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PRIMARY RESEARCH ARTICLE

Differential response of soil CO₂, CH₄, and N₂O emissions to edaphic properties and microbial attributes following afforestation in central China

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Abstract

Land use change specially affects greenhouse gas (GHG) emissions, and it can act as a sink/source of GHGs. Alterations in edaphic properties and microbial attributes induced by land use change can individually/interactively contribute to GHG emissions, but how they predictably affect soil CO₂, CH₄, and N₂O emissions remain unclear. Here, we investigated the direct and indirect controls of edaphic properties (i.e., dissolved organic carbon [DOC], soil organic C, total nitrogen, C:N ratio, NH₄⁺-N, NO₃⁻-N, soil temperature [ST], soil moisture [SM], pH, and bulk density [BD]) and microbial attributes (i.e., total phospholipid fatty acids [PLFAs], 18:1ω7c, nitrifying genes [ammonia-oxidizing archaea, ammonia-oxidizing bacteria], and denitrifying genes [*nirS*, *nirK*, and *nosZ*]) over the annual soil CO₂, CH₄, and N₂O emissions from the woodland, shrubland, and abandoned land in subtropical China. Soil CO₂ and N₂O emissions were higher in the afforested lands (woodland and shrubland) than in the abandoned land, but the annual cumulative CH₄ uptake did not significantly differ among all land use types. The CO₂ emission was positively associated with microbial activities (e.g., total PLFAs), while the CH₄ uptake was tightly correlated with soil environments (i.e., ST and SM) and chemical properties (i.e., DOC, C:N ratio, and NH₄⁺-N concentration), but not significantly related to the methanotrophic bacteria (i.e., 18:1ω7c). Whereas, soil N₂O emission was positively associated with nitrifying genes, but negatively correlated with denitrifying genes especially *nosZ*. Overall, our results suggested that soil CO₂ and N₂O emissions were directly dependent on microbial attributes, and soil CH₄ uptake was more directly related to edaphic properties rather than microbial attributes. Thus, different patterns of soil CO₂, CH₄, and N₂O emissions and associated controls following land use change provided novel insights into predicting the effects of afforestation on climate change mitigation outcomes.

KEYWORDS

greenhouse gas, land use type, methane uptake, soil microbial attribute, soil microenvironment

1 | INTRODUCTION

Global warming is one of the most serious environmental problems due to increasing emissions of greenhouse gases (GHGs) into the atmosphere. The concentrations of CO₂, CH₄, and N₂O have reached new highs at 410.5 ppm, 1877.0 ppb, and 332.0 ppb at the end of 2019, the abundance relative to 1750s, respectively (World Meteorological Organization, 2020). The increased CH₄ and N₂O concentrations have more drastic global warming due to its global warming potential being approximately 28 and 265 times higher than CO₂ estimated on a mass basis over a 100-year scale, respectively (IPCC, 2013). Especially, different from CH₄ emission in the wetland, the CH₄ uptake in upland soils has removed approximately 9–51 Tg CH₄ year⁻¹ from the atmosphere (Kirschke et al., 2013). Land use change has been identified as the second largest anthropogenic sink and source of GHG emissions due to its impacts on the global biogeochemical cycle and hydrological properties of terrestrial ecosystems (Arneeth et al., 2017). Ideally, afforestation and reforestation are the strategies to mitigate anthropogenic emissions of GHGs because they can potentially sequester 2.3–5.7 Gt CO₂ eq year⁻¹, and hence partly offset the global emission of 49 Gt CO₂ eq year⁻¹ (IPCC, 2013). With afforestation and reforestation expanded largely worldwide, it is indispensable to quantify soil GHG emissions and associated drivers following afforestation.

Numerous studies have attempted to investigate the effects of afforestation on soil GHG emissions, but the results are not consistent. Previous studies have reported positive response (Deshmukh et al., 2020; Han & Zhu, 2020; Nazaries et al., 2011), negative responses (Galbally et al., 2010; Shvaleva et al., 2013), and no effect on soil CO₂, CH₄ and N₂O emissions/uptakes (Maljanen et al., 2012). The discrepant effects of afforestation on soil GHG emissions either by meta-analysis or by experimental approaches could be attributed to differences in study sites and land use change types (Tan et al., 2020), human managements (Petitjean et al., 2019), and climate zone (van Kessel et al., 2013; van Lent et al., 2015). Meanwhile, Li et al., (2012) have indicated that the net balance between soil C or N input (e.g., litter input) and output (e.g., GHG emissions), as the soil C or N accumulation, is huge in the subtropical zone. In recent decades, afforestation has rapidly expanded in most subtropical regions due to socioeconomic reasons, however, the effects of afforestation on soil GHG emissions in subtropical regions have not been well considered to date. This gap in knowledge may constrain our understanding of the feedbacks of land use changes to global climate, particularly in subtropical regions where both afforestation and deforestation occur intensively.

Land use change is usually accompanied by changes in soil substrate, soil microbial attributes and chemical properties (Chiti et al., 2018; Hong et al., 2021; Taeumer et al., 2021). Although these changes could individually/interactively affect soil CO₂, CH₄, N₂O production, consumption and diffusion processes (Lagomarsino et al., 2016; Lubbers et al., 2013), the predominant controls over soil CO₂, CH₄, and N₂O emissions are different. Generally, soil

CO₂ emission arises from the production of respiration by roots (autotrophic respiration) and soil decomposers (heterotrophic respiration), CH₄ emission is produced by the balance between methanogenesis and methanotrophs, and N₂O emission is mediated by microbial nitrification (autotrophic/heterotrophic nitrification) and denitrification (Bond-Lamberty et al., 2004; Guetlein et al., 2018). For instance, afforestation enhanced C input which could accelerate soil C decomposition and CO₂ emission (Liu et al., 2017; Nazaries et al., 2015). While heterotrophic respiration enhancement is closely coupled with increased microbial activities (Chen et al., 2016). Methanotrophs, which utilize atmospheric CH₄ as energy source, are the primarily microbial driver of soil CH₄ uptake in upland soils (Nazaries et al., 2013). Nitrifying (ammonia-oxidizing archaea, AOA; ammonia-oxidizing bacteria, AOB) and denitrifying genes [nitrite reductase (encoded by *nirS/nirK*)], are considered to be the rate-limiting step in nitrification and denitrification, respectively, which are main process in the production of N₂O (Jones et al., 2014; Kits et al., 2019).

Meanwhile, soil GHG emissions can be strongly regulated by soil moisture (SM) and temperature under land use change. It has been reported that afforestation increased soil CH₄ uptake, due to the reduced SM, which resulted in facilitated diffusion of atmospheric CH₄ into soil (Hiltbrunner et al., 2012). In contrast, higher SM created an anaerobic environment, thereby decreased CO₂ emissions but increase CH₄/N₂O emissions (Ishikura et al., 2018). Increased temperature stimulates microbial activities and simultaneously promoting soil release of CO₂, CH₄, and N₂O (Frey et al., 2013; Nottingham et al., 2020; Voigt et al., 2017). In a word, although soil CO₂, CH₄, and N₂O emissions could be sensitive to changes in soil substrate, soil microbial attributes, and chemical properties following land use change, it is still unresolved what main factors play a decisive role in influencing GHG emissions.

The Danjiangkou Reservoir, the largest freshwater reservoir in Asia, is the water source for the Middle Route Project named the South-to-North Water Transfer Project in China (Zhang, 2009). In recent decades, afforestation has been carried out on a large scale to repair soil erosion caused by human activities. Our previous studies in this region have found that afforestation significantly increased soil organic C (SOC) and CH₄ uptake (Wu et al., 2018). However, the effect of land use change on soil GHG emissions has largely been neglected. The specific purpose of the present research was to examine the influences of the afforestation on soil GHG emissions, and explore the underlying mechanisms on how variations in the soil environmental/microbial properties control soil GHG emissions in a subtropical China. It has been suggested that soil CO₂ and N₂O emissions are primarily regulated by changes in the soil microbial properties, while soil CH₄ uptake is more sensitive to changes in environment/chemical factors following afforestation (Deshmukh et al., 2020; Wu et al., 2020). In this study, we tried to test the following hypotheses (I) afforestation would increase soil GHG emissions with increased soil organic matter providing sufficient substrate for soil GHG emissions in the subtropical China; and (II) soil CO₂, CH₄, and N₂O emissions would respond differently to changes in soil

substrate, soil microbial attributes, and chemical properties following land use change.

2 | MATERIAL AND METHODS

2.1 | Study area

Field experiments were carried out at the Wulongchi Experiment Station (32°45'N, 111°13'E; 280–400 m a.s.l.) in the Danjiangkou Reservoir area, Shiyan City, Hubei Province, China. In 1980s, following a government's reorganization of the land use, large areas of croplands with the corn (*Zea mays* Linn.) and rape (*Brassica campestris* Linn.) were converted to woodlands with coniferous plants (*Platycladus orientalis* (Linn.) Franco), and shrublands (*Sophora davidii* (Franch.) plantation; Zhu et al., 2010). The mean annual temperature is 15.7°C, with 4.2°C in January to 27.3°C in July, and the mean annual precipitation is 749.3 mm, with 70%–80% occurs between April and October (Cheng et al., 2013). The soil is classified as silt soil in the abandoned land where the corn (*Z. mays* Linn.) and rape (*B. campestris* Linn.) cultivations have been followed over several years, a loam in the shrubland, and a sandy loam in the woodland following the USDA soil Taxonomy.

2.2 | Experimental design and soil physico-chemical analysis

The field experimental plots were set up in each land use type using randomized complete block design with three blocks (600 m × 50 m), the distance between each plot was approximately 100 m. Each block included the abandoned land, shrubland, and woodland. In July 2017, three sub-plots (2 m × 2 m) were set up randomly in each land use type from three blocks. Three soil samples (0–10 cm) were collected using 3.5 cm diameter stainless steel cylinder after litter removal once a month from July 2017 to July 2018. A total of 27 soil samples were harvested to represent each land use type monthly. A part of soil samples was stored at –80°C for microbial analysis and the other was stored at 4°C for the soil physico-chemical analysis.

Bulk density (BD) was sampled from 0 to 10 cm soil depth using 5 cm diameter soil core. Besides, all soil samples were sieved through 2 mm sieve. Soil NH₄⁺-N and NO₃⁻-N concentrations were extracted 1 M KCl solution (soil: solution = 1:5) immediately and then determined on a Smart Chem Discrete Auto Analyzer (Advanced Micro Systems Inc.). SM was obtained by oven-drying fresh soil overnight (105°C). Soil pH was measured at soil water suspension (soil: water suspension = 1:2.5) after shaking 30 min with a pH electrode (SevenEasy pH; Metler Toledo). SOC and total nitrogen (TN) contents were determined using an element analyzer (Vario EL; Elementar Analysensysteme) after air drying and removing inorganic C by using 1 M HCl. Dissolved organic C (DOC) was obtained by ddH₂O extraction (soil:solution = 1:5) and then analyzed using a TOC analyzer (Vario TOC; Elementar).

2.3 | Measurement of GHG emissions

Emissions of soil GHGs were measured once a month using static chambers and the gas chromatography technique from July 2017 to July 2018. Static chambers were inserted into each plot of different land types. The static chamber (PVC collars) consisted of two parts: one was a cylindrical bottom pedestal (30 cm diameter, 15 cm height), a half of the pedestal was permanently inserted into the soil, and the other was a removable cover (30 cm diameter, 30 cm height) with a 15 cm long silicic tube (4 mm diameter) for air collection. A small fan was installed to mix the air in the chamber. Thirty milliliter air samples were collected by syringe throughout 30 min incubation period (at 0, 15, and 30 min) and transferred to 12 ml pre-evacuated bottles. To minimize any effects of diurnal variation in gas emissions, gas samples were collected at the same time between 9:00 AM and 11:00 AM of day on each sampling occasion (Cheng et al., 2010). The air temperature of each experimental plot was measured with a mercurial thermometer at the same time. Soil GHG concentration was measured in a gas chromatography (Agilent 7890). Soil GHG emissions were calculated using linear least-squares fit to the three points in the time series of gas concentration in each chamber with an average chamber temperature (Metcalf et al., 2007):

$$F = \frac{dc}{dt} \times \frac{273}{273 + T} \times \frac{M}{22.4} \times \frac{V}{A},$$

where F is soil GHG emissions, dc/dt is the rate of change in gas concentration in the chamber, T is the air temperature in the chamber, and M is the molecular weight of GHGs (CH₄: 16, CO₂: 44, N₂O: 44). 22.4 is the molar volume of gas at standard temperature and pressure (1 mol⁻¹), V is the chamber volume (m³) and A is the chamber area (m²). Data were omitted if the slope of the linear fitting had a coefficient of determination (R^2) of <0.90.

Annual and seasonal cumulative soil GHG emissions were calculated using the following equation (Yuan et al., 2019):

$$E = \sum_{i=1}^n \frac{f_i + f_{i+1}}{2} \times (t_{i+1} - t_i) \times 24 \times 10^{-2},$$

where E is the annual or seasonal cumulative CH₄ (kg CH₄ ha⁻¹), CO₂ (kg CO₂ ha⁻¹) or N₂O (kg N₂O ha⁻¹) emissions, f represents the emission of CH₄ (mg CH₄ m⁻² h⁻¹), CO₂ (mg CO₂ m⁻² h⁻¹) or N₂O (mg N₂O m⁻² h⁻¹), i is the i th measurement, $(t_{i+1} - t_i)$ is the days between two adjacent measurements, and 24×10^{-2} is used for unit conversion.

2.4 | Phospholipid fatty acids

Soil phospholipid fatty acids (PLFAs) were extracted following the descriptions by (Bossio & Scow, 1998). Briefly, lipid was extracted from 3 g freeze-dried soils in 20 ml extraction mixture (chloroform:methanol:phosphate buffer = 1:2:0.8), and then split it into neutral, glyco- and phospholipids. Subsequently, mild-alkali methanolysis transformed the recovery of fatty acid methyl esters.

The fatty acid methyl esters were identified using an Agilent 6890 gas chromatograph (Agilent Technologies) and a MIDI Sherlock Microbial Identification System (MIDI, Inc.). Peak areas were converted to nmol g^{-1} dry soil using the internal standard, nonadecanoic acid methyl ester (19:0). Total extractable PLFAs were used as microbial biomass, and the PLFA 18:1 ω 7c was used as an indicator for quantifying the relative abundance of methanotrophic bacteria (Smith et al., 2015).

2.5 | Quantitative real-time PCR

Genomic DNA was extracted from 0.25 g fresh soil using the MoBio PowerSoil™ DNA isolation kit (MoBio Laboratories Inc.) according to the manufacturer's instructions. Afterwards, the copy numbers of nitrifying (AOA and AOB) and denitrifying genes (*nirS*, *nirK*, and *nosZ*), were determined by the real-time PCR with a CFX96 Optical Real-Time Detection System (Bio-Rad Laboratories Inc.). The 15 μl quantitative reaction mixture contained 7.5 μl 2 \times SYBR Green Mix, 0.7 μl of primers, 1 μl of DNA template, and 15 μl ddH₂O. The primer sequence and thermal cycling procedures were listed in Table S1. The standard curves were established with a 10-fold diluted series of plasmids. Finally, the gene copy numbers were obtained for each sample by comparing with the standard gene and standard curves, and presented in per gram dry soil (copies/g).

2.6 | Statistical analyses

One-way ANOVA and two-way ANOVA were used to examine the effects of different land use types and seasons on GHG emissions, edaphic properties, and soil microbial attributes. Duncan's test was used for multiple comparisons among types or between seasons if the effect was significant. Multivariable stepwise regression analyses were used to select the optimal explanatory variables for soil GHG emissions from biotic and abiotic variables. The final explanatory variables based on the optimal model were selected the smallest Akaike information criterion (AIC_c; Burnham & Anderson, 2004). Based on the optimal explanatory variables obtained above, we conducted analytic hierarchy process to explore the relative importance of various variables in regulating soil GHG emissions. All the statistical analyses were performed in R software v3.6.1 (R Core Team, 2019) using the *vegan* and *rdacca.hp* package (Lai et al., 2021; Oksanen et al., 2010).

Structural equation modeling (SEM) was applied to evaluate the relationship of the soil GHG emissions, soil microbial attributes with edaphic properties. We constructed pathways based on the principal component analysis (PCA) to create a multivariate functional index before SEM construction (Figure S2). The first component (PC1), which explained 50.4%–65.1% of the total variance for three groups, the second component (PC2), which explained 83.7% of the total variance for soil microbial properties especially represented the nitrifying genes, were then introduced as a new variable into the

subsequent analysis (Table S3; Chen et al., 2019). The best fit model was evaluated using the non-significant paths ($p > 0.05$) and χ^2 test using AMOS 21.0 (Amos Development Corporation).

3 | RESULTS

3.1 | Soil GHG emissions

The annual soil CO₂ and N₂O emissions were higher in the woodland ($18.64 \pm 1.11 \text{ Mg CO}_2 \text{ ha}^{-1}$; $1.13 \pm 0.12 \text{ kg N}_2\text{O ha}^{-1}$) than the shrubland ($16.34 \pm 0.39 \text{ Mg CO}_2 \text{ ha}^{-1}$; $0.89 \pm 0.05 \text{ kg N}_2\text{O ha}^{-1}$) and the abandoned land ($11.67 \pm 0.56 \text{ Mg CO}_2 \text{ ha}^{-1}$; $0.45 \pm 0.11 \text{ kg N}_2\text{O ha}^{-1}$), respectively (Figure 1a,c; Table 1), with higher level of CO₂ emission on average in summer compared to winter, whereas most of seasonal/monthly N₂O emission showed opposite trend of CO₂ emission (Figure 2a,c; Figure S1; Table 1). The annual cumulative CH₄ uptake did not significantly change among all land use types (Figure 1b; Table 1), with the higher level on average in winter ($0.79 \pm 0.13 \text{ kg CH}_4 \text{ ha}^{-1}$) compared to summer ($0.28 \pm 0.02 \text{ kg CH}_4 \text{ ha}^{-1}$) in the abandoned land (Figure 2b; Table 1).

3.2 | Seasonal variation in soil microbial attributes

Total PLFAs and content of specific PLFA biomarker (18:1 ω 7c) which represented methanotrophic bacteria significantly differed across different land use types, with the significantly higher levels in the woodland and shrubland compared to abandoned land. The total PLFAs showed higher levels in summer compared to winter in the woodland and abandoned land (Figure 3a,b). In contrast, the abundance of nitrifying genes (AOA and AOB) was lower in shrubland compared to other lands (Figure 3c,d), with the higher AOA gene in winter than in summer (Figure 3c). Whereas the abundance of denitrifying genes (*nirS*, *nirK*, and *nosZ*) showed same changing trend of nitrifying genes with the highest levels in the woodland among land use types, but the differences were not statistically significant between seasons (Figure 3e–g).

3.3 | Drivers over GHG emissions

All soil microenvironments (i.e., soil temperature [ST], SM, pH, and BD), soil chemical properties (i.e., DOC, SOC, TN, C:N ratio, NH₄⁺-N, and NO₃⁻-N), and soil microbial properties (i.e., total PLFAs, 18:1 ω 7c, nitrifying genes [AOA and AOB], and denitrifying genes [*nirS*, *nirK*, and *nosZ*]) directly controlled the response of GHG emissions (CH₄, CO₂, and N₂O; (Figure S5). Variation partitioning analysis also indicated that soil microenvironments, soil chemical properties, and their interactions explained much more of variation in CO₂ and CH₄ emissions than soil microbial properties (Figure 4a,b), while soil microbial properties explained more of variation in N₂O emission compared to soil microenvironments and chemical properties (Figure 4c).

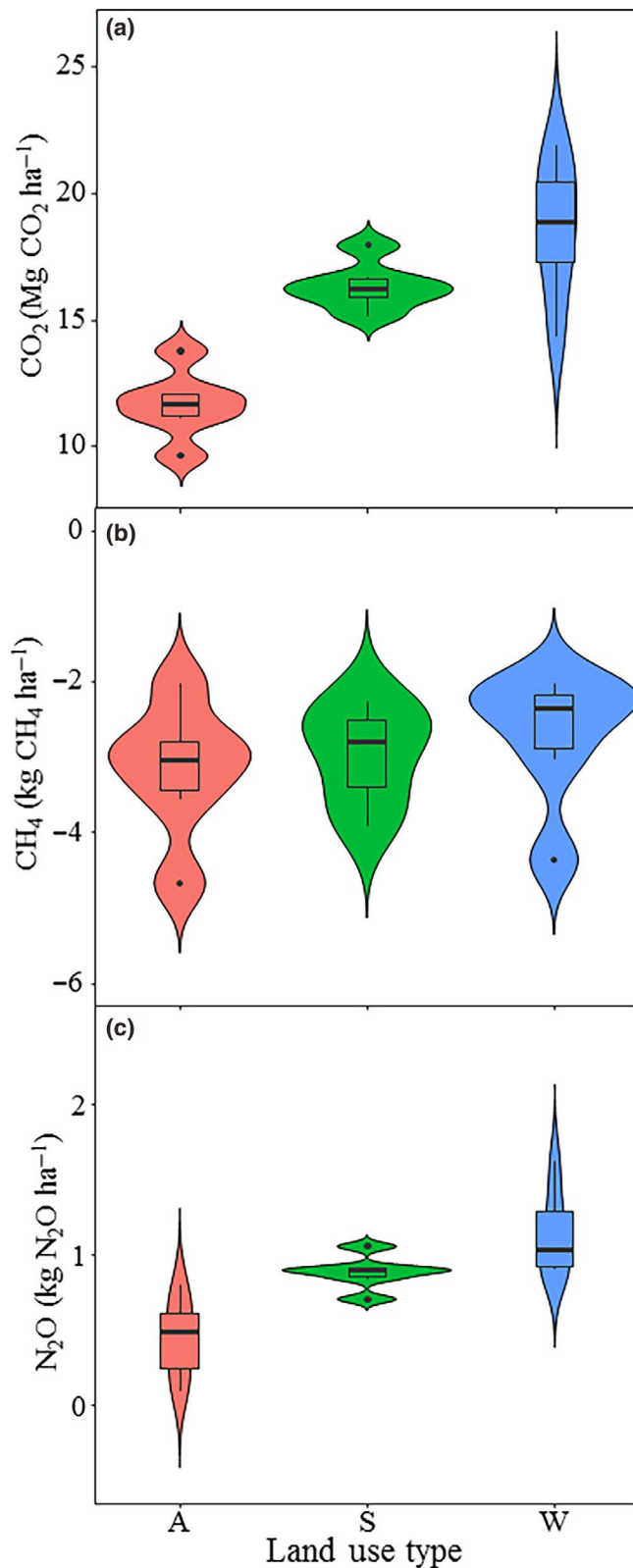


FIGURE 1 Annual CO₂ (a), CH₄ (b), and N₂O (c) emissions from different land use types. A, abandoned land; S, shrubland, W, woodland.

The SEM further illustrated that there was a different key factor in regulating the GHG emissions. Soil microenvironments exerted a negative effect on CO₂ emission, and a positive effect on CH₄

uptake. In contrast, soil chemical properties had indirect effect on CO₂ emission through the positive association with soil microbial properties (Figure 5a,b). Meanwhile, soil microenvironments and chemical properties indirectly affected N₂O emission via its effect on denitrifying genes (PC1) and nitrifying genes (PC2; Figure 5c). There were also strong correlations of soil microbial properties with soil microenvironments and chemical properties (Figure 5; Figure S4). Total PLFAs and 18:1 ω 7c were negatively correlated with the SM, BD, and NO₃⁻-N concentration, and positively correlated with almost soil chemical properties (Figure S4).

The multivariable stepwise regression analyses and analytic hierarchy process revealed the significant relationships between GHG emissions and potential drivers. Specifically, the CO₂ emission was positively associated with the ST, DOC, NO₃⁻-N, and total PLFAs, but marginally correlated with soil pH ($R^2 = 0.95$, Figure 6a; Figure S4a). The CH₄ uptake was positively associated with the ST, SM, and NH₄⁺-N, but negatively correlated with the DOC, and marginally related to the pH and BD, but it was not significantly dependent on the 18:1 ω 7c ($R^2 = 0.58$; Figure 6b; Figure S3b). The N₂O emission was positively associated with the TN, AOB, and C:N ratio, but negatively correlated with the ST, SOC, and *nosZ* ($R^2 = 0.49$; Figure 6c).

4 | DISCUSSION

Being partially supported hypothesis I, our results showed that afforestation increased soil CO₂ and N₂O emissions but did not significantly affect CH₄ uptake in the subtropical China. As expected, we found that soil CO₂ emission was higher in the woodland followed by the shrubland and the abandoned land (Table 1; Figure 1a), possibly due to high substrate availability. This point was supported by the positive relationship of soil CO₂ emission with DOC (Figure 6a), which was considered the most active form of fresh C. Higher plant productivity in afforested land could import C to soil in the form of litter and root exudates, and further stimulate CO₂ emission (Dube et al., 2009; Lange et al., 2015). Interestingly, we found significant positive correlations between with CO₂ emission and NO₃⁻-N concentration (Figure 6a), and that this agreed well with CO₂ emission being promoted at the NO₃⁻-N addition, and this finding indicated the promotion to root autotrophic respiration was greater than or equal to the inhibition to microbial heterotrophic respiration with high NO₃⁻-N concentration (Li et al., 2015). Thus, the greater soil substrate availabilities such as SOC, DOC, and NO₃⁻-N concentrations in the woodland were able to support greater microbial activities, and in turn could control CO₂ emission from the soil to atmosphere (Figure 5a; Iqbal et al., 2010; Straathof et al., 2014).

Indeed, we found that soil CO₂ emission was closely related to total PLFAs (Figure 2a) with a positive relationship between them (Figures 5a and 6a; Figures S3a and S5). This result was consistent with other studies showed that afforestation enhanced soil microbial activities, primarily because alteration in plant residue and root exudation inputs induced by afforestation could facilitate the available resources to microorganisms (Bradford, 2013; Lange et al., 2015).

Source of variation	CO ₂ (Mg CO ₂ ha ⁻¹)	CH ₄ (kg CH ₄ ha ⁻¹)	N ₂ O (kg N ₂ O ha ⁻¹)
Land use type	23.3 ^{***}	0.028	9.844 ^{***}
Season	643.65 ^{***}	19.939 ^{***}	13.145 ^{**}
Land use type × Season	17.66 ^{***}	4.37 [*]	3.565 [*]

TABLE 1 Significant of the effects of seasons, land use types and their interactions on GHGs based on the two-way ANOVA ($p < 0.05$; $**p < 0.01$; $***p < 0.001$; numbers are F-values)

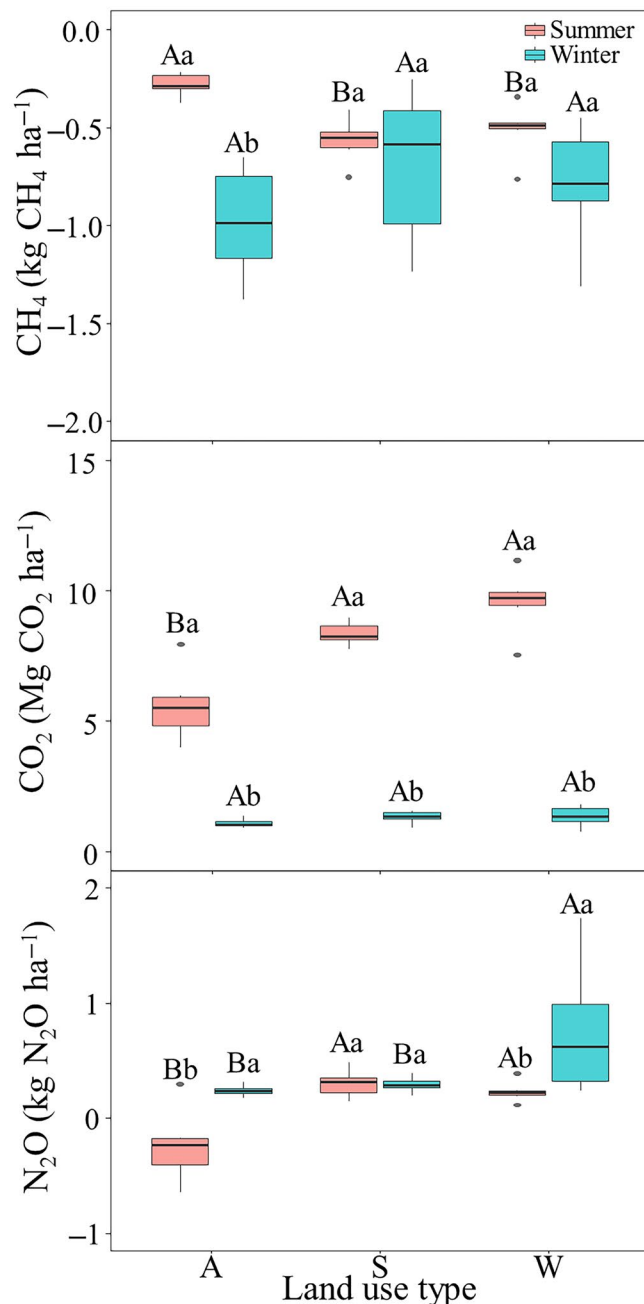


FIGURE 2 Seasonal variations in CO₂ (a), CH₄ (b), and N₂O (c) emissions under different land use types. Different capital letters indicate statistically significant difference at $p < 0.05$ between seasons within the same land use types. Different lowercase letters indicate statistically significant difference at $p < 0.05$ among different land use types within the same season. See Figure 1 for abbreviations

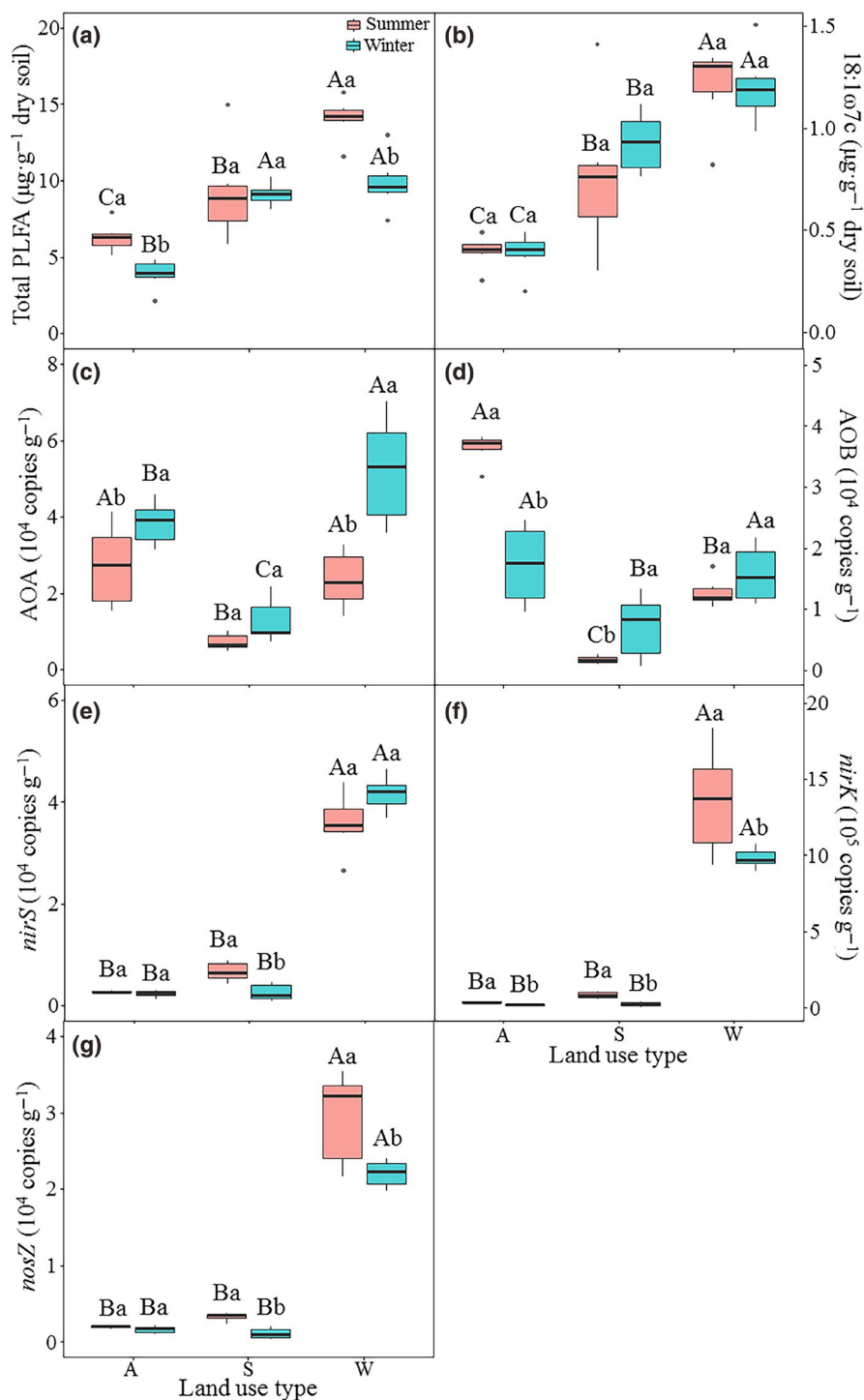
Major of studies have identified that soil pH was one of variables driving soil microorganisms (Fierer & Jackson, 2006; Jones et al., 2019), however, soil pH was not an explanatory variable for the soil microbial properties (Figure S4), possibly due to the pH range in this study could not have been as narrow and alkaline as in other studies (Brockett et al., 2012).

Meanwhile, soil respiration increased with enhanced ST (Figure 6a; Figure S5). To confirm this point, we observed a clear seasonal pattern of CO₂ emission with higher levels in summer compared to winter in all land use types (Table 1; Figure 2a), because substrate depletion by soil microbial thermal adaptation could enhance CO₂ emission on warming conditions (Davidson, 2020). We also found that SM played an important role in regulating soil CO₂ emission (Figures 5a and 6a), low moisture impeded soil respiration rate by reducing solute transport through soil and hence could force microorganisms into dormancy under dry conditions (Li et al., 2018; Manzoni et al., 2012, 2014). Additionally, marginally correlation of soil CO₂ emission with soil pH (Figure 6a) could be due to enhanced plant growth in association with increased soil pH, leading to the higher autotrophic respiration from living root and aboveground biomass (Chen et al., 2015).

In contrast, soil CH₄ uptake did not significantly vary with different land use types (Figure 1b), being inconsistent with the part of hypothesis I. These results were in line with Wachiye et al., (2020) that demonstrated CH₄ uptake did not show any differences across different land use types. However, higher 18:1 ω 7c was found in afforested compared to abandoned land (Figure 3b). Whereas, CH₄ uptake was not correlated with 18:1 ω 7c, regardless of land use types (Figures 4b, 5b and 6b; Figure S3b), which was according to our expectation. Moreover, we found the weak control of the soil BD over CH₄ uptake (Figure 6b), possibly due to the decreased soil BD leading to faster diffusion of CH₄ under higher porosity and pore status in the afforested lands (Tate, 2015). Previous studies manifested that soil CH₄ uptake could be limited by N availability in tropical soils (Hassler et al., 2015; Veldkamp et al., 2013). Our result coincided with it especially NH₄⁺-N concentration (Figure 6b), which might also be possibly limited by N availability in subtropical area. With the influence of aforementioned factors, CH₄ uptake should increase under afforestation. Nevertheless, CH₄ uptake was the net fluxes by methane oxidation and methane reduction, thus, the two processes in disparate soil conditions could be offset, leading to no significant differences in CH₄ uptake following afforestation.

The ability of soil CH₄ uptake in upland soils was not attributed to microbial attributes but closely related to soil environmental

FIGURE 3 Seasonal variations in soil microbial properties under different land use types, with total phospholipid fatty acids (PLFAs; a), 18:1 ω 7c (b), nitrifying genes (AOA, ammonia-oxidizing archaea; AOB, ammonia-oxidizing bacteria; c, d), and denitrifying genes (*nirS*, *nirK*, *nosZ*; e–g). See Figure 1 for abbreviations and Figure 2 for detail information



properties (Figures 4b, 5b and 6b). We observed that seasonal variations in CH₄ uptake showed parallel changing trend with CO₂ emission (Figure 2b). The increased temperature could stimulate soil CH₄ uptake (Figure 6a; Liu et al., 2020), leading to a considerable effect on seasonal variations on methane uptake. SM usually controlled over soil CH₄ oxidation through the diffusion of oxygen and the active of methanotrophs (Castaldi & Fierro, 2005; Malyan et al., 2016; Ni & Groffman, 2018). Surprisingly and rarely, soil CH₄ uptake rate increased with SM in our findings (Figure 6b), possibly because all microbes were inactive in summer, for the input of rain to severely

dry soil could enhance methanotrophic activities, leading to more CH₄ consumption than CH₄ production under the wetter soil conditions (Shvaleva et al., 2013; Singh et al., 1997).

Soil N₂O emission also increased following afforestation (Figure 1c) primarily caused by soil microbial properties (Figures 4c, 5c and 6c; Figure S5). Higher substrate availability enhanced the activities of soil microbes, causing an increasing in N₂O emission (Figure S5; Blagodatskaya et al., 2014). There were significant correlations among copies of the AOB and *nosZ* genes with N₂O emission (Figures 5c and 6c). Nitrification by either AOB (Lipschultz

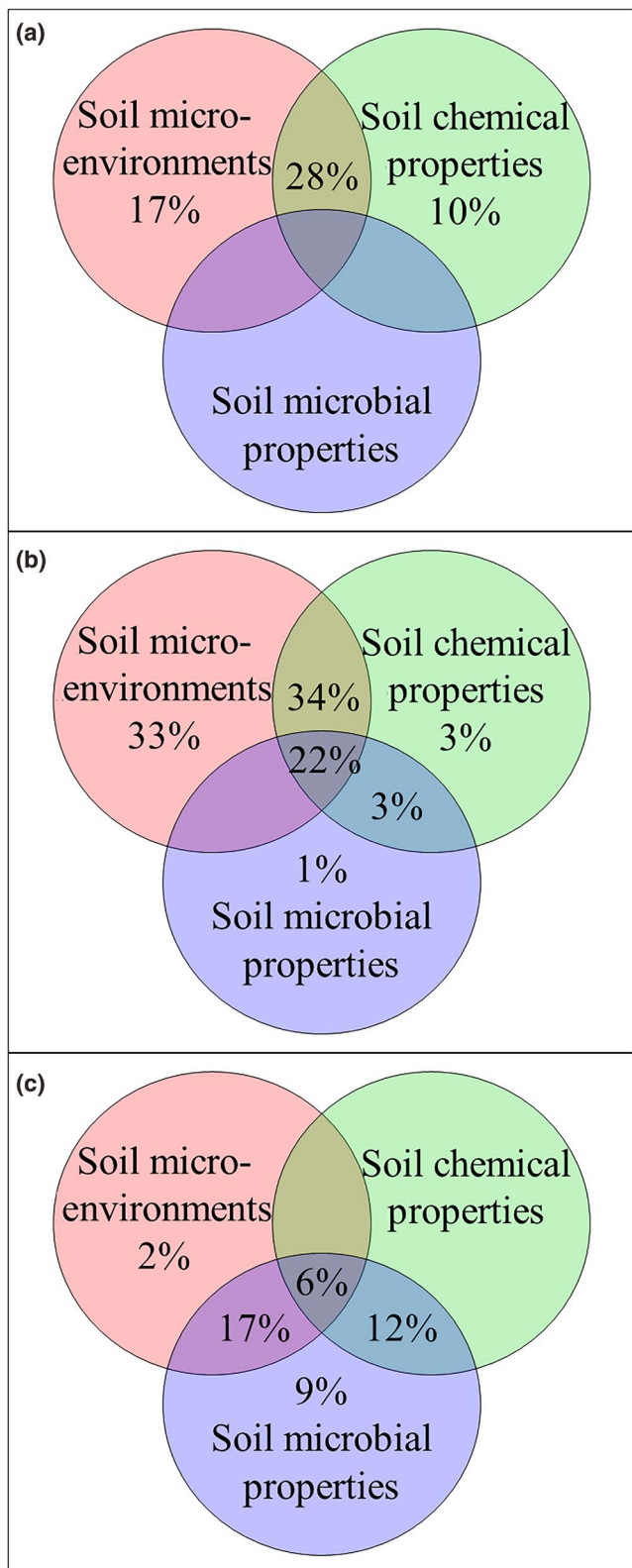


FIGURE 4 Relative contributions of soil microenvironments, chemical properties, and microbial properties to greenhouse gas emissions. Variation partitioning analysis was conducted to identify the variance in the CO₂ (a), CH₄ (b), and N₂O (c) emissions explained by these three groups of biotic and abiotic factors. Values <0 are not shown

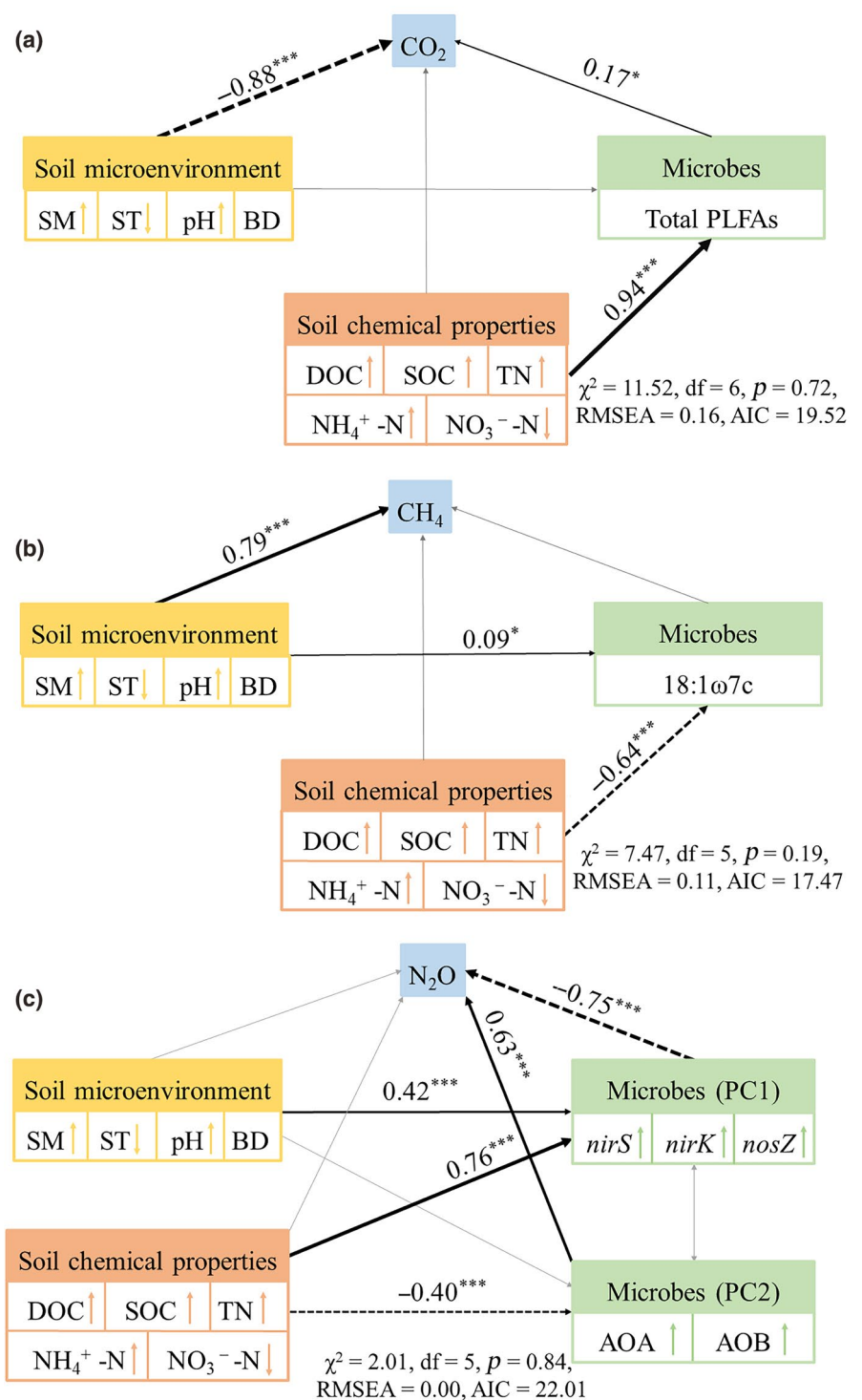
et al., 1981) or AOA (Kozłowski et al., 2014) produces N₂O emission. Interestingly, we found that the AOB, not AOA, was related to N₂O emission following afforestation (Figure 6c), due to the alkaline environment making AOB dominated in our study area. These results provided compelling evidences for soil pH has been recognized as a critical factor for niche separation of AOA and AOB, with AOA generally dominating in acid environments and AOB at neutral and/or alkaline pH (Prosser & Nicol, 2012). The *nosZ* gene associated with the final step of denitrification process (N₂O to N₂). Thus, it is possible that the high copies of *nosZ* gene can contribute for low N₂O emission (Pajares & Bohannan, 2016). The interaction of soil microbial/chemical properties totally explained 44% of the variation (Figure 4c), which is in agreement with earlier studies (Beaulieu et al., 2011; Hassler et al., 2017). Soil C was an important resource for the population of functional genes (Benanti et al., 2014), combined with an increased N availability accelerates soil nitrification (Yang et al., 2021) and denitrification process (Regan et al., 2017), which are both important for N₂O emission.

In addition, high soil DOC and NH₄⁺-N levels could enhance denitrifying genes, which would provide energy and benefit for soil N₂O emission (Song et al., 2011). We also found that soil micro-environment and soil chemical properties indirectly affected N₂O emission via its effect on nitrifying (AOA and AOB) and denitrifying genes (*nirS*, *nirK*, and *nosZ*) (Figure 5c). Actually, the activity and abundance of nitrifying and denitrifying genes could be stimulated by higher temperature to produce more N₂O (Li et al., 2020). The decreased SM declined nitrogen mineralization and provided favorable aerobic environment for nitrifying genes, conversely, the increased SM constructed favorable anaerobic environment for denitrifying genes (Davidson et al., 2008; Larsen et al., 2011). Thus, SM could be considered as an important regulation and thus predict the production pathway of soil N₂O emissions, although it was only selected into the model but have no significant differences (Figure 6c).

5 | UNCERTAINTIES AND IMPLICATIONS

Beyond our expectations, although with the increased substrate availability, variations in soil GHG emissions were inconsistent, with the changing tendency of the increased CO₂ and N₂O emissions, and no significant change in CH₄ uptake following afforestation. The response of soil CO₂ and N₂O emissions to afforestation was mainly regulated by changes in the soil microbial attributes (total PLFAs, AOB, and *nosZ*, respectively). Conversely, soil environmental/chemical properties (i.e., ST, SM, BD, pH, and NH₄⁺-N concentration), rather than soil microbial attributes, controlled over soil CH₄ uptake. Previous meta-analysis showed that afforestation increased CO₂ and CH₄ emissions, but had no effect on soil N₂O emission (Han & Zhu, 2020). Other studies found that afforestation significantly decreased soil CH₄ emission but had no impact on soil CO₂ and N₂O emissions in tropical regions, which was inconsistent with

FIGURE 5 Structural equation models (SEMs) depicting the direct and indirect effects of soil microenvironments, chemical properties, and microbial properties on greenhouse gases CO₂ (a), CH₄ (b), and N₂O (c) emissions. Single-headed arrows indicate the hypothesized direction of causation. The black solid arrows indicate the positive relationship, the black dashed arrows indicate the negative relationship, and the gray arrows indicate insignificant relationship. The arrow width is proportional to the strength of the relationship. Multiple-layer rectangles represent the first component from the PCA conducted for the soil microenvironments, chemical properties, and the first and second component from PCA for the soil microbial properties. The arrows "↑" and "↓" indicate positive and negative correlations between the variables and the first or second component from the PCA, respectively. The soil microenvironments include SM, ST, pH, and BD; the soil chemical properties include the DOC, SOC, TN, NH₄⁺-N, and NO₃⁻-N concentration; the soil microbial properties include the total PLFAs, 18:1ω7c, as well as denitrifying (PC1) and nitrifying genes (PC2). The numbers adjacent to the arrows are the standardized path coefficients. BD, bulk density; DOC, dissolved organic C; SM, soil moisture; SOC, soil organic C; ST, soil temperature; TN, total N; microbes, soil microbial properties. **p* < 0.05, ***p* < 0.01, ****p* < 0.001. See Figure 3 for abbreviations



our findings (Hergoualc'h & Verchot, 2011; van Lent et al., 2015). Definitely, some studies have attempted to synthesize the effects of land use change on soil GHG emission, but there are not consistent results which primarily depend on different study regions (Han & Zhu, 2020; Hergoualc'h et al., 2020). Thus, our case study provided insightful support for further studies to quantify the impact of afforestation on GHG emissions.

In spite of soil respiration increased soil CO₂ emission following afforestation in our finding, it does not mean we must deny

contribution of afforestation to the mitigation of GHG emissions. Trees sequestered CO₂ from atmosphere through photosynthesis offset the increase in soil CO₂ emission following afforestation (Wehr et al., 2016). Soil GHG emissions from land use change have been substantially underestimated because processes such as field management activities from shifting cultivation and large variability depending on forest age have not been considered (Arneeth et al., 2017), thus, future studies should consider it for the evaluation of integrated effects on GHG emissions, and also the long-term

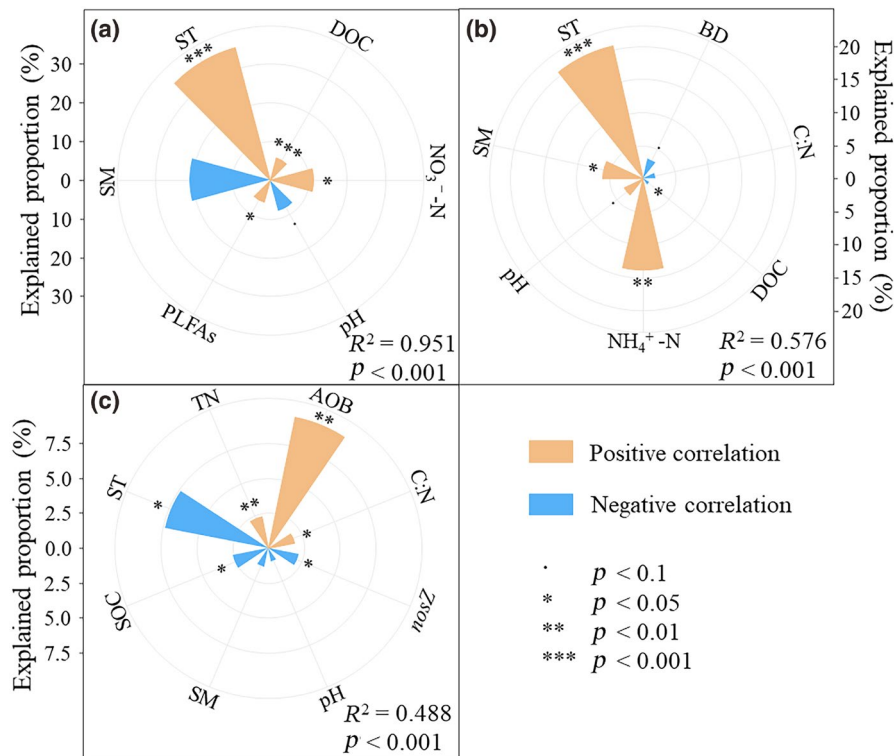


FIGURE 6 Proportions for the CO_2 (a), CH_4 (b), and N_2O (c) emissions explained by the biotic and abiotic variables. The values of the radiuses of the gray circles are shown as the vertical scales. The lengths of the bars are proportional to the radiuses of the gray circles and represent the explained proportions. The orange bars indicate positive correlations and blue bars indicate negative correlations between greenhouse gas emission and the explanatory variables, respectively. $p < 0.1$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. See Figures 3 and 4 for abbreviations

measurements are for better understanding on the underlying driving mechanisms. Nevertheless, our results are important for better understanding uncertainties in soil GHG emissions and identifying reliable and meaningful climate change mitigation interventions by informing the relevant policies.

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CONFLICT OF INTEREST

We declare that there are no conflicts of interest to this work.

AUTHOR CONTRIBUTION

Qiong Chen conducted the experiment with contributions from Chunyan Long and Jingwen Chen; Qiong Chen visualized data and wrote the manuscript; Xiaoli Cheng reviewed and edited the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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