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Biochar

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Opposing effects of maize straw and its biochar on soil N_2O emissions by mediating microbial nitrification and denitrification in a subtropical Moso bamboo forest

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Abstract
Straw and biochar amendments markedly influence soil N_2O emissions in subtropical Moso bamboo forests, but the microbial mechanisms driving these responses remain elusive. This study aimed to assess the contrasting influences of maize straw and its derived biochar on soil N_2O emissions in a subtropical Moso bamboo forest. Straw amendment (5 t C ha^{-1}) stimulated N_2O emission by 16–27% ($P < 0.05$). However, biochar addition (5 t C ha^{-1}) decreased the concentrations of NH_4^+ by 11–14%, NO_3^- by 11–15% and water-soluble organic nitrogen for 14–17%, and decreased the abundances of ammonia-oxidising bacterial *amoA* by 40–45%, *nirK* by 30–36%, *nirS* by 24–32% and associated genera *Nitrosospira*, *Mesorhizobium*, *Bradyrhizobium*, *Rhizobium*, *Pseudomonas*, and *Cupriavidus*. Biochar also decreased the activities of enzymes related to organic N hydrolysis (protease and urease) and denitrification (nitrate reductase and nitrite reductase), and thus decreased N_2O emissions by 17–20% ($P < 0.05$). Furthermore, biochar enhanced the abundance of *nosZ* gene (by 40–46%) and its dominant genera (*Mesorhizobium*, *Bradyrhizobium*, and *Azospirillum*), which facilitated N_2O reduction. In contrast, straw inhibited the growth of these dominant genera and lowered the abundance of *nosZ* gene (by 24–38%). These results highlight the varied responses of nitrification and denitrification processes and hence N_2O emission to the application of straw and biochar in soils of a subtropical Moso bamboo forest.

Highlights

- Maize straw enhances but its biochar lowers N_2O emissions
- Biochar decreases organic N hydrolysis and denitrifying enzyme activities
- Biochar reduces the abundances of AOB *amoA*, *nirK* and *nirS* and dominant genera
- Biochar promotes the abundances of *nosZ* gene and its dominant genera

Keywords Nitrous oxide emission, Microbial functional community, Microbial gene abundance, Nitrogen dynamics, Organic amendments

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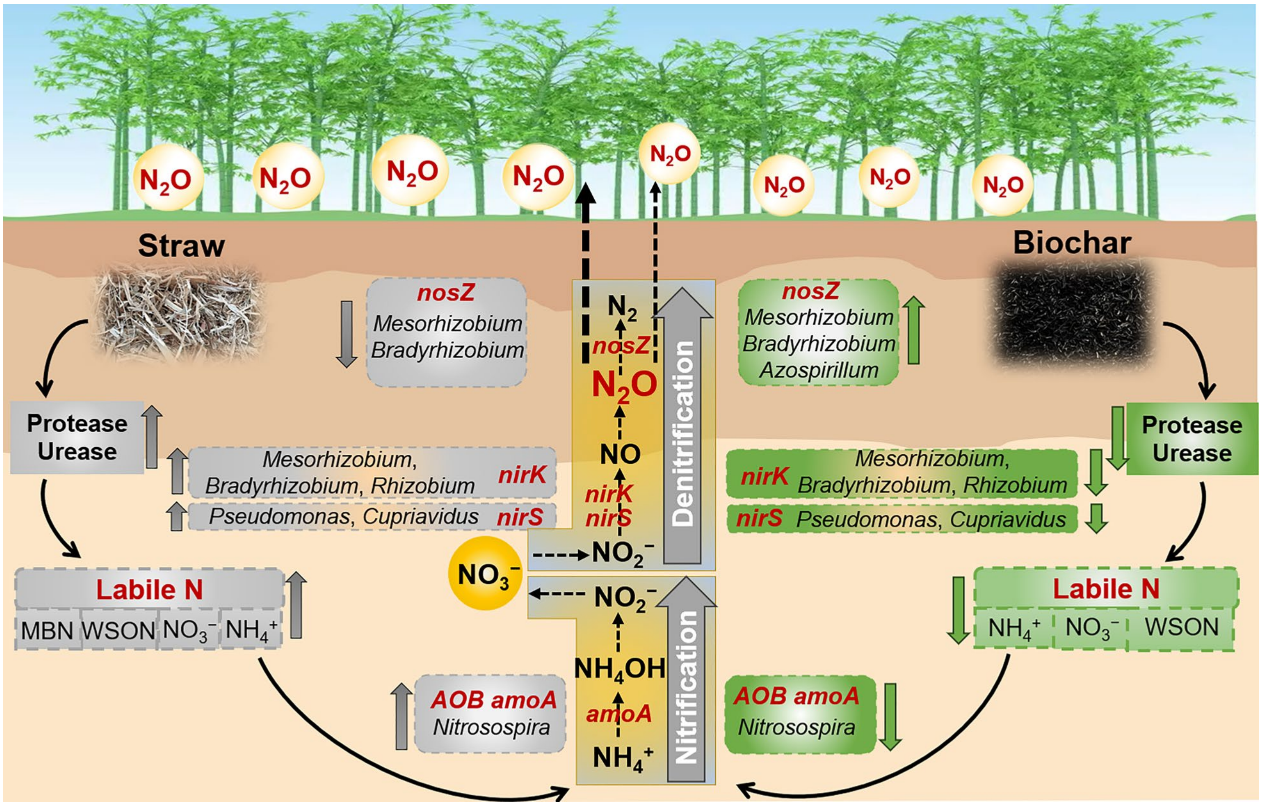
Graphical Abstract



1 Introduction

Moso bamboo (*Phyllostachys edulis*) forests are an important forestry resource in subtropical China, covering an area of 6.73×10^6 hectares (Chen et al. 2018). Moso bamboo forest soils generally emit less N_2O than broadleaf forest soils (Li et al. 2017) because plant litter decomposition produces secondary metabolites, such as phenolic constituents, that induce potent allelopathic effects (Hoyweghen et al. 2012). These released metabolites may alter the function of microbial communities and activities of N-cycling enzymes, resulting in decreased ammonification and nitrification rates (Gao et al. 2025). Nevertheless, Moso bamboo forests are still an important source of N_2O emissions, particularly when under intensive management (Cao et al. 2020). Fertilization serves as a routine practice to enhance productivity in Moso bamboo forests (Zhao et al. 2024); however, the introduction of inorganic N into the soil facilitates ammonification and nitrification, which translate to significant N_2O emissions (Zhu et al. 2022). More specifically, amendments of organic fertilizers and straw are conventional practices for the intensive management of Moso bamboo plantations, as they stimulate the proliferation of fine roots that facilitate growth (Zhao et al. 2024). However, these same amendments may release organic N compounds that increase N_2O emissions (Jiang et al. 2023; Xie et al. 2024). Therefore, in the context of a rapidly changing climate, understanding the impacts of chemical fertilization and organic amendments on soil N_2O effluxes within forests is of great importance for the development of management practices to mitigate environmental damage.

The production of N_2O is strongly associated with the degradation of organic N, ammonification, nitrification and denitrification processes (Kuypers et al. 2018). Ammonium produced from ammonification can fuel aerobic oxidation of ammonium and nitrite, while the nitrate produced during nitrification can fuel the denitrification under anoxic conditions (Kuypers et al. 2018). The *amoA* gene encodes ammonia monooxygenase, an enzyme responsible for oxidizing ammonia to hydroxylamine, which constitutes the rate-limiting step in nitrification. Conversely, *nirK* and *nirS* genes, which encode distinct forms of nitrite reductase, drive the conversion of nitrite to nitric oxide, a critical reaction in the denitrification pathway (Kuypers et al. 2018). Additionally, *nosZ* gene, which encodes N_2O reductase, plays a crucial role in the completion of denitrification, influencing N_2O emissions (Xiong et al. 2024). The dynamics of nitrification and denitrification are governed by soil attributes such as aggregation stability, pH, aeration status, labile C and N fractions, and the structure of microbial community (Zhu et al. 2022). However, field investigations exploring the linkages of N_2O fluxes to soil physicochemical properties and N-cycling functional genes in forest ecosystems remain limited.

Biochar is a critical soil improvement agent that can enhance soil fertility and increase soil carbon (C) stocks; thus, serving as an important amendment during soil tillage (Ding et al. 2016; Zhou et al. 2026). The application of biochar to Moso bamboo forest soils alters its physical, chemical and microbial properties, which subsequently changes N-associated biogeochemical processes (Jiang. 2025; Li et al. 2024; Zhou et al. 2024a, b). For example, biochar may reduce soil bulk density and enhance the formation of macroaggregates, which alters microbial ecological niches (Zhang et al. 2019). The pH of biochar is determined during pyrolysis, with soil amendments often increasing soil pH, which then elevates the abundance of *nosZ* gene, thereby reducing soil N_2O emissions (Aamer et al. 2020). While labile N increases soil N_2O emissions through the promotion of nitrification and denitrification, biochar may mediate N availability due to its sorption capacity; thus, reducing the microbial utilization of N and (by extension) N_2O emissions (Zhou et al. 2025; Zhang et al. 2023). In addition, the effects of biochar on nitrification and denitrification vary between soils from different ecosystems (Ji et al. 2020). For instance, biochar increased the nitrification rates of soils that produce greenhouse vegetable cabbage, green tea, and Jerusalem artichokes. However, soil N_2O emissions under green tea and Jerusalem artichokes were lower than under greenhouse vegetable cabbage, which correlated to an increased abundance of *nosZ* (Ji et al. 2020). This suggests that biochar-induced N_2O emissions from different soils are regulated by predominantly microbial pathways. Thus, elucidating the responses of the key functional genes and dominant microbial species involved in nitrification and denitrification is essential toward revealing the microbial mechanisms behind N_2O emissions under biochar amendments in Moso bamboo forests.

Crop straw production in the main producing areas of China exceeds 550 Mt year^{-1}, and straw return to agricultural soils is one of the effective strategies for its utilization (Li et al. 2018; Liu et al. 2023). Although the incorporation of straw has been shown to enhance soil nutrient and energy supply to activate the microbial N mineralization, which in turn enhances N_2O emissions, the effect of its biochar on N transformation in forest soils is not well known (Zhou et al. 2025). Further investigation is needed to clarify the microbial mechanisms underlying the effects of biochar on N_2O emissions from Moso bamboo forests. Here, maize straw and its biochar were amended into Moso bamboo forest soils to explore the impacts of these exogenous materials on N_2O emissions. The aims of this study were to compare the responses of the key functional microbial genes and communities involved in nitrification and denitrification processes to the application of maize straw and its biochar, and to characterize the microbial mechanisms that regulate the generation of N_2O under these two amendments. We hypothesize that (1) straw will increase N_2O emissions from Moso bamboo forest soils through the acceleration of nitrification and denitrification processes; (2) biochar will exert contrasting effects on N_2O emissions by modulating key microbial communities and functional genes involved in nitrification and denitrification. This study contributes to the growing body of evidence demonstrating that biochar mitigates N_2O emissions by mediating soil functional microbial communities. It also highlights the potential of optimized management of Moso bamboo forests as a strategy for climate change mitigation through suppression of soil N_2O emissions.

2 Materials and methods

2.1 Experimental site

The study was conducted in Gaohong Township (30°13’N, 119°47’E), situated within Hangzhou City, China. This area experiences a subtropical monsoon climate, with average annual sunlight, precipitation and temperature of 1950 h, 1564 mm and 17.8 ℃, respectively. The soil is categorized as a Ferralsol and exhibited the following physicochemical characteristics when air-dried: pH of 4.82, soil organic C (SOC) of 19.8 g kg^{-1}, total N of 1.88 g kg^{-1}, available P of 7.8 mg kg^{-1}, and available K of 89.4 mg kg^{-1}. The soil texture comprised 40% sand, 32% silt, and 28% clay.

The experiment was carried out within a Moso bamboo forest (with a stand density of 3×10^3 stems per hectare and mean breast-height diameter of 101 mm) that originated from an evergreen broadleaf forest converted in 2002. The forest was fertilized with urea, superphosphate, and potassium chloride at rates of 200 kg N ha^{-1}, 57 kg P ha^{-1}, and 67 kg K ha^{-1}, respectively, which were applied annually in late May during 2002–2019.

2.2 Experimental design

The study employed a randomized block design with three treatments and four replicates. The three treatments included: (1) control without straw or biochar application; (2) application of maize straw at 5 × 10^3 kg C ha^{-1}; (3) incorporation of maize straw-derived biochar at 5 × 10^3 kg C ha^{-1}. Twelve plots (10 m × 10 m each) were established with 5 m buffer zones between plots on August 31, 2020.

The biochar was produced from maize straw by Intellect, Integration & Connection, Ltd., Nanjing, Jiangsu. Thermal processing proceeded with a constant heating rate (8.5 °C min^{-1}) to the terminal temperature (500 °C), followed by 10 h of maintained pyrolysis, with process completion determined by the disappearance of smoke from the effluent gas stream. The biochar had a specific surface area of 11.3 m^2 g^{-1}, pH of 9.24 (measured at a 1:20 w:v in water), total C of 550 g kg^{-1} and total N of 11.9 g kg^{-1}. Maize straw contained 412 g kg^{-1} of total C and 6.6 g kg^{-1} of total N. The C to N ratio of biochar and straw were 46 and 62, respectively. The specific surface area of the biochar was determined using the procedure outlined by Rafiq et al. (2016). An elemental analyzer (CHN-O-RAPID, Germany) was used to determine the total C and N contents in both biochar and straw. Both straw and biochar were pulverized to pass through a 2 mm mesh and tilled into the topsoil (0–20 cm) on August 31, 2020.

2.3 Soil N_2O efflux measurements

The soil N_2O was collected by a static chamber on the third and twelfth months after the straw and biochar amendments. The static chamber consisted of a ground-inserted frame (0.3 m × 0.3 m × 0.1 m) and a removable upper box (0.3 m × 0.3 m × 0.3 m). The ground-inserted frame was permanently embedded vertically in the plot center of each treatment. Gas samples from the static chamber were extracted with a 100 ml plastic syringe by puncturing the rubber stopper with the needle during rain-free mornings (9:00–11:00 AM), with a total of four gas samples collected for each chamber. The calculation of N_2O emissions was carried out using the formula below.

$$F = \rho \frac{V}{V} \frac{P}{P_0} \frac{T_0}{T} \frac{dC_t}{d_t}$$

where F is the N_2O efflux (μg m^{-2} h^{-1}); ρ is the density of N_2O in standard conditions (mg m^{-3}); A is the area of chamber base frame (m^2); V is the volume of chamber (m^3); P_0 and P are the atmospheric pressure under standard conditions and in the chamber, respectively; T_0 and T are the absolute temperature in standard conditions and in chamber, respectively; dC_t/d_t denotes the temporal variation of N_2O concentration.

2.4 Soil sampling and analyses

Topsoil (0–20 cm) was collected from five random locations within each plot on the same days of gas collection. Soils from each plot were thoroughly mixed and transferred to the laboratory to determine soil pH and the concentrations of SOC, total N, microbial biomass C (MBC) and N (MBN), water-soluble organic N (WSON), NH_4^+, NO_3^-, available P and K, as well as the activities of enzymes related to N cycling (nitrate reductase, nitrite reductase, protease, and urease), and the abundances of nitrification/denitrification genes (*amoA*, *nirK*, *nirS* and *nosZ*).

The SOC and total N were determined by an elemental analyzer (CHN-O-RAPID, Germany). Soil available P was analyzed by the Bray method (Lu 2000). Available K in the soil was quantified using the flame photometric technique following extraction with 1 M CH_3COONH_4 (Lu 2000). The soil NH_4^+ and NO_3^- were extracted by 2 M KCl and measured using a Dionex ICS 1500 ion chromatograph (Dionex Co., Sunnyvale, CA). The WSON was the difference between total N and NH_4^+ plus NO_3^- in water extracts after the total N was measured using a TOC-TN analyzer (Multi N/C 2100, Analytik Jena, Germany), and NH_4^+ and NO_3^- were analyzed using ion chromatography (Dionex Co., Sunnyvale, CA). Soil MBC and MBN were measured following the chloroform fumigation-K_2SO_4 extraction method (Wu et al. 1990). The activities of soil protease, urease, nitrate reductase and nitrite reductase were determined according to the methods of Greenfield et al. (2021), Cordero et al. (2019), Abdelmagid and Tabatabai (1987), and Hulse et al. (1988), respectively.

2.5 Real-time PCR and sequencing of microbial genes

Total DNA was obtained from 0.2 g soil employing the Fast DNA Spin Kit (MP Biomedicals, USA). Purification of DNA was performed using the OMEGA Pure kit (Omega Bio-Tek, USA). Nitrification and denitrification genes (*amoA*, *nirK*, *nirS*, and *nosZ*) were amplified using an ABI GeneAmp® 9700 PCR System, with primers and reaction conditions detailed in Table S1. The amplified DNA fragments were isolated and purified employing agarose gel electrophoresis followed by a commercial DNA extraction kit (PCR Clean-Up Kit). Real-time qPCR was conducted on a QuantiFluor™-ST fluorescent quantitative System (Promega, USA) following the provided protocol. Sequencing libraries were generated via the TruSeq™ DNA Library Prep Kits (Illumina, USA) in accordance with the manufacturer's guidelines. DNA library sequencing was conducted using Illumina MiSeq technology with paired-end reads (Majorbio Technology Co. Ltd., Shanghai, China). Raw sequencing reads were archived in the NCBI-SRA (accession: SRP502198).

2.6 Bioinformatics

Microbiome sequencing analysis was performed using the QIIME2 bioinformatics platform. Paired-end reads were first merged and barcode-filtered, then processed through quality control (q2-demux) before DADA2-based denoising for ASV production (Callahan et al. 2016). SILVA version 138 (https://www.arb-silva.de/) was used for taxonomic identification (McDonald et al. 2012). All samples were rarefied to achieve uniform library sizes for comparative analysis.

2.7 Statistical analysis

All data were expressed as the mean of four replicates + standard deviation (SD). A one-way ANOVA followed by Tukey's post-hoc test was conducted to assess the differences between treatments at each sampling time. Correlation analyses were performed between the soil properties, N pools, enzyme activities, and the abundance of functional species using Pearson's correlation test. The Mantel test was conducted using a Bray method for species distance and Euclidean method for environmental distance. Correlation heat maps were rendered using an online ChiPlot platform (https://www.chiplot.online/). To evaluate soil variable impacts on N_2O emissions, a covariance-based SEM approach was constructed in AMOS using robustified maximum likelihood estimation. The labile N (including NH_4^+, NO_3^-, WSON and MBN), activities of enzymes (including protease, urease, nitrate reductase, nitrite reductase), Shannon diversity, Chao 1 diversity, nitrification and denitrification gene copies of ammonia-oxidizing bacteria (AOB), and archaea (AOA) *amoA*, *nirK*, *nirS*, *nosZ*, and other soil biochemical properties (e.g., SOC, total N, MBC, WSOC, available P and K) were reduced in dimensions. All data were standardized prior to modeling.

3 Results

3.1 N_2O emissions, soil properties, N pools, and enzyme activities

Compared with the control, maize straw increased but its biochar amendment decreased N_2O emissions ($P<0.05$) (Fig. 1). The incorporation of straw significantly promoted the concentrations of total N, NH_4^+, NO_3^-, WSON, and MBN in the Moso bamboo forest soil, while biochar decreased the concentrations of WSON, NO_3^- and NH_4^+ ($P<0.05$) (Fig. 1). Specifically, straw application increased the NH_4^+ concentration by 16% and 10% and NO_3^- by 17% and 11% on the third and twelfth months, respectively, whereas the biochar amendment decreased NH_4^+ by 14% and 11%, and NO_3^- by 15% and 11%, respectively.

On the third month following straw application, the activities of protease, urease, nitrate reductase and nitrite reductase increased by 20%, 18%, 22%, and 20%, respectively. By the twelfth month, the activities of these enzymes increased by 13%, 13%, 16%, and 15%, respectively (Fig. 2). In contrast, the application of biochar decreased the activities of these four enzymes by 15%, 15%, 18%, and 17%, respectively on the third month, and by 13%, 12%, 15%, and 16%, respectively, on the twelfth month.

3.2 Microbial gene abundance and microbial communities

Both straw and biochar enhanced the diversities of AOA and AOB *amoA* gene-bearing microbial communities but did not significantly affect the abundance of AOA *amoA* gene compared with the control (Fig. 3). In comparison, straw increased the abundance of AOB *amoA* gene by 56% and 40% ($P<0.05$), whereas the biochar decreased it by 45% and 39% ($P<0.05$), in the third and twelfth months, respectively (Fig. 3). The addition of straw increased the abundances of *nirK* and *nirS* genes by 45% and 42%, respectively, at the third month, and 32% and 28% at the twelfth month ($P<0.05$). By contrast, biochar decreased the abundances by 36% and 32%, respectively, at the third month, and 30% and 24% at the twelfth month ($P<0.05$) (Fig. 4). The abundances of *nosZ* genes in the control in the third and twelfth months were 1.3×10^7 and 1.5×10^7 copies g^{-1}, respectively. Straw amendment decreased the *nosZ* abundance by 38% and 24%; whereas, biochar application increased it by 46% and 40%, in the third and twelfth month, respectively ($P<0.05$) (Fig. 4). Both straw and biochar enhanced Shannon and Chao1 indices of *nirK*-denitrifying microbial communities at the two sampling days ($P<0.05$) (Fig. 4). While biochar enhanced the Chao1 index of *nirS*-denitrifying microbial communities in the third month, straw and biochar increased the Chao1 index of *nosZ*-bearing microbial communities in the third and twelfth months ($P<0.05$) (Fig. 4).

Nitrosospira was the dominant genus of nitrifiers, and was significantly stimulated by straw (7–19%) but inhibited by biochar (11–14%) amendment ($P<0.05$) (Fig. 3). The dominant bacterial genera of *nirK* denitrifiers in the third month were *Bradyrhizobium*, *Mesorhizobium*, *Afipia*, and *Bosea*, with their relative abundances accounting for 13–27%, 0.8–6%, 0.1–4%, and 0.1–1%, respectively. Straw increased the relative abundances of *Bradyrhizobium* (35%), *Mesorhizobium* (24%), and *Bosea* (1150%), while biochar increased the abundances of *Afipia* (2862%) and *Bosea* (735%) but decreased those of *Bradyrhizobium* (34%) and *Mesorhizobium* (84%) ($P<0.05$) (Fig. 4). *Rhizobium*, *Achromobacter*, and *Bosea* were the dominant genera of the *nirK* denitrifiers in the twelfth month. The relative abundances of *Rhizobium* and *Achromobacter* were enhanced by the straw (157% and 79%) but decreased under the biochar (65% and 45%) ($P<0.05$) (Fig. 4). The dominant genus of the *nirS*

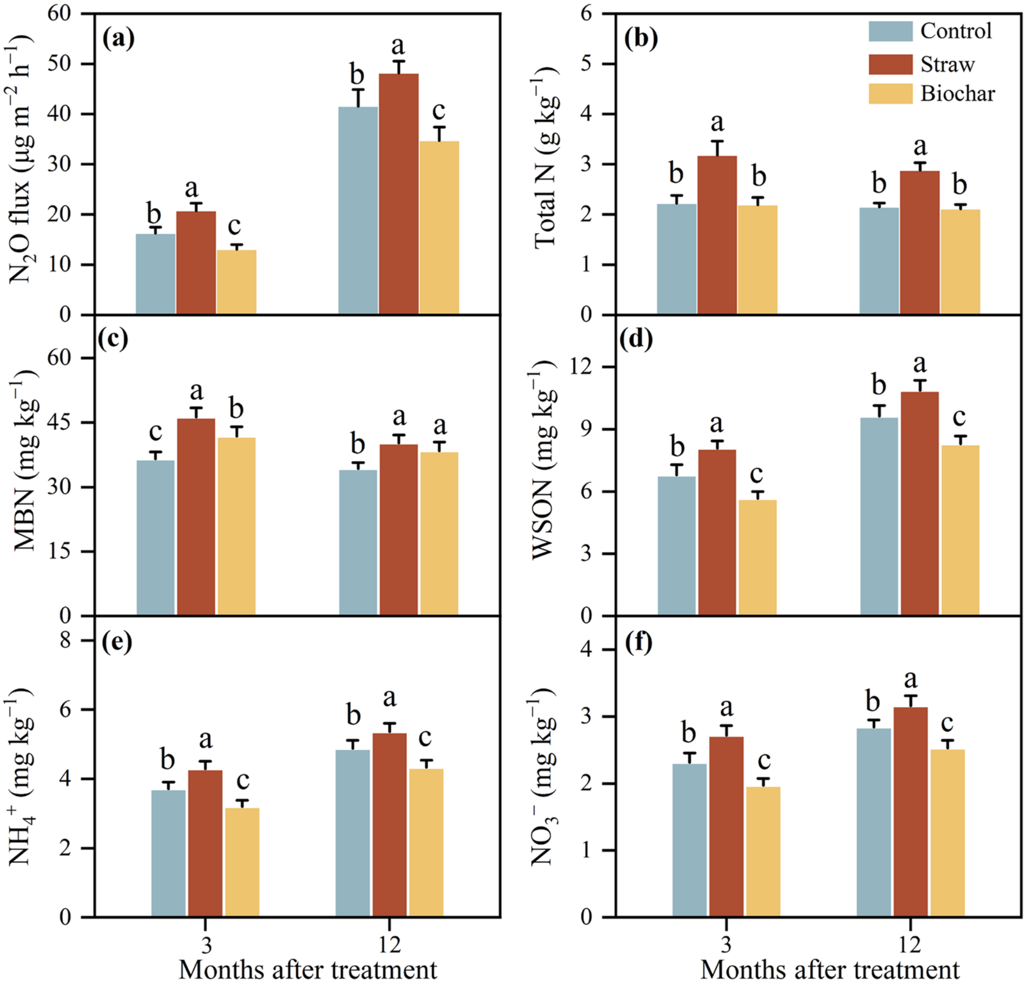


Fig. 1 Effects of maize straw and its biochar addition on N_2O flux and the concentrations of total N, microbial biomass N (MBN), water-soluble organic N (WSON) and mineral N in soils from a Moso bamboo forest. Different lowercase letters indicate significant differences between amendment treatments at a given sampling time ($P < 0.05$). Values represent means + SD ($n = 4$)

denitrifier in the third month was *Pseudomonas*, accounting for 50–75%. Its abundance was enhanced by straw and diminished by biochar ($P < 0.05$) relative to the control (Fig. 4). The dominant bacterial genera in the twelfth month were *Cupriavidus* (16–31%), *Rhodanobacter* (10–19%), and *Pseudomonas* (2%), with *Pseudomonas* being the only detected genus in the straw amended soil. Straw-increased the relative abundance of *Cupriavidus* (32%) but decreased that of *Rhodanobacter* (51%), while biochar reduced the relative abundances of both by 32% and 44%, respectively ($P < 0.05$) (Fig. 4). The dominant genera of *nosZ* denitrifiers in the third month were *Mesorhizobium* and *Bradyrhizobium*, which accounted for 16–33% and 0.3–3%, respectively. The relative abundances of *Mesorhizobium* and *Bradyrhizobium* were decreased by straw but promoted by biochar ($P < 0.05$) (Fig. 4). The dominant genera of *nosZ* denitrifiers in the twelfth month were *Mesorhizobium* (2–5%) and *Azospirillum* (1–2%). Straw decreased while biochar enhanced the abundance of *Mesorhizobium* ($P < 0.05$) (Fig. 4).

3.3 Factors influencing soil N_2O emissions

The Mantel test and correlation analyses revealed that N_2O emissions at the two sampling times were significantly correlated with the activities of protease, urease, nitrate, and nitrite reductase, pH, total N, and labile N (NH_4^+, NO_3^- and WSON) (Fig. 5). The N_2O emissions showed a positive association with the abundances of nitrification and denitrification genes, which were in turn positively associated with the activities of N cycling-related enzymes and the N pools, and negatively associated with the pH (Fig. 5). Most dominant genera of nitrifiers (e.g., *Nitrosospira*) and denitrifiers (e.g., *Bradyrhizobium*, *Mesorhizobium*, *Afipia*, *Rhizobium*, *Achromobacter*, *Bosea*, *Pseudomonas*, and *Cupriavidus*)

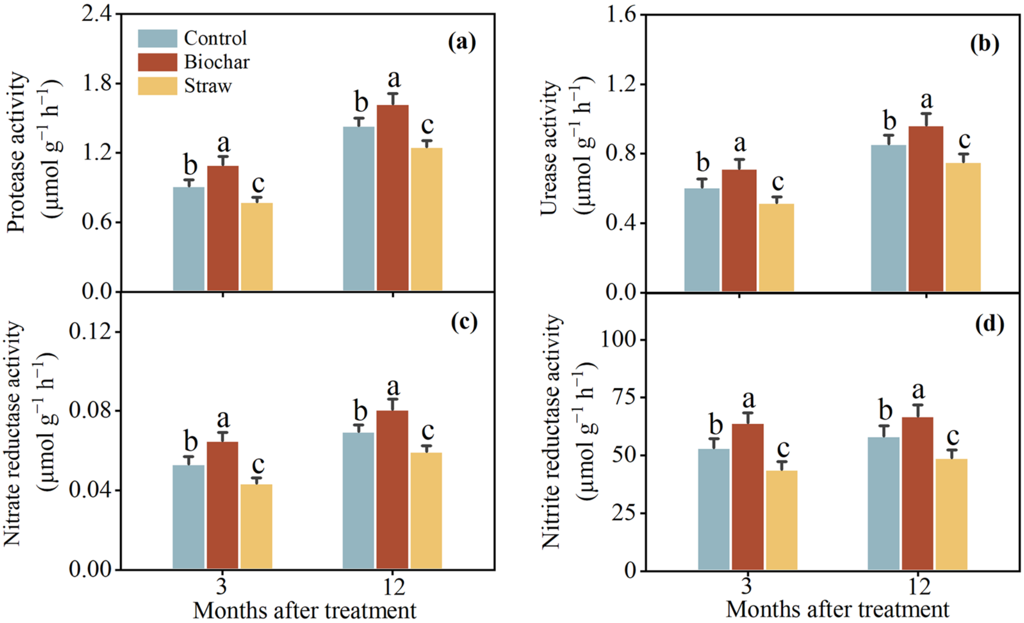


Fig. 2 Effects of maize straw and its biochar addition on the activities of soil protease (**a**), urease (**b**), nitrate reductase (**c**), and nitrite reductase (**d**) in a Moso bamboo forest. Different lowercase letters indicate significant differences between amendment treatments at a given sampling time ($P < 0.05$). Values represent means + SD ($n = 4$)

positively influenced N_2O emissions, except the *nirK*-bearing denitrifiers in the third month. However, the dominant *nosZ*-bearing denitrifiers (*Mesorhizobium*, *Bradyrhizobium*, and *Azospirillum*) negatively influenced N_2O emissions (Fig. 6). The SEM revealed that labile N was the most important factor affecting N_2O emissions, followed by the activities of N-cycling enzymes. Soil pH was an important indirect factor that influenced N_2O emissions by regulating labile N and the abundances of nitrification and denitrification genes (Fig. 7).

4 Discussion

4.1 Labile N pool mediated the effects of straw and its biochar on soil N_2O emissions

This study demonstrates the opposing effects of maize straw and its biochar on soil N_2O emissions (Fig. 1). Such contrasting effects were likely mediated by differences in their regulation of labile N pools, with straw promoting and biochar lowering labile-N availability (Fig. 1). It is evident that soil N_2O emission was positively correlated with the soil available N pools (NH_4^+, NO_3^-, and WSON) (Fig. 5). These findings align with earlier studies demonstrating that increased N availability accelerated nitrification and denitrification processes, thereby increasing soil N_2O emissions within subtropical forest ecosystems (Zhou et al. 2021, 2025; Shi et al. 2024). This is likely because available N not only stimulates soil microbial growth but also serves as a substrate for soil nitrification and denitrification, thereby promoting N_2O production (Zhang et al. 2023).

Most N in biochar is recalcitrant and exhibits low bioavailability (Knicker 2010). A previous study revealed that biochar may enhance soil microbial activity by providing easily mineralizable aliphatic compounds and improving soil physicochemical properties, thereby promoting the release of available N from organic matter (Liu et al. 2018a). However, release of available N from biochar-enhanced mineralization of soil organic matter is somewhat limited, and available N can be readily depleted by plant uptake (Nguyen et al. 2017). Consequently, the available N decreased, although the total N was not altered by biochar (Fig. 1). In addition, physicochemical properties of biochar, including its microporous structure, charged functional groups on the surface, and extensive surface area, all of which enhance its adsorption capacity and thereby reduce the availability of labile N (Liu et al. 2018a). Notably, biochar with a lower C/N ratio (46) supported higher *nifH* gene abundances (36% and 28% greater than the control at months 3 and 12, respectively) (Fig. S1), suggesting a promotion of biological N_2 fixation that could partially compensate for N retention (Xia et al. 2023). In contrast, the addition of maize straw with a high C/N ratio (62) provided a large source of labile C, which likely enhanced soil microbial activity and induced transient N immobilization, e.g. promoted the MBN content (Fig. 1). Critically, the

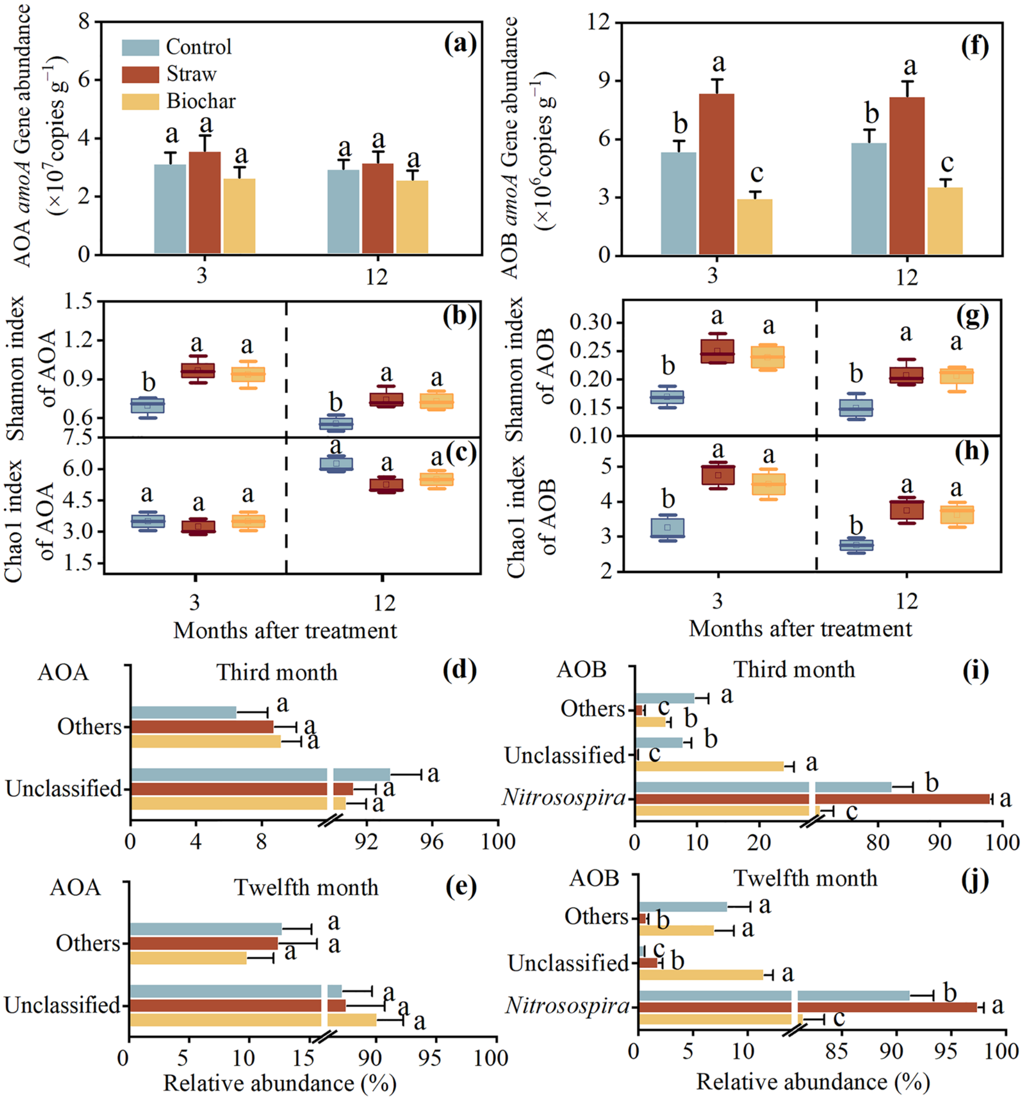


Fig. 3 Effects of maize straw and its biochar addition on the *amoA* gene abundances (**a**, **f**), Shannon (**b**, **g**) and chao1 (**c**, **h**) indices and dominant species at genus level of ammonia-oxidizing archaea (AOA) (**d**, **e**) and ammonia-oxidizing bacteria (AOB) (**i**, **j**) in a Moso bamboo forest soil. Different lowercase letters indicate significant differences between amended treatments at each sampling time ($P < 0.05$). Values represent means + SD ($n = 4$)

concurrent release of labile N compounds from straw (e.g., amino acids) reduced the soil microbial reliance on biological N_2 fixation, as was reflected by the promoted protease and urease activities and the reduced *nifH* gene abundance (34% and 23% lower than the control at months 3 and 12, respectively) (Figs. 2 and S1). The subsequent remineralization of immobilized N, coupled with the ongoing mineralization of straw-derived organic N, ultimately led to the observed increase in soil available N pools (Fig. 1). Thus, the high C/N ratio of maize straw shifted the N mineralization-fixation dynamics toward enhanced net mineralization and N availability, which in turn promoted soil N_2O production via nitrification and denitrification.

Ammonium constitutes the principal substrate for nitrification, whose products in turn provide substrates for denitrification, thereby coupling and accelerating both processes (Kuypers et al. 2018). In soils, an important source of ammonium is derived from the hydrolysis of applied urea, mediated by urease activity (Cordero et al. 2019). The inhibitory effect of biochar on NH_4^+ availability may be attributed to its capacity to create alkaline microsites, generate reactive oxygen species, and release polycyclic aromatic hydrocarbons, all of which can suppress urease activity and thereby limit NH_4^+ release

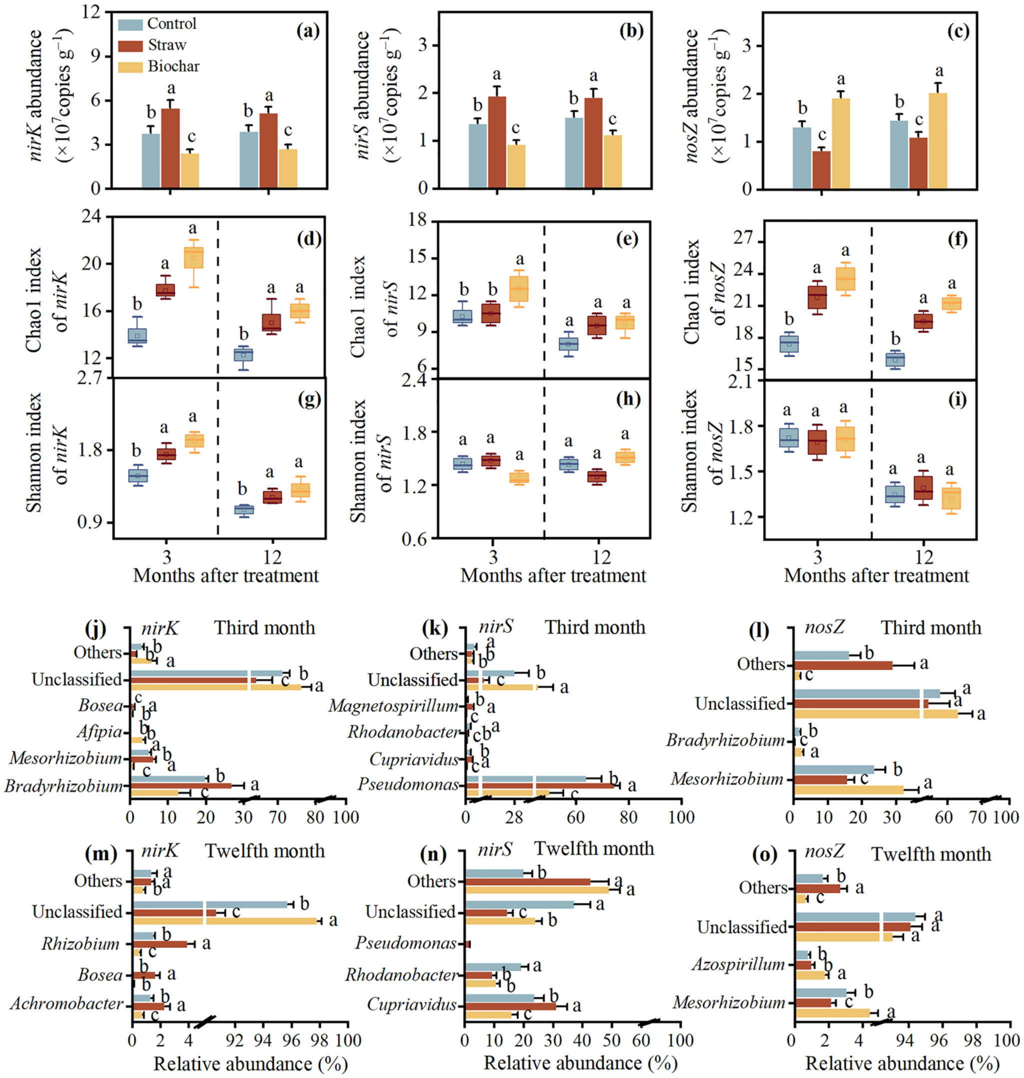


Fig. 4 Effects of maize straw and its biochar addition on the abundances of denitrification bacterial genes (*nirK*, *nirS*, *nosZ*; **a**–**c**), diversity indices (**d**–**i**), and dominant species at the genus level (**j**–**o**) of soil denitrification bacterialcommunities (*nirK*, *nirS*, *nosZ*) in a Moso bamboo forest soil. Different lowercase letters indicate significant differences between amended treatments at each sampling time ($P < 0.05$). Values represent means + SD ($n = 4$)

(Liu et al. 2018b). In contrast, straw incorporation likely enhanced urease-mediated urea hydrolysis, as the labile organic N compounds released from straw (e.g., amino acids) serve as direct substrates that stimulate both urease synthesis and activity (Li et al. 2019; Xu et al. 2024). Moreover, straw promotes the formation of organo-mineral complexes and macroaggregates (e.g., humus-clay bonds), both of which contribute to the stability of urease activity (Ji et al. 2024). Additionally, straw input reshapes the ureolytic microbial community that is induced by the labile organic C and N components, thereby accelerating urea hydrolysis (Lv et al. 2024; Xu et al. 2024). Collectively, by modulating the supply of NH_4^+ to nitrification and denitrification processes, maize straw enhanced soil N_2O emissions, whereas biochar exerted a suppressive effect (Fig. 1).

4.2 Microbial mechanisms involved in the effects of straw on soil N_2O emissions

Straw amendment increased soil N_2O emissions by upregulating nitrification (e.g., *amoA*) and denitrification (e.g., *nirK*/*nirS*) genes and stimulating their associated enzyme activities (Fig. 5), supporting the first hypothesis. Ammonium oxidation, a crucial step that limits the rate of nitrification process, is mediated by AOA and AOB communities (He et al. 2012). Here, while AOA *amoA* gene exhibited greater abundance than AOB *amoA* gene (Fig. 3), straw treatment significantly increased the

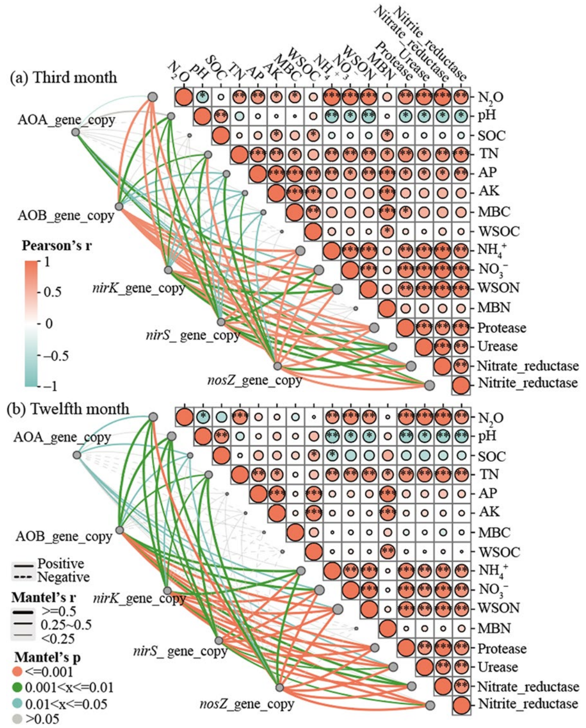


Fig. 5 Relationships between soil N_2O emissions, soil factors, and nitrification/denitrification-related gene abundance in a Moso bamboo forest. The abundances of nitrification/denitrification bacterial genes were correlated with each single index by Mantel tests. Edge width corresponds to the Mantel's *r* statistics for relative distance correlations, and the edge color denotes statistical significance. SOC, TN, AP, AK, MBC, MBN, WSOC, WSON, NH_4^+, NO_3^- represent Soil organic C, total N, Available P, available K, microbial biomass C and N, and water-soluble organic C and N, Amonium, Nitrate, respectively. Asterisks indicate significant correlations with *, ** and *** indicating $P < 0.05$, $P < 0.01$, and $P < 0.001$, respectively

abundance of the AOB *amoA* gene without affecting that of AOA *amoA* gene. This suggests that straw-induced stimulation of the nitrification process was primarily driven by the AOB community (Fig. 3). The contrasting responses of AOB and AOA to straw addition may be attributed to their distinct physiological and ecological characteristics. AOB possess larger cell sizes and utilize different ammonia oxidation pathways, rendering them more responsive to increased NH_4^+ availability under nutrient-enriched conditions (Ouyang et al. 2018). Conversely, AOA are better adapted to oligotrophic environments and exhibit high substrate affinity; the ammonia monooxygenase enzyme encoded by AOA *amoA* reaches saturation at relatively low NH_4^+ concentrations (Prosser and Nicol 2012).

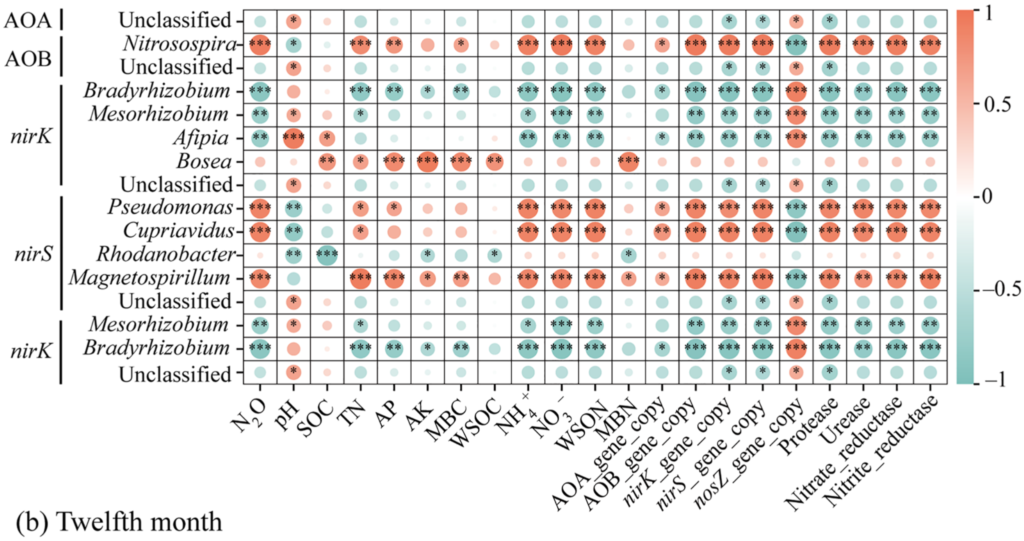
In the straw-amended soil, intensified ammonia oxidation occurred concurrently with elevated abundances of *nirK* and *nirS* genes (Fig. 4), which encode nitrite reductases, leading to enhanced conversion of nitrate into N_2O compared to the biochar treatment. This pattern is further supported by the positive correlations observed among nitrate concentrations, nitrite reductase activities, and the abundance of denitrifying microorganisms in the straw-amended soils (Fig. 5). A previous study has shown that straw contains substantial amounts of labile organic C, which can serve as a readily available energy source for denitrifiers and thereby stimulating their activity and proliferation (Starr et al. 2024). In addition, the supply of labile C enhanced overall microbial respiration, contributing to localized oxygen depletion and consequently formation of anaerobic microsites, which are favorable for denitrification and subsequent N_2O production (Zhu et al. 2022). Furthermore, the straw treatment resulted in a lower abundance of the *nosZ* gene, which encodes N_2O reductase (Fig. 4), potentially limiting the reduction of N_2O to N_2, thereby contributing to greater N_2O accumulation. Collectively, straw addition increased the abundances of AOB *amoA*, *nirK*, and *nirS* genes, thereby intensifying both nitrification and denitrification processes and ultimately leading to elevated N_2O emissions from the soil.

4.3 Effect of biochar on soil N_2O emissions and underlying microbial mechanisms

Biochar manifested opposing effects on soil N_2O emissions compared with straw amendment, primarily due to their contrasting effects on the nitrifier/denitrifier communities and its associated functional genes (Figs. 3 and 4). During soil nitrification, *Nitrosospira* was the dominant AOB nitrifier genus, which utilizes ammonium for its energy source (Kuypers et al. 2018). Biochar is a highly adsorbent soil amendment that may promote the immobilization of soil labile N (Gai et al. 2014). Therefore, the decrease in NH_4^+ availability may have contributed to the decreased abundance of *Nitrosospira* observed under the biochar treatment (Fig. 3). Furthermore, the incorporation of biochar may increase soil aromatic compound levels, which could subsequently lower the availability of labile C substrates required for microbial growth (Zhou et al. 2024b; c). These conditions may have lowered the abundance of the AOB *amoA* gene (Fig. 3), thereby exerting a negative effect on ammonium oxidation. Therefore, the reduction in soil N_2O emissions observed under biochar treatment may be attributed to the inhibition of nitrifier abundance and activity, resulting in the net suppression of nitrification.

The decreased abundances of *nirK* and *nirS* by biochar (Fig. 4) suppressed denitrification and resulted in a decline in soil N_2O emissions. Denitrification is preferential anaerobic process; thus, limited O_2 supply is a critical factor for denitrifiers (Kuypers et al. 2018). Highly porous biochar can develop enriched oxic

(a) Third month



(b) Twelfth month

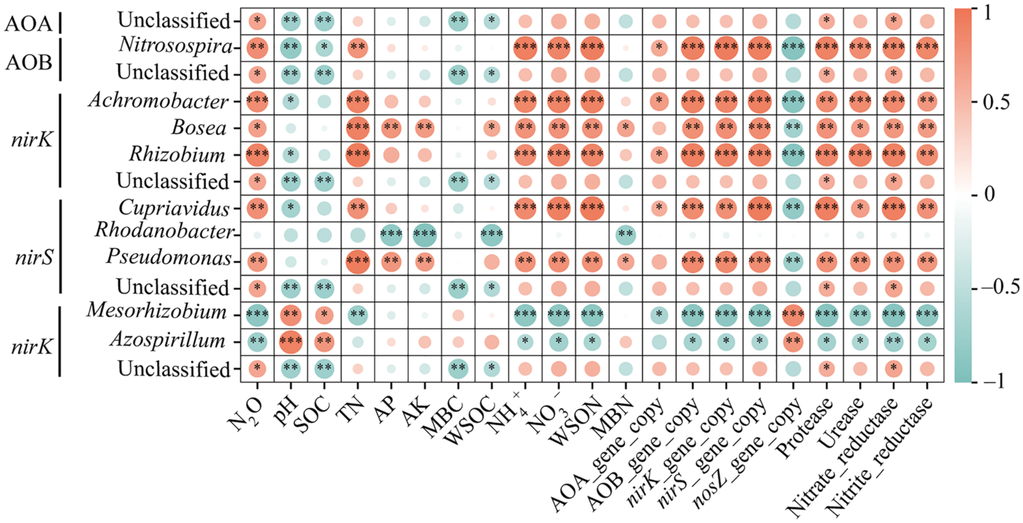


Fig. 6 Pearson's correlation between soil N_2O efflux, soil factors, abundance of nitrification/denitrification microbial genes, and dominant species of nitrification/denitrification bacteria at the genus level in a Moso bamboo forest. SOC, TN, AP, AK, MBC, MBN, WSOC, WSON, NH_4^+, NO_3^- represent Soil organic C, total N, Available P, available K, microbial biomass C and N, and water-soluble organic C and N, Amonium, Nitrate, respectively. Asterisks indicate significant correlations with *, ** and *** indicating $P < 0.05$, $P < 0.01$, and $P < 0.001$, respectively

patches surrounding biochar particles, subsequently promoting soil aeration (Zhu et al. 2022). Thus, the improved soil aeration creates unfavorable conditions for denitrifying microorganisms (Kuypers et al. 2018). In addition, the smaller amounts of nitrate under biochar than other treatments provided insufficient substrates for these denitrifiers. Furthermore, *Bradyrhizobium*, a dominant denitrifying genus that declined under biochar amendment in this study (Fig. 4), is known to participate in soil N_2O reduction through harboring key denitrification genes (e.g., *nirK*) (Sciotti et al. 2003). However, its growth is constrained by oxygen supply and it preferentially thrives under acidic conditions (Sciotti et al. 2003; Lin et al. 2018); thus, the greater O_2 diffusion and higher pH surrounding biochar patches may inhibit the growth of this important denitrifier. Collectively, by lowering the abundances of *nirK* and *nirS* genes and their bearing denitrifiers such as *Bradyrhizobium*, *Rhizobium*, *Pseudomonas*, and *Cupriavidus* (Fig. 4), biochar decreased soil N_2O emissions.

Biochar can induce elevated pH zones at soil-biochar interfaces, which facilitates the production of N_2O reductases (Zhu et al. 2022). This will promote the reduction process of N_2O and reduce its emission (Fig. 1). In

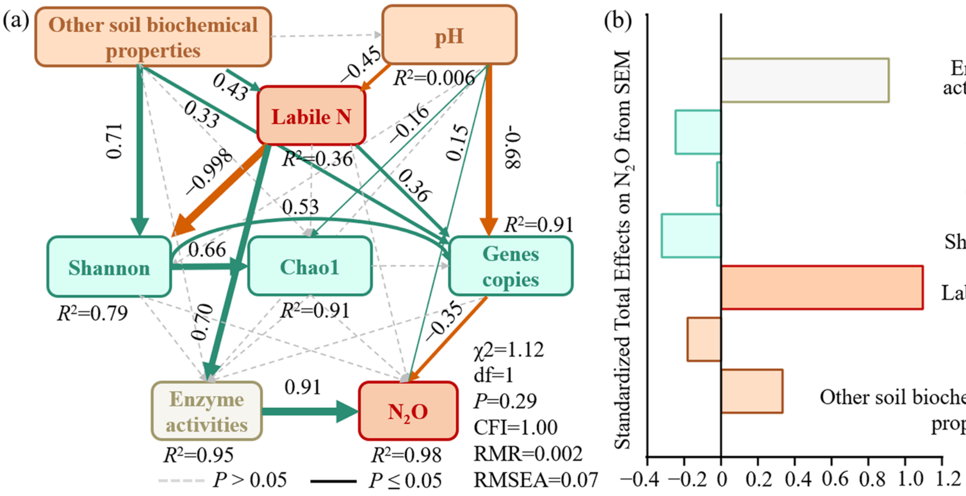


Fig. 7 Structural equation model (SEM) to assess multivariate effects (**a**) and the standardized total effects of individual variances (**b**) on the soil N_2O efflux. Brown and blue arrows represent significant negative and positive pathways, respectively. Numbers associated with solid lines show the path coefficients. Solid and dashed lines denote path coefficients at $P \leq 0.05$ and $P > 0.05$, respectively. R^2 values indicate the proportion of the variance explained for each dependent variable in the model. Labile N includes NH_4^+, NO_3^-, water-soluble organic N and microbial biomass N

addition, *Mesorhizobium*, one of the denitrifiers that bear the *nosZ* nitrification gene encoding N_2O reductase, was the dominant taxon in the present study (Fig. 4). It is known to exhibit a strong adaptability to alkaline environments (Zhang et al. 2017). This may have promoted its capacity to compete for nutrients in the biochar-amended soil. Furthermore, *Mesorhizobium* is an aerobe that thrives in biochar-amended soil, which enhances O_2 diffusion (Sánchez et al. 2013).

Ultimately, with the decreases of AOB *amoA*, *nirK* and *nirS* genes, and an increase in the *nosZ* gene abundance, biochar decreased soil N_2O emissions by inhibiting the production of N_2O but accelerating its reduction. These findings support the second hypothesis that biochar exert the effects contrasting to straw on N_2O emissions by modifies soil microbial communities, which harbor the nitrification and denitrification genes responsible for governing soil N_2O production.

5 Conclusion

The novel finding of our study was that maize straw and its biochar manifested opposing effects on N_2O emissions from Moso bamboo forests soils. Such effects were mediated by key functional microbial genes and the associated microbial communities responsible for nitrification and denitrification. In the acidic Moso bamboo forest soil, the application of alkaline biochar decreased the abundances of AOB *amoA*, *nirK* and *nirS* genes and their specific associated species, *Nitrosospira*, *Mesorhizobium*, *Bradyrhizobium*, *Rhizobium*, *Pseudomonas* and *Cupriavidus*, contributing to the decreased production of N_2O. Biochar also promoted N_2O reductases via enhanced the abundances of *Mesorhizobium*, *Bradyrhizobium* and *Azospirillum*, further suppressing N_2O emissions. In contrast, straw amendment promoted the activities of soil protease and urease, and increased the abundance of functional genes that facilitate soil nitrification and denitrification. Straw also decreased the abundance of N_2O reductases by inhibiting the growth of its specific species, facilitating N_2O emissions. This study highlights the potential risk of elevated N_2O emissions through the application of straw to the soil in subtropical Moso bamboo forest, and importantly, demonstrates that the associated biochar alleviates this risk. Future investigations should cover a range to straw and biochar types in in different soils and climatic zones; work should also focus on the combined effects of straw and biochar on N_2O emissions in subtropical Moso bamboo forests.

Supplementary Information

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Supplementary material 1

Author contributions
Mouliang Xiao: Investigation, Methodology, Formal analysis, Visualization, Writing—Original Draft, Writing—Review & Editing. Caixian Tang: Writing—Review & Editing. Zhenhui Jiang: Writing—Review & Editing. Jiashu Zhou: Methodology, Writing—Review & Editing. Yu Luo: Writing—Review & Editing. Tida Ge: Writing—Review & Editing. Lixia Pan: Investigation, Writing—Review & Editing. Bing Yu: Writing—Review & Editing. Yanjiang Cai: Writing—Review & Editing. Jason C. White: Writing—Review & Editing. Yongfu Li: Conceptualization, Supervision, Investigation, Methodology, Validation, Data curation,

Writing—Original Draft, Writing—Review & Editing. The authors read and approved the final manuscript.

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Data availability

The main data supporting the findings of this study are available at Figshare: https://doi.org/10.6084/m9.figshare.28955522 (Xiao et al. 2025).

Declarations

Competing interests

Yu Luo is an EBM of the journal Biochar, and he was not involved in the peer-review or handling of the manuscript. The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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