013). The average EC_{50} value for pyrene toxicity affecting denitrification activity was 60 mg kg^{-1} (Guo et al., 2011), which is far above the PAH concentrations typically found in properly manufactured biochar. Our estimations show that standard biochar application increases soil PAH concentrations by only ~0.06 mg kg^{-1}, which is three orders of magnitude below the toxicity threshold (EC_{50}) required to inhibit denitrification (**Text S6**). EPFRs and trace metals may also influence microbial processes or enzyme activity (e.g., N_2OR), but their effects are generally transient and poorly constrained under field conditions (Odinga et al., 2020; Pan et al., 2019). When biochar complies with quality standards, concentrations of these compounds are typically too low to exert strong or persistent inhibition (EBC, 2022). Therefore, while inhibitory compounds may locally suppress specific pathways, their role in regulating N_2O emissions is likely minor.

5. Conclusions and research gaps

The mechanism controlling N_2O emissions in agricultural soils emerge from the interaction between multiple microbial pathways, environmental conditions, and soil physicochemical properties. In this review, we established a mechanistic framework linking (i) the biological and abiotic pathways involved in N_2O production and consumption, (ii) the environmental factors regulating the contribution of these pathways, and (iii) the physicochemical properties of biochar capable of modifying such controls. We further discussed how biochar functions within the soil matrix to influence N_2O dynamics through interconnected effects on pH, substrate availability, redox processes, oxygen diffusion, sorption interactions, and microbial activity. Overall, current evidence suggests that biochar reduces N_2O emissions primarily by altering the environmental conditions that regulate N_2O production and consumption pathways rather than by directly suppressing a single microbial process. The most consistently supported mechanisms include increases in soil pH promoting N_2O reduction to N_2, changes in oxygen diffusion and redox conditions affecting the balance between nitrification and denitrification, modulation of carbon and nitrogen substrate availability, and electron transfer-mediated enhancement of denitrification. However, the relative importance of these mechanisms varies strongly with soil type, biochar properties, environmental conditions, and the dominant microbial pathways active in the system.

5.1. Research gaps

A major limitation in understanding biochar-induced changes in N_2O emissions is the poor quantification of the relative contribution of distinct N_2O production and consumption pathways under different soil conditions. While nitrification and denitrification are generally considered the dominant biological sources of N_2O, the relative importance of other N_2O producing pathways (e.g., nitrifier-denitrification, co-denitrification, chemodenitrification), the tight linkage of the two processes in coupled nitrification-denitrification, as well as interactions with N substrate competing processes (e.g., DNRA and ANAMMOX), remains poorly constrained. This uncertainty limits mechanistic interpretation of how biochar properties (i.e., carbon availability, pH regulation, sorption capacity, and redox activity) affect specific microbial pathways. In particular, the effects of biochar on denitrification remain difficult to predict due to unresolved interactions among carbon accessibility, pH regulation of enzyme activity, and controls over the N_2O:N_2 product ratio. Future progress will require integrated approaches combining isotopic tracing techniques with molecular and enzymatic analyses capable of distinguishing pathway-specific microbial activity and functional responses to biochar in soil systems.

Another major challenge is the inconsistent reporting of biochar properties, largely resulting from the lack of standardized characterization protocols. Although important efforts have been made through biochar initiatives (e.g., EBC and IBI) and published books (e.g., Singh et al., 2017), comparisons among studies remain difficult due to inconsistent descriptions of biochar production conditions and physicochemical properties. In addition, several biochar properties directly linked to N_2O mechanisms should be systematically characterized, including particle size, porosity, surface area, ion exchange capacity, alkalinity, degree of carbonization, dissolved organic carbon release, and electrochemical properties. Here we bring a particular attention to the characterization of biochar carbon fractions. While total organic carbon is routinely reported, much less is known about the accessibility and turnover of distinct carbon pools released by biochar and their short- and long-term effects on microbial processes. This is especially relevant for heterotrophic pathways, where carbon availability simultaneously regulates microbial growth, oxygen consumption, electron donor supply, and denitrification completeness. Similarly, the role of biochar electrochemical properties under natural soil conditions remains poorly understood despite increasing evidence that electron transfer processes may contribute to enhanced N_2O reduction.

Mechanistic understanding of biochar effects on N_2O emissions also requires a stronger focus on microscale soil processes. Biochar-induced changes in pH, oxygen availability, redox gradients, and substrate distribution are highly heterogeneous and often occur at spatial scales not captured by bulk soil measurements. Advanced approaches in imaging (Zhu et al., 2022), microsensors (Chakraborty et al., 2025), and light-based techniques (Weng et al., 2022) could substantially improve understanding of microscale interactions between biochar particles, microbial communities, and N_2O production pathways. Integrating these approaches with molecular techniques may help differentiate the contribution of specific pathways and identify the environmental conditions favoring N_2O production versus reduction. Particular attention should also be given to the temporal evolution of biochar properties following soil application. Aging processes progressively modify biochar surface chemistry. However, the long-term implications of these changes for N_2O emissions remain poorly understood. Current knowledge is limited by the widespread use of artificial aging approaches, which may overestimate biochar decomposition and produce physicochemical transformations that differ from those occurring under natural soil conditions. Consequently, long-term studies using naturally aged biochars are essential.

Finally, additional research is needed to better understand biochar sorption and buffering processes within soil matrices. Key unresolved questions include the extent to which biochar modifies the availability of DOC, nitrogen substrates, trace metal co-factors, extracellular enzymes, and microbial signaling compounds, as well as the temporal relevance of N_2O entrapment within biochar pores. Future studies should combine sorption isotherms and kinetic approaches with soil-based experiments across different soil types and nitrogen sources in order to evaluate how these interactions evolve over time and influence N_2O dynamics. Advancing the mechanistic understanding of biochar-mediated regulation of N_2O emissions will require interdisciplinary approaches integrating soil physics, biogeochemistry, microbial ecology, and electrochemistry across multiple spatial and temporal scales. Such integration is essential for improving mechanistic understanding and optimizing biochar application strategies aiming climate mitigation.

CRediT authorship contribution statement

Xiao Wang: Conceptualization, Funding acquisition, Investigation, Methodology, Validation, Visualization, Writing – original draft, Writing – review & editing. **Camille Nunes Leite:** Conceptualization, Investigation, Validation, Visualization, Writing – review & editing. **Bo Thamdrup:** Validation, Writing – review & editing. **Sander Bruun:** Conceptualization, Funding acquisition, Supervision, Validation, Writing – review & editing. **Hans Chr. Bruun Hansen:** Conceptualization, Funding acquisition, Supervision, Validation, Writing – review & editing.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Xiao Wang reports financial support was provided by University of Copenhagen. Xiao Wang reports a relationship with China Scholarship Council that includes: funding grants. Xiao Wang reports a relationship with Innovation Fund Denmark that includes: funding grants. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary data

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