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Asymmetric responses of functional microbes in methane and nitrous oxide emissions to plant invasion: A meta-analysis

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ABSTRACT

Plant invasion increases methane (CH_4) and nitrous oxide (N_2O) emissions, however, the changes of soil functional microbes governing CH_4 and N_2O emissions are poorly understood. We conducted a meta-analysis based on 112 published papers to explore soil functional microbes driving CH_4 and N_2O emissions under plant invasion. The result showed that CH_4 and N_2O emission rates were increased by 94.6% and 27.3% under plant invasion, respectively, and the increments of CH_4 and N_2O emission were ascended with time since invasion. The copies of soil functional microbes in the production of CH_4 (*mcrA*) and N_2O (*nirS* and *nirK*) were increased by 105.7%, 24.4%, and 55.1% under plant invasion, respectively, whereas the copies of soil functional microbes in the consumption of CH_4 (*pmoA*) and N_2O (*nosZ*) were decreased by 50.4% and 24.5%, respectively. Plant invasion influenced soil functional microbes via increasing above-ground biomass, soil organic carbon, total nitrogen, and microbial biomass carbon. This study highlighted the vital roles of soil functional microbes in CH_4 and N_2O emission rates under plant invasion. This study also revealed that the increased CH_4 and N_2O emission rates under plant invasion were time-dependent, which challenged the constant estimation of ecosystem warming potential under plant invasion in the long term.

1. Introduction

Currently, 17% of earth's surface (excluding Antarctica and glaciated Greenland) is endangered by non-native plants (Early et al., 2016). Plant invasion alters ecosystem functionality across terrestrial ecosystems. For instance, invasive plant increases soil carbon contents and alters greenhouse gas emissions (Qiu, 2015; Vila et al., 2011). A growing number of studies have revealed that the increment in greenhouse gas emissions offset the increases in ecosystem primary production under plant invasion (Bezabih et al., 2022; Qiu, 2015). Methane (CH_4) and nitrous oxide (N_2O) amplify global warming, with higher warming potential being 25 and 298 times that of carbon dioxide (CO_2), respectively (Yin et al., 2015). Thus, a comprehensive elucidation of the impacts of plant invasion on CH_4 and N_2O emissions and their underlying mechanisms are of particular importance in estimating changes in ecosystem services (e.g., the total warming potential) (Bellard et al., 2014; Qiu, 2015). The meta-analyses summarized CH_4 and N_2O emission rates under invasion (Qiu, 2015), and revealed dominant factors underlying the responses of CH_4 and N_2O emission rates to plant invasion from the perspective of climatic and edaphic factors (Bezabih et al., 2022). However, the microbial mechanism underlying these responses is unclear yet.

Plant invasion might alter CH_4 and N_2O emission rates through changing carbon and nitrogen contents, as well as soil physicochemical properties (Ehrenfeld, 2010; Liao et al., 2008). Invasive plants improve the net primary productivity of ecosystem, whereby more carbon and nitrogen consequently enter soil in the form of plant litter and root exudates in an ecosystem (Xu et al., 2014; Zhang et al., 2018). High levels of soil organic carbon and total nitrogen provide plenty substrates for the production of CH_4 and N_2O (Kim et al., 2020a; Yu et al., 2020).

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Furthermore, canopy shading effects and more soil organic detritus increase soil moisture, which is more likely to lead to an anaerobic condition for CH_4 and N_2O production (Alexandrou and Earl, 1998; Bu et al., 2019). Hence, we speculated that the invasive plants may lead to the increment of CH_4 and N_2O emission rates. Current researches mainly revealed the mechanisms underlying the changes in CH_4 and N_2O emission rates under plant invasion from the perspective of soil physicochemical properties (Gao et al., 2019; Yin et al., 2015; Yuan et al., 2015). Yet, the changes in CH_4 and N_2O emission under plant invasion are generally functioned by soil microbes, and it is necessary to reveal the mechanisms of changed CH_4 and N_2O emission from the microbial perspective.

The production of CH_4 and N_2O primarily involves biological processes. CH_4 produced by microbes accounts for 69% of total CH_4 (Conrad, 2009) and the N_2O from microbes can reach up to 90% of total N_2O (IPCC et al., 2021). The CH_4 emission rate is determined by the balance between the CH_4 production and consumption (Song and Liu, 2016). Methanogens (e.g., marker gene, *mcrA*) convert substrates (e.g., acetate and CO_2) to CH_4 (Kim et al., 2020a), whereas methanotrophs (e.g., marker gene, *pmoA*) oxidize CH_4 to CO_2 (Song and Liu, 2016; Yu et al., 2020). It is well known that N_2O is the byproduct of nitrification and denitrification, and the denitrification may contribute to the majority of N_2O in some ecosystems, e.g., wetlands. In denitrification, two nitrite reductase enzymes (marker genes: *nirS* and *nirK*) reduce nitrite to nitric oxide, and nitric oxide is subsequently reduced to N_2O via nitric oxide reductase (Kim et al., 2020b). Nitrous oxide reductase (marker gene, *nosZ*) governs the last step of denitrification, in which N_2O is reduced to dinitrogen under anoxic conditions (Kim et al., 2020b). It has been reported that the copies of *mcrA*, *nirK*, and *nirS* genes were increased, while the copies of *pmoA* and *nosZ* were lowered under exotic *Spartina alterniflora* compared with native plant counterparts (Gao et al., 2018; Lin et al., 2019; Zeleke et al., 2013; Zhang et al., 2013). The alteration of soil functional microbes may influence the production and consumption of CH_4, as well as the production and consumption of N_2O via denitrification, and ultimately influences CH_4 and N_2O emission rates (Wang et al., 2016; Yu et al., 2020). Therefore, we postulated that the asymmetric alterations of soil functional microbes shape the changes in CH_4 and N_2O emission rates under plant invasion. Surprisingly, the understanding of the changes in soil functional microbes in response to plant invasion remain quite rudimentary at the global scale. Consequently, it is crucial to quantify the effects of plant invasion on soil functional microbes, which can elucidate the microbial mechanisms governing CH_4 and N_2O emissions.

The changes in CH_4 and N_2O emission rates under plant invasion may be temporal (time-dependent phenomenon) (Geddes et al., 2014). This phenomenon may be attributed to that the impacts of invasive species on ecological processes vary over time since invasion (Strayer et al., 2006). For instance, the changes in species richness and biomass may differ with time since invasion (Dostal et al., 2013). Further, Xiang et al. (2015) found that soil organic carbon and total nitrogen contents under *Spartina alterniflora* invasion were increased over time since invasion. The changes in soil organic carbon and total nitrogen influence the functional microbial community compositions involving the carbon and nitrogen cycling (Zhang et al., 2009, 2013), thus alter the magnitude of alterations in CH_4 and N_2O emission rates. The effects of invasive species on ecosystems may be cumulative over time since invasion (Peltzer et al., 2010). Hence, we posited the changes in CH_4 and N_2O emission rates under plant invasion might be more severe with time since invasion. However, most of previous studies have ignored to take the invasion chronosequence into consideration (Chen et al., 2018; Geddes et al., 2014). Further, two previous meta-analyses have not tested the time-dependent changes in CH_4 and N_2O emission rates under plant invasion (Bezabih et al., 2022; Qiu, 2015).

To address the knowledge gaps on how plant invasion affects CH_4 and N_2O emission rates, a meta-analysis was performed to reveal microbial mechanisms underlying changes in CH_4 and N_2O emissions under plant invasion at the global scale, and to explore the dynamics of CH_4 and N_2O emissions with time since invasion. Specifically, the objectives of this study were to: (a) differentiate the responses of CH_4 and N_2O emission rates to plant invasion in different categories; (b) explore the microbial mechanisms underlying the responses of CH_4 and N_2O emission rates to plant invasion; (c) reveal how the responses of CH_4 and N_2O emission rates were altered with time since invasion.

2. Materials and methods

2.1. Data collection

We conducted a systematic review of published articles to examine the effects of plant invasion on CH_4 and N_2O emission rates. Articles were collected via ISI Web of Science database up to March 2022, using keywords: (invader* OR invasive* OR invasion* OR exotic species OR alien species OR nonnative species OR nonindigenous species) AND ((CH_4 OR methane* OR N_2O OR "nitrous oxide"*) OR (*mcrA* OR *pmoA* OR *nirS* OR *nirK* OR *nosZ*)).

We screened the articles according to following criteria: 1. 'Invasive species' refers to alien species with self-sustaining populations and the potential to spread beyond their native environments. Studies regarding the expansion or transplantation of native species were excluded; 2. The study should pairwise compare targeted variables (e.g., CH_4 emission rate, N_2O emission rate, and soil functional microbes) between invasive species and native species; 3. The study also included other specific details, such as soil organic carbon, total nitrogen, carbon:nitrogen ratio, above-ground biomass, stem density, microbial biomass carbon, soil temperature, moisture, salinity, pH, sulfate, etc; 4. Article contained the details on experimental sites, ecosystem types, invasive species, as well as experimental duration that lasted at least one growing season.

Following a thorough examination, 112 articles were eligible for the next analyses. For each case study, control (native species) and treatment (invasive species), means (X), standard deviations (SD) ($SD = SE * \sqrt{n}$), and sample sizes (n) of CH_4 and N_2O emission rates and environmental variables were directly extracted from either tables or graphs using GetData software. We also compiled latitude, longitude, climate zones, and invasive species from each study. The identification of ecosystem types, included forests, grasslands, freshwater, mangrove, salt marsh, and oligohaline marsh, was extracted from original articles.

Finally, a dataset was constructed from 112 studies (Fig. S1). We quantified the responses to explore the effects of plant invasion on CH_4 and N_2O emission rates and the associated microbial mechanisms based on this dataset. Additionally, we quantified the responses of CH_4 and N_2O emission rates under different conditions, by dividing invasive plants into different categories, e.g., climate zones, ecosystem types, plant life-forms (woody and herbaceous), and N-fixing traits [N-fixing plants including both symbiotic and associative fixers (e.g., *Myrica*, *Acacia*, and *Spartina*) and non-N-fixing plants, respectively]. N-fixing traits were identified based on plant trait database (TRY) (Kattge et al., 2020).

2.2. Data analyses

We calculated the effect size and conducted the statistical analyses with OpenMEE software (Wallace et al., 2017). The natural logarithm of response ratio (lnRR) was used to calculate the effect size of CH_4 and N_2O that can be easily compared with other studies, despite few negative CH_4 and N_2O fluxes, since there were robust results in effect size of CH_4 and N_2O using lnRR and Hedge'd (Fig. S2). A lnRR value of zero for targeted variable indicates that plant invasion has no impact on it. A positive lnRR value indicates that targeted variable is increased by plant invasion, and *vice versa*. The lnRR and variance (v_i) were calculated via Eqn. (1) and Eqn. (2), respectively.

$$\ln RR = \ln(X_t/X_c) = \ln(X_t) - \ln(X_c) \quad \text{Eqn(1)}$$

$$v_i = \frac{S_t^2}{N_t X_t^2} + \frac{S_c^2}{N_c X_c^2} \quad \text{Eqn(2)}$$

where X_t and X_c are means of control (native species) and treatment (invasive species), respectively; N_t and N_c are sample sizes of control and treatment, respectively; S_t and S_c are standard deviations of control and treatment, respectively.

Subsequently, we performed a weighted summation of all cases to reveal overall impact of plant invasion on CH_4 and N_2O emission rates and other variables. Various case studies have different backgrounds, therefore, a random-effects model was selected to determine the weight of each case (Castro-Diez et al., 2014). The weight (w_i) of observations and weighted natural logarithm of response ratio (RR_{++}) were estimated by Eqn. (3) and (4).

$$w_i = \frac{1}{v_i + \tau^2} \quad \text{Eqn(3)}$$

$$RR_{++} = \frac{\sum_{i=1}^{m} w_i \ln RR}{\sum_{i=1}^{m} w_i} \quad \text{Eqn(4)}$$

where m is number of observations between control and treatment, and τ^2 represents the between-study variance, which was determined by Restricted Maximum Likelihood method.

We also calculated 95% confidence interval (CI) of RR_{++} using Eqn. (5).

$$CI = RR_{++} \pm 1.96 S(RR_{++}) \quad \text{Eqn(5)}$$

where $S(RR_{++})$ is standard error of the weighted natural logarithm of response ratio (RR_{++}) that was estimated by Eqn. (6).

$$S\left(RR_{++}\right) = \sqrt{\frac{1}{\sum_{i=1}^{m} w_i}} \quad \text{Eqn(6)}$$

The significance of the weighted natural logarithm of response ratio was set at $p < 0.05$.

Finally, changes in targeted variables under plant invasion were transformed as $(e^{RR_{++}} - 1) \times 100\%$ (Liao et al., 2008). Additionally, to comprehensively understand how plant invasion affected CH_4 and N_2O emission rates through plant traits, soil properties, and soil functional microbes, thirteen variables with significant effects on CH_4 and N_2O emission rates were selected to build the conceptual framework. We constructed and tested the structural equation models initially, however, the models were not eligible. Alternatively, we used regression and correlation analyses after data normalization to quantify the relationships between variables.

Furthermore, the observations about CH_4 emission rate were categorized into <5 years, 5~10 years, 10~15 years, and >15 years, and the studies about N_2O emission rate were categorized into <5 years, 5~10 years, and 10~15 years. We separately calculated the weighted lnRR for each group. The relationship between the effect size of CH_4 emission rate and time since invasion was explored using linear mixed-effect model, as did for the effect size of N_2O emission rate.

3. Results

3.1. Effects of plant invasion on CH_4 and N_2O emission rates

On average, the weighted lnRR of CH_4 and N_2O emission rates were 0.67 (95% CI: 0.52~0.82) and 0.24 (95% CI: 0.11~0.37) under plant invasion, respectively (Fig. 1), with large variations among different categories (e.g., climate zones, ecosystem types, plant life-form, and N-fixing traits). CH_4 emission rate was increased under plant invasion in subtropical monsoon (0.80; 95% CI: 0.63~0.97), temperate monsoon (077; 95% CI: 0.09~1.63), temperate continental climates (0.66; 95% CI: 0.11~1.20) and mediterranean (0.63, 95% CI: 0.24~1.01), whereas was decreased in temperate marine (−0.34; 95% CI: 0.55~−0.14). CH_4 emission rate was increased in coastal wetlands, e.g., salt marshes (0.83; 95% CI: 0.66~1.00), oligohaline marshes (2.91; 95% CI: 1.38~4.43), and mangroves (0.73; 95% CI: 0.43~1.04) (Fig. 1a), whereas the responses of CH_4 emission rate was not significant in grasslands, forests, and freshwaters. Meanwhile, CH_4 emission rate under herbaceous invasion was significantly increased with the weighted lnRR of 0.79 (95%

Fig. 1. Effects of plant invasion on a) CH_4 and b) N_2O in different categories. Error bars represent 95% confidence intervals (CI). The weighted natural logarithm of response ratio is significantly different from zero when 95% CI does not overlap with zero. The number of observations for each group is given in brackets.

CI: 0.62~0.96). The invasion of N-fixing plant could increase CH_4 emission rate with the weighted lnRR of 0.81 (95% CI: 0.64~0.98).

Moreover, significantly increased N_2O emission rate was only observed under subtropical monsoon (0.34; 95% CI: 0.21~0.46) and temperate monsoon (0.64; 95% CI: 0.40~0.88) among climate zones (Fig. 1b). N_2O emission rate were only enhanced in salt marshes (0.19; 95% CI: 0.02~0.36) and grasslands (0.52; 95% CI: 0.24~0.80) (Fig. 1b). Herbaceous invaders increased N_2O emission rate by 0.29 (95% CI: 0.16~0.42), whereas the responses of N_2O emission rate were not significant in woody invasion. The N-fixing and non-N-fixing plants increased N_2O emission rate by 0.48 (95% CI: 0.16~0.79) and 0.17 (95% CI: 0.03~0.31), respectively.

3.2. Responses of soil properties, plant traits, and soil functional microbes to plant invasion

Plant invasion increased soil moisture, salinity, and sulfate concentrations, with the weighted lnRR of 0.14 (95% CI: 0.10~0.18), 0.16 (95% CI: 0.08~0.24), and 0.54 (95% CI: 0.42~0.66), respectively (Fig. 2a), whereas plant invasion didn't significantly affect soil temperature. Soil pH tended to be increased under invasion (0.01; 95% CI: 0.00~0.02). Further, plant invasion substantially increased soil organic carbon by 0.32 (95% CI: 0.25~0.39), total nitrogen by 0.16 (95% CI: 0.07~0.25), and soil carbon:nitrogen ratio by 0.14 (95% CI: 0.06~0.21) (Fig. 2b). For plant traits, plant stem density was decreased by −1.21 (95% CI: 1.69~−0.73) under plant invasion, while above-ground biomass was increased by 0.57 (95% CI: 0.43~0.72).

Soil microbial biomass carbon was increased by 0.23 (95% CI: 0.00~0.45) (Fig. 2c). Furthermore, the copies of *mcrA*, *nirK*, and *nirS* were increased by 0.72 (95% CI: 0.23~1.21), 0.44 (95% CI: 0.03~0.84), and 0.22 (95% CI: 0.04~0.39) under plant invasion, respectively, while the copies of *pmoA* (−0.41; 95% CI: 0.80~−0.01) and *nosZ* (−0.28; 95% CI: 0.54~−0.02) were decreased (Fig. 2d).

3.3. The influences of plant traits, soil physicochemical properties, and soil functional microbes on the CH_4 and N_2O emission rates

Plant invasion altered plant traits and soil properties, which consequently influenced microbes that directly affected CH_4 and N_2O emission rates (Fig. 3). Plant invasion increased the above-ground biomass. Soil moisture, sulfate concentrations, organic carbon, and total nitrogen were related positively to the higher plant above-ground biomass, and the coefficient values were 0.78 ($p < 0.05$), 0.84 ($p < 0.001$), 1.11 ($p < 0.001$), and 0.56 ($p < 0.05$), respectively. The lnRR of microbial biomass carbon was related positively to the changes of soil moisture with the coefficient of 0.20 ($p < 0.001$), soil organic carbon with the coefficient of 0.13 ($p = 0.09$), and total nitrogen with the coefficient of 0.01 ($p = 0.96$). The change of microbial biomass carbon was related negatively to sulfate concentrations with the coefficient of −0.59 ($p < 0.001$).

Furthermore, the copies of *mcrA* were increased (0.47; $p < 0.001$), and the copies of *pmoA* were decreased (−0.04; $p = 0.19$) with higher soil organic carbon. The copies of *nirK*, and *nirS* were significantly and positively correlated with the total nitrogen with the coefficient of 0.77 ($p < 0.001$) and 0.40 ($p < 0.001$), respectively. The copies of *nosZ* were related negatively to the higher total nitrogen with the coefficient of −0.40 ($p < 0.001$). The copies of *mcrA*, *nirK*, and *nirS* were linked positively with higher microbial biomass carbon, and the coefficient were 1.16 ($p < 0.001$), 1.24 ($p < 0.001$), and 0.62 ($p < 0.001$), respectively. The copies of *pmoA*, and *nosZ* were decreased with higher microbial biomass carbon, with the coefficient of −0.06 ($p = 0.28$) and −0.67 ($p < 0.001$), respectively.

The CH_4 and N_2O emission rates were increased with higher microbial biomass carbon contents, with the coefficient of 0.26 ($p = 0.14$) and 0.04 ($p = 0.88$), respectively. There were different responses of soil functional microbes governing CH_4 and N_2O emissions under plant invasion. The CH_4 emission rate was increased with higher copies of *mcrA* (0.77; $p < 0.001$) and lower copies of *pmoA* (−0.05; $p = 0.70$). The positive relationship was detected between N_2O emission rate and the copies of *nirK* and *nirS* with the coefficient of 0.45 ($p < 0.001$) and 0.53 ($p < 0.001$), respectively. The N_2O emission rate was decreased with higher copies of *nosZ* (−0.99; $p < 0.001$) (Fig. 3).

3.4. Responses of CH_4 and N_2O emission rates against time since invasion

The responses of CH_4 emission rate to plant invasion were changed

Fig. 2. Effects of plant invasion on a) soil physical and chemical properties, b) soil carbon and nitrogen contents, c) plant traits and soil microbial biomass carbon and d) functional microbes. Error bars represent 95% confidence intervals (CI). The weighted natural logarithm of response ratio is significant different from zero where 95% CI does not overlap with zero. The number of observations for each grouping of variables is given in brackets. AGB, MBC, SOC, TN and C/N is mean above-ground biomass, microbial biomass carbon, soil organic carbon, total nitrogen and carbon:nitrogen ratio, respectively.

Fig. 3. Conceptual framework on CH_4 and N_2O emission rates in response to plant invasion. Black and red lines are the positive and negative relationships, respectively. Solid and dashed lines represent significance and insignificance relationships, respectively, where statistically significant level is p-value ≤ 0.05. AGB, SOC, TN, MBC, N_2O, and CH_4 is mean above-ground biomass, soil organic carbon, total nitrogen, microbial biomass carbon, nitrous oxide emission rate, and methane emission rate, respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

over time since invasion, as did for N_2O emission rate (Fig. 4). In general, significant changes in CH_4 and N_2O emission rates under plant invasion were occurred after 5 years. When time since invasion was less than 5 years, plant invasion tended to increase the CH_4 emission rate (0.33, 95% CI: 0.36~1.01), but likely decrease the N_2O emission rate (−0.24, 95% CI: 0.56~0.09) (Fig. 4a–b).

In contrast, plant invasion significantly increased CH_4 and N_2O emission rates when time since invasion was longer than 5 years. While time since invasion ranged from 5 to 10 years, CH_4 and N_2O emission rates were increased by 0.95 (95% CI: 0.72~1.18) and 0.75 (95% CI: 0.47~1.03), respectively. When time since invasion ranged from 10 to 15 years, the weighted lnRR of CH_4 emission rate was 1.94 (95% CI: 1.54~2.34). In addition, the weighted lnRR of CH_4 emission rate was 3.13 (95% CI: 1.55~4.72) with time since invasion longer than 15 years (Fig. 4a). The weighted lnRR of N_2O emission rate was 0.54 (95% CI: 0.27~0.80) for 10~15 years, which was slightly smaller than the peak value for 5~10 years (Fig. 4b). Along invasion chronosequence, the lnRR of CH_4 emission rate increased over time since invasion with the slope being 0.19 (p-value <0.001, Fig. 4c). The relationship between the lnRR of N_2O emission rate and time since invasion was not significant (Fig. 4d).

4. Discussion

This work revealed the microbial mechanisms on the response of CH_4 and N_2O emission rates to plant invasion, and explored the changes of lnRR in CH_4 and N_2O emission rates with time since invasion. The asymmetric responses of soil functional microbes to plant invasion led to

Fig. 4. Changes of weighted natural logarithm of response ratio with invasion time. a) CH_4 and b) N_2O. Error bars represent 95% confidence intervals (CI). The weighted natural logarithm of response ratio is significant where 95% CI does not overlap with zero (a, b). The number of observations for each group is given in brackets. Changes in the natural logarithm of response ratios in CH_4 (c) and N_2O (d) emission rates with invasion time.

the greater production and smaller consumption capacity of CH_4 and N_2O. Here, we emphasized the roles of soil functional microbes to pinpoint the changes in CH_4 and N_2O emission rates under plant invasion on the basis of two previous meta-analyses (Bezabih et al., 2022; Qiu, 2015). Moreover, the impacts of plant invasion on CH_4 and N_2O emission rates were distinct at different invasion stages, and the increments of CH_4 emission increased with longer times since invasion.

4.1. Roles of soil functional microbes in CH_4 and N_2O emissions responding to plant invasion

It is an important ecological issue now that plant invasion changes CH_4 and N_2O emissions. Bezabih et al. (2022) suggested non-native plants increased N_2O emissions by 77.6% in grasslands. The N_2O emission rate under plant invasion was increased by 60.8 ± 32.2% in grasslands based on a bigger dataset (Fig. 1) that the result was compatible with an earlier meta-analysis (Bezabih et al., 2022). The changes in CH_4 emissions were also compatible with Bezabih et al. (2022). However, dominant factors underlying the responses of CH_4 and N_2O emission rates under plant invasion are distinct. Although Bezabih et al. (2022) stressed that climate and soil properties were responsible for the changes in CH_4 and N_2O emissions under plant invasion. We found that asymmetric changes of soil functional microbes under plant invasion could enhance the responses of CH_4 and N_2O emissions.

Microbes are important participants in carbon and nitrogen cycling and play a vital role in CH_4 and N_2O emissions (Kim et al., 2020a; Yu et al., 2020). Asymmetric changes in the copies of soil functional microbes in carbon cycling, stimulated methanogens and lowered methanotrophs, lead to a higher CH_4 emission rate under plant invasion. The production of CH_4 was increased with higher abundances of *mcrA* gene (Kim et al., 2020b). Gao et al. (2018) found the soil with lower copies of *pmoA* also possessed the higher CH_4 emission rates. The out-of-step oscillations between *mcrA* and *pmoA* result in the changes in CH_4 emission rate, which was also suggested in previous case studies (Song and Liu, 2016; Yu et al., 2020). In denitrification, the N_2O production was determined by two main nitrite reductases (in general, encoding genes *nirS* and *nirK*) (Zhang et al., 2013). Generally, the copies of *nirS* gene were one order of magnitude higher than that of *nirK* gene, and the denitrification rate was correlated with the number of *nirS* gene (Volesky et al., 2018). Several studies have documented microbes without the *nosZ* gene cannot complete the whole denitrification process, which result in N_2O as the end product (Gordon et al., 2020; Juhanson et al., 2017; Shan et al., 2021). Hence, N_2O emissions from denitrification are jointly determined by two nitrite reductases (*nirS* and *nirK*) and nitrous oxide reductase (*nosZ*) (Kim et al., 2020b; Soper et al., 2018). More copies of *nirS* and *nirK* in conjunction with less copies of *nosZ* leaded to the higher N_2O emissions under plant invasion.

Our results showed that plant invasion significantly increased the copies of methanogens (*mcrA*) and reduced the copies of methanotrophs (*pmoA*), which were consistent with Gao et al. (2018). The changes of soil microbes under plant invasion may be due to several reasons. Plants invasion supplies more available substrates (e.g., 'non-competitive' substrate trimethylamine) for methanogens through litter and root exudates than native plants (Gao et al., 2018; Xu et al., 2014). Liu et al. (2010) suggested that the abundance of methanogens (*mcrA*) was increased by 401.2% with the soil organic carbon rising from 7.2 g C kg^{-1} soil to 262.4 g C kg^{-1} soil, enhancing the CH_4 production. Invasive plants (e.g., *Spartina alterniflora*) also promotes the diffusion of CH_4 from soil to atmosphere by the aerenchyma tissue. Moreover, the abundance of methanotrophs (*pmoA*) was decreased by 50.4% under plant invasion (Fig. 2). Higher soil water content forms the anoxic condition that restrains CH_4 oxidation under plant invasion, since the methanotrophs are generally aerobes. Gao et al. (2018) found that the abundance of *pmoA* dropped from 8.82×10^8 copies g^{-1} soil to 5.26×10^8 copies g^{-1} soil, while the soil water content increased from 44.78% to 50.47%. Plant invasion increased the copies of *mcrA* and decreased the copies of *pmoA*, thus more methyl-coenzyme M reductase and less methane-oxidizing monooxygenase (Kim et al., 2020b), and eventually increased CH_4 emissions. As for denitrification, our results showed that plant invasion significantly increased the copies of soil functional microbes with nitrite reductases (*nirS* and/or *nirK*) and decreased the copies of soil functional microbes with nitrous oxide reductase (*nosZ*). The asymmetric changes of soil functional microbes (e.g., *nirS*, *nirK*, and *nosZ*), governing the N_2O emission rate, may be ascribed to the changes in soil properties and amounts of substrate. Plant invasion lowers soil bulk density and increases moisture by higher above-ground and litter biomass, as a result, the soil denitrifiers' community is altered (Aulakh et al., 1991; Yang and Chen, 2021). Cantarel et al. (2020) found that the abundance of *nirK* and *nirS* were increased by 37.83% and 34.07% under *Fallopia x bohemica* invasion, respectively. Plant invasion also increases soil nitrogen (e.g., total nitrogen, ammonium, and nitrate) contents (Liao et al., 2008), and different types of soil functional microbes exerted distinct responses. The abundances of *nirK* and *nirS* were increased with higher nitrogen concentrations (Yang et al., 2017). At the same time, the abundance of *nosZ* was decreased by 16.2% with the soil nitrogen contents increasing from 1.21 g N kg^{-1} soil to 1.25 g N kg^{-1} soil (Li et al. (2022). Moreover, plant invasion may import some secondary metabolites (e.g., tannins and phenolics) into soil (Coats and Rumpho, 2014). The abundance of *nosZ* was related negatively to these secondary metabolites with the coefficient of −0.51 for hydrolysable tannins and −0.25 for phenolics (Laanbroek et al., 2018). Collectively, the responses of soil functional microbes in denitrification under plant invasion, promoting the production of N_2O and inhibiting the consumption of N_2O to dinitrogen, ultimately stimulated N_2O emissions.

Plant invasion can regulate the structures of plant communities in recipient ecosystems and subsequently alter the abundance of soil functional microbes, which eventually impact CH_4 and N_2O emissions. Invaded plants typically possess a high leaf area index that can overshadow soil. Moreover, invaded plants with greater above-ground biomass and litter (Mueller et al., 2016; Vila et al., 2011) can increase soil water holding capacities (Alexandrou and Earl, 1998; Bu et al., 2019). Higher soil moisture changes the redox potential, and consequently alters microbial community compositions (Zhou et al., 2002) as well as the copies of methanogenic (*mcrA*), methanotrophic (*pmoA*), and denitrifying microbes (*nirK*, *nirS*, and *nosZ*) (Rankin et al., 2018; Zhang et al., 2018). Therefore, CH_4 and N_2O emission rates were ultimately altered. Meanwhile, invasive plants increased the copies of sulfate-reducing bacteria (Xia et al., 2015), and the methanogens were generally co-existed with sulfate-reducing bacteria whereby CH_4 production was increased under plant invasion (Yuan et al., 2014).

Additionally, the weighted lnRR of CH_4 emission rate to plant invasion tended to be greater in wetlands compared with those in grasslands. The different weighted lnRR between categories might be attributed to the various changes in plant traits (e.g., above-ground biomass) and soil properties (e.g., soil moisture, soil organic carbon, and total nitrogen) (Bezabih et al., 2022; Mueller et al., 2016; Qiu, 2015). Plant invasions generally resulted in more biomass in wetlands (Liao et al., 2008). The high levels of biomass increase soil organic carbon and total nitrogen (Xu et al., 2014; Zhang et al., 2018) that provide more substrates for microbes. Meanwhile, wetlands usually have higher soil moisture than grasslands, thus, a bit more soil water may lead to an anaerobic environment for microbes (Zhou et al., 2002), which eventually elicit differences in CH_4 emissions between wetlands and grasslands. Soil anaerobic environment can impact microbial community compositions, and thereby affect the production and oxidation of CH_4 (Bu et al., 2019; Vila et al., 2011).

4.2. The mechanisms of changes in CH_4 and N_2O emission rates with time since invasion

This study revealed different changes in CH_4 and N_2O emission rates with time since invasion. In general, microbial community compositions are time-dependent to plant invasion. Soil microbial biomass was increased with time since invasion; however, the changes in different microbes were not the same (Zhang et al., 2019a, 2019b). Although the abundance of *Methanosaetaceae* and *Methanosarcinaceae* were increased under *Spartina alterniflora* invasion (Yuan et al., 2016), the abundance of the acetotrophic family *Methanosaetaceae* was changed to a much higher degree than the facultative family *Methanosarcinaceae*. Therefore, different pathways of CH_4 production are altered to different extents. With time since invasion, CH_4 production rate was positively correlated with the relative abundance of facultative methanogens, but was negatively correlated with the relative abundance of acetotrophic and hydrogenotrophic methanogens. The dominant methanogenic archaea species shifted from the acetotrophic family *Methanosaetaceae* in one-year invaded plots to the facultative family *Methanosarcinaceae* in 13-year and 16-year invaded plots (Wang and Wang, 2017; Yuan et al., 2014). This may be caused by the competition between sulfate-reducing bacteria and methanogens (Yuan et al., 2015). Yuan et al. (2014) found that sulfate concentration under *Spartina alterniflora* invasion was increased from 28% (one-year of invasion) to 236% (16-years of invasion), and the abundance of sulfate-reducing bacteria was increased (Zeleke et al., 2013). With increases in the abundance of sulfate-reducing bacteria, CH_4 production in coastal salt marshes was increased from trimethylamine by 61~90% (King et al., 1983; Yuan et al., 2014).

Soil carbon contents can be cumulated after plant invasion (Peltzer et al., 2010), which might influence soil functional microbes. Xiang et al. (2015) found that *Spartina alterniflora* increased soil organic carbon in aggregates, and the accumulation rate of soil organic carbon was increased exponentially with time since invasion. The ratio of aerobic to anaerobic microbes was reduced with the increase of soil organic carbon in aggregates (Xiang et al., 2015; Zhang et al., 2014), thus, changes in microbial community compositions may further impact CH_4 and N_2O emissions. With invasion chronosequence of *Spartina alterniflora*, significantly positive relationships between CH_4 emissions and soil organic carbon were observed (Xiang et al., 2015). In addition, the increased abundance of methanogens with time since invasion also facilitated CH_4 emissions (Xiang et al., 2015). To sum up, the changes in soil properties were time-dependent under plant invasion and then the changes in microbes were also time-dependent, resulting in the different CH_4 and N_2O emissions with time since invasion.

4.3. Limitations

There are another pathways of N_2O production other than denitrification, e.g., soil nitrification. But seldom data are available on N_2O emission from nitrification, and soil functional microbes regulating the production and consumption of N_2O in nitrification have not been well documented other than AOA-*amoA* and AOB-*amoA* (Soper et al., 2018). Consequently, our study failed to take the nitrification process into account; thus, there were some limitations in fully elucidating the microbial mechanisms underlying N_2O emissions under plant invasion. The changes in soil functional microbes for N_2O emissions in nitrification under plant invasion remain to be further studied. Meanwhile, the abundance of soil functional microbes only reflects the metabolic potential other than actual activity. It is better that actual activity is incorporated into analyses in future studies. Furthermore, invasive species also increased net primary productivity of ecosystems and the carbon sequestration potential (Bu et al., 2019; Prater et al., 2006; Qiu, 2015). Hence, the joint consideration of the radiative forcing equivalents of CO_2, CH_4, and N_2O, as well as soil carbon dynamics in ecosystems are essential to comprehensively evaluate the impacts of plant invasion on ecosystem services in future research.

5. Conclusions

This study emphasized the microbial mechanisms underlying the changes in CH_4 and N_2O emission rates in response to plant invasion. Plant invasion significantly increased the abundance of *mcrA*, *nirS*, and *nirK*, but decreased the abundances of *pmoA* and *nosZ*. The production capacity of CH_4 and N_2O were increased, whereas the consumption capacities of CH_4 and N_2O were decreased under plant invasion. Furthermore, changes in soil physicochemical properties, such as moisture and organic carbon, influenced CH_4 and N_2O emission rates by altering soil microbial biomass carbon and soil functional microbes. Meanwhile, we found that the increments of CH_4 and N_2O emission rates tended to be increased with longer times since invasion, particularly for CH_4 emission rate. The roles of microbes in CH_4 and N_2O emissions are critical in understanding the changes in greenhouse gas emissions under plant invasion.

Author contributions

Zhaolei. Li and Naishun. Bu conceptualized the research plan. Yaozhong. Yao and Pinjie. Su collected the data. Yaozhong. Yao, Pinjie. Su, Jing. Wang, and Congke. Miao analyzed the data. Yanzhong. Yao, Yifu. Luo, Qiqi. Sun, Jiale.Wang, and Guohui. Zhang. visualized the data. Yanzhong. Yao and Zhaolei. Li wrote the manuscript. Zhaolei. Li, Naishun. Bu and Youtao. Song reviewed and edited later versions of the manuscript. Naishun. Bu and Zhaolei. Li provided the funding acquisition.

Declaration of competing interest

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.

Data availability

I have shared the link to my data at the Attach File step.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.soilbio.2022.108931.

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