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Climatic zone effects of non-native plant invasion on CH_4 and N_2O emissions from natural wetland ecosystems

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Abstract

Plant invasion markedly alters carbon and nitrogen cycles, and possibly influences the emission of greenhouse gases from wetlands in different climatic zones. In this study, data pertaining to 207 paired observational cases from studies on global ecosystems were retrieved for evaluating the effect of non-native plant invasion on the emission of CH_4 and N_2O from tropical/sub-tropical (TS) and temperate (TE) wetlands. The mean CH_4 emission rate from TS wetlands increased significantly from 337 to 577 kg CH_4 ha^{-1} yr^{-1} in sites populated with native and invasive plants, respectively, while that of TE wetlands increased from 211 to 299 kg CH_4 ha^{-1} yr^{-1} in sites populated with native and non-native plants, respectively. The increase in CH_4 emissions in invaded sites was possibly attributed to the increases in plant biomass, soil organic carbon (SOC), and soil moisture (SM). Plant invasion did not affect the emission of N_2O from TS wetlands, but reduced the emission of N_2O from TE wetlands, and this was primarily attributed to the depletion of NH_4^+ and NO_3^- in soils and the lower soil temperature in temperate regions. Plant invasion increased the global net CH_4 emissions from natural wetlands by 10.54 Tg CH_4 yr^{-1}, which varied across different climatic zones. The net increase in CH_4 emissions was 9.97 and 0.57 Tg CH_4 yr^{-1} in TS and TE wetlands, respectively. Our finding not only highlights that plant invasion exhibited strong stimulation effect on CH_4 emission in TS wetland and suppression effect on N_2O emission in TE wetland but also improves our current understanding of major controlling factors, which is vital to producing curving mechanisms.

Keywords: Climate zones; plant invasion; CH_4 emission; N_2O emission; wetland ecosystem

1. Introduction

Natural wetlands are a major contributor to carbon sequestration, and it is estimated that they play a crucial role in atmospheric CO_2 fixation (Schlesinger and Bernhardt, 2013). However, wetlands are the largest source of CH_4 worldwide, and contribute 100 to 231 Tg CH_4 annually (IPCC, 2007; IPCC, 2013). The proportion of CH_4 emitted from the northern, temperate, and tropical wetlands is estimated to be 34%, 5%, and ~60%, respectively (Wang et al., 1996). Cao et al. (1996) reported that the annual emission of CH_4 from natural wetlands is 92 Tg CH_4, of which the tropical wetlands release 51.4 Tg CH_4. Bartlett and Harriss (1993) estimated that the global CH_4 emission of wetlands is 109 Tg CH_4 yr^{-1}, and tropical and temperate wetlands account for 61% and 5% of the total emission, respectively. Previous studies have reported that the CH_4 fluxes of tropical wetlands are generally higher than those of temperate wetlands (Frank and Hein, 2021), which is possibly attributed to the warmer conditions and longer growth season in tropical regions (Hendriks et al., 2007; Jungkunst and Fiedler, 2007). The natural wetlands are presently under immense pressure with a dramatic increase in global consumption and the proliferation of invasive plants (Pegg et al., 2022), which represents a major global challenge in natural ecosystems with the potential to significantly modify greenhouse gas (GHG) emissions (Mantoani et al., 2021).

Numerous previous studies have found that plant invasion alters CH_4 and N_2O emissions in natural ecosystems (Cheng et al., 2007; Gao et al., 2019; Qiu, 2015; Yao et al., 2023). Yuan et al.

(2015) reported that the invasion of *Spartina alterniflora* increased the emission of CH_4 in a coastal salt marsh in China by 57–505%. The introduction of *Phragmites australis* into a temperate tidal marsh in Korea populated by the native *Suaeda japonica* increased the emission of CH_4 by up to 2000% (Kim et al., 2020). Another study reported that the invasion of *Typha* × *glauca* in a temperate coastal marsh in USA increased the emission of CH_4 by more than 50-fold compared to that induced by the native species, *Carex stricta* (Lawrence et al., 2017). Gao et al. (2019) showed that the invasion of *S. alterniflora* in the mangrove wetlands of China increased the emission of N_2O by 2500%. However, Grand and Gaidos (2010) observed that the emission of CH_4 from a tropical wetland in USA did not increase following plant invasion, and similar observations were reported by Jiang et al. (2009) in a sub-tropical wetland in China. Additionally, some studies have reported that the invasion of plant species reduced the emission of CH_4 and N_2O in tropical and sub-tropical wetlands (Sheng et al., 2021; Yin et al., 2015; Zhang et al., 2018). Bezabih et al. (2022) estimated that plant invasion increased CH_4 emissions in wetland ecosystems by 68% and N_2O emissions in grassland ecosystems by 78%. A recent meta-analysis by Yao et al. (2023) found that plant invasion in natural ecosystems enhanced CH_4 and N_2O emissions by 94.6% and 27.3%, respectively. As for regions, the net increase in CH_4 emissions from *S. apetala* invaded mangrove wetland in Hainan Island, China, was 0.04 Tg CH_4 yr^{-1} and accounts for 2.5% of the global mangrove wetland CH_4 emission (1.6 Tg yr^{-1}) (He et al., 2019). Gao et al. (2019) estimated that the total N_2O emission from invasive *Spartina alterniflora* wetlands in China covering 55181 ha was approximately 0.06 Tg N_2O yr^{-1}, and accounts for ~0.60% of the global N_2O emission (9.6–10.8 Tg N_2O yr^{-1}) (IPCC, 2013).

Plant invasion altered several biotic and abiotic factors, including soil properties (Stefanowicz et al., 2016; Tong et al., 2012; Xiang et al., 2015; Zhang et al., 2010; Zhou et al., 2015) and plant biomass (Su et al., 2020; Zhang et al., 2010; Zhou et al., 2015). Plant invasion can modify soil properties by increasing the deposition of litter and rhizodeposits (Liao et al., 2008; Ravichandran and Thangavelu, 2017). It has been reported that the quantity and chemical quality of litter and rhizodeposits differ among species (Chen et al., 2015; Zhu et al., 2020). Invading plants can also modify fundamental ecosystem processes, including the decomposition of organic matter and nitrogen fixation (Hawkes et al., 2005; Liao et al., 2008; Rice et al., 2004; Stefanowicz et al., 2016; Tharayil et al., 2013). Invading plants can affect the structure of vegetation by displacing the native species and altering the rates and patterns of nutrient cycling (D'Antonio and Vitousek, 1992; Ravichandran and Thangavelu, 2017), which alter the composition of soil microbes (Windham and Ehrenfeld, 2003). In turn, soil microbes are one of the key components that facilitate or inhibit plant invasion (Beckstead and Parker, 2003; Inderjit and van der Putten, 2010; van der Putten et al., 2013).

Plant invasion considerably increases the aboveground biomass (AGB), belowground biomass (BGB) (Lunstrum and Chen, 2014; Su et al., 2020; Zhang et al., 2010), and the diversity of soil microbes (Stefanowicz et al., 2016). A previous study by Angeloni et al. (2006) demonstrated that the invasion of the cattail species, *Typha* × *glauca*, nearly doubled the aboveground biomass (AGB) and belowground biomass (BGB) of sites in the temperate coastal wetland of the USA compared to those of sites populated with native sedges, rushes, and bulrushes. In Yancheng Natural Reserve in China, plant carbon storage following *S. alterniflora* invasion was increased by 16.9 and 1.4-fold compared with native *Suaeda salsa* and *P. australis*, respectively (Zhou et al., 2015). The increase in biomass production directly increases the organic carbon input of soils in the form of exudates and root debris for methanogenesis (Christensen et al., 2002). Zhang et al. (2019) reported that the increase in the SOC of a wetland populated with *S. alterniflora* was 5-fold higher than that of a wetland occupied by the native *S. salsa*. Xu et al. (2014) and Xiang et al., (2015) estimated that the invasion of *S. alterniflora* increased the SOC in a coastal wetland in China by 3-fold compared to that of the native plants, *S. glauca* and *Salix glauca*, and depended on the time of invasion (Zhang et al., 2010b). The increase in SOC due to an increase in plant biomass also provides more substrates for the production of CH_4 (Christensen et al., 2002; Zhao et al., 2017).

Up to date, however, there has been less work on the net GHG emissions induced by plant invasion at the global climatic zone level. In this study, the emission of CH_4 and N_2O from natural wetlands populated by invasive and native plants in different climatic zones was evaluated at the global level based on published peer-reviewed studies. The present study aimed to evaluate the effect of the invasion of non-native plants on the emission of CH_4 and N_2O in different climatic zones and identify the key factors that affect the annual emission of CH_4 and N_2O following plant invasion in different climatic zones. The study also aimed to estimate the effects of plant invasion on the net global budgets of CH_4. We hypothesized that plant invasion would more efficiently increase CH_4 emissions in tropical/sub-tropical wetlands than in temperate wetlands due to higher temperatures and a longer growth season.

2. Materials and Methods

2.1. Data retrieval

Scientific articles and reports in the Web of Science, Google Scholar, and China National Knowledge Infrastructure, published between December 1999 and May 2022, were searched in this study. The keywords used for the literature searches were "plant invasion" OR, "invasive" AND "non-invasive", "native" AND "non-native plant", "exotic" AND "non-exotic" plant species, "effects" OR "impacts" on "greenhouse gases", and "CH_4" OR "N_2O". A systematic review was conducted to avoid bias during data retrieval using the criteria described hereafter. Field observation studies not involving field manipulation or experimental studies at sites populated with invasive and native plants were included. Studies in which each of the treatments included at least three replicates were included. Studies in which the period of measurement covered one or more growth seasons were included. Studies in which additional treatments, including fertilization, burning, and warming were excluded. Studies addressing the effects of expanding or colonizing native species, such as woody or shrub encroachment were excluded. The densely invaded sites were considered for studies in which a site populated with native plants was compared to sites populated with varying densities of invasive species. Lastly, if a paper included data from multiple sites, the data from each site was regarded as separate and independent.

The Web Plot Digitizer tool (version 3.11; https://automeris.io/WebPlotDigitizer) was used to extract the data presented in the figures and plots in the articles. Both manual and automatic data-extraction algorithms were used after calibration with the corresponding values from the plots and images. Alternative descriptive sources, including the global invasive species database (GISD; http://www.issg.org), were used if the study did not specify whether the plants were invasive or native to the case study area. The data pertaining to CH_4 and N_2O fluxes were converted to kg ha^{-1} yr^{-1}. Auxiliary information, including the location (longitude, LON and latitude, LAT), climatic data (annual mean air temperature, MAT and mean annual precipitation, MAP), plant biomass, plant height, and soil properties such as soil pH, SOC, total nitrogen (TN), bulk density (BD), contents of NO_3^- and NH_4^+, soil temperature (ST), and soil gravimetric water content (SM), were additionally obtained. The mean values, standard deviation (SD), and sample sizes of all the variables in ecosystems populated with invasive and native species were retrieved. In c cases where the articles reported the standard error (SE) of the variables instead of the SD, the SD was determined using the formula: SE $\times\sqrt{n}$, where n represents the sample size. However, in case where the values of SD or SE were not reported, the SD was calculated as 1/10th of the mean (Luo et al., 2006). The authors of the relevant studies were contacted to obtain any useful information not published in the articles. If the authors were unable to provide the requested information, the data pertaining to soil properties were retrieved from the Harmonized World Soil Database, version 1.2 (FAO, 2012), based on the geographic coordinates of the study location. Data pertaining to the atmospheric deposition of nitrogen were retrieved from global nitrogen deposition maps (Ackerman et al., 2018). Data pertaining to the environmental factors were also extracted from published studies performed at the same experimental sites at which the CH_4 and/or N_2O fluxes had been measured. Data pertaining to the GHG fluxes and environmental variables were subjected to outlier detection using a simple empirical-based method in which values higher than 2 × SD or lower than the mean values were excluded (Williams and Baker, 2012).

2.2. Data organization and estimation of net CH_4 and N_2O emissions induced by plant invasion

Owing to spatial variations in the CH_4 and N_2O fluxes across wetland ecosystems in different climatic regions, the dataset was subcategorized into (1) tropical/sub-tropical (TS) wetlands and (2) temperate (TE) wetlands. The datasets obtained from tropical and sub-tropical regions were merged to increase the number of paired observational cases. The net emission of CH_4 induced by plant invasion was estimated for each species by calculating the difference in CH_4 fluxes between wetland sites populated with non-native plants and those occupied by native species. The fluxes were subsequently multiplied by the area invaded by each species. The regional and net global CH_4 emissions were then summed for each species based on their global distribution and geographic locations. However, net global N_2O emission estimations were not included in our present estimation because of the paucity of data about the area coverage of invasive plants that were considered for N_2O measurements in each region.

2.3. Data analyses

The effect size of the CH_4 and N_2O fluxes from wetlands in different climatic regions was estimated using Hedge's d (RRd) method. Hedge's d is a unit-free index that ranges from $-\infty$ to $+\infty$ (Qiu, 2015). This index weights cases according to the number of replicates, and the inverse of their variance is calculated as Xt/Xc < 0, where Xt and Xc represent the mean values of GHG fluxes from sites populated with invasive and native species, respectively (Wu et al., 2022). The index is not biased by small sample sizes or unequal variances (Koricheva et al., 2013). Large differences in the flux of GHGs between sites populated by invasive species and those occupied by native species indicate a greater effect size. Additionally, zero d-values indicate no difference, whereas positive and negative d-values indicate a general increase and decrease in the response variable, respectively, following plant invasion (Qiu, 2015). The effect of plant invasion on environmental factors was evaluated using natural logarithm-transformed response ratios (RRs). The RRs for a given case study were calculated using the following formulas:

$$\mathrm{RR} = \ln(\mathrm{Xt} \,/\, \mathrm{Xc}) \tag{1}$$

$$\mathrm{RRd} = \frac{(Xt - Xc) \times \mathrm{J}}{\sqrt{\frac{(Nt-1)St^2 + (Nc-1)Sc^2}{Nt+Nc-2}}} \tag{2}$$

where X_t and X_c represent the mean values of the selected GHG fluxes or environmental variables in sites populated with invasive and native species, respectively; Nt and Nc represent the sample sizes obtained from sites populated with invasive and native species, respectively; and St and Sc represent the corresponding SDs of sites populated with invasive and native species, respectively. J is a bias correction factor that was used to remove the small sample-size bias of the standardized differences of means. The value of J was calculated using the following formula:

$$J = 1 - \frac{3}{4(Nt+Nc-2)-1} \quad (3).$$

The RRs of the environmental factors, plant parameters, soil properties, and RRd of the GHG fluxes were calculated using the rma.mv function in the "metafor" package of R, version 4.2.1 (Balduzzi et al, 2019). A random-effects model was preferred because it accounts for the random component of variation in effect sizes among studies besides sampling error (Castro-Díez et al., 2014). The relationships of the environmental factors, plant parameters, and soil properties with the weighted RRd of CH_4 and N_2O fluxes following plant invasion in different climatic regions were calculated using the OriginPro 2022b software. The violin and box plots of plant biomass and CH_4 and N_2O fluxes in response to plant invasion in wetland ecosystems across different climatic regions were prepared using OriginPro 2022b. The relative importance of the environmental factors, plant parameters, and soil properties that affect the CH_4 and N_2O fluxes following plant invasion was determined by random forest analysis. The Random Forest algorithm is a machine learning technique that can handle both linear and nonlinear classification and regression problems with non-parametric data. This algorithm is robust to outliers and missing values, enabling the integration of complex data from various sources in high-dimensional spaces without overfitting (Hengl et al., 2015; Guo et al., 2015). For our study, the total number of observations used to predict CH_4 emissions in TS and TE wetlands was 104 and 82, respectively, while 36 and 10 observations were used to predict N_2O emissions in TS and TE wetlands, respectively. Any missing values for soil and environmental factors were imputed by using the nearest neighbor algorithm (Beretta and Santaniello, 2016; Troyanskaya et al., 2001; Tang and Ishwaran, 2017). Plant characteristics, including aboveground biomass, belowground biomass, stem density, and plant height were not included in the random forest model and SEM because of data scarcity. Finally, the predictors were ranked in order of importance according to the percent increase in mean square error (%IncMSE), and negative values of %IncMSE indicated a lack of importance (Liaw and Wiener, 2002). Additionally, structural equation model (SEM) was used to assess the multivariate effects of environmental factors and soil properties on regulating the responses of CH_4 and N_2O fluxes to invasive plants in TS and TE wetlands. We conducted a correlation matrix, and then "lavaan" packages of R were used for SEM. Maximum likelihood estimation was used to fit the SEM, and the model was evaluated based on the modification indices and goodness of fit after stepwise exclusion of non-significant paths. Fit indices including the degree of freedom (df), chi-square, probability level ($p > 0.05$), comparative fit index (CFI) closer to 1.0, and root mean squared error of approximation index (RMSEA < 0.05) were used to evaluate the adequacy of the SEM (Grace et al., 2012; Schermelleh-Engel et al., 2003; Zhou et al., 2022).

3. Results

3.1. Effects of plant invasion on the biomass of wetland plants and soil properties

Plant invasion significantly increased ($p < 0.05$) the AGB and BGB of the plants by 229% and 29%, respectively, in TS wetlands, and by 142% and 48%, respectively, in TE wetlands (Fig. 1). Plant invasion in TS wetlands significantly increased ($p < 0.05$) the SOC, TN, soil NH_4^+ content, and soil moisture (SM) content by 68%, 106%, 38%, and 17%, respectively, reduced soil bulk density (BD) and soil NO_3^- content by 9% and 17%, respectively (Fig. 2). Plant invasion significantly increased ($p < 0.05$) the soil TN by 18%, but did not affect SOC. In contrast, plant invasion decreased soil NO_3^- and NH_4^+ by 114% and 76%, respectively, in TE wetlands. Additionally, plant invasion increased SM in TE wetlands by 5% but decreased BD by 9%.

3.2. Effect of plant invasion on CH_4 and N_2O fluxes

The findings revealed that plant invasion significantly increased ($p < 0.05$) CH_4 fluxes by 62% in global wetland ecosystems (Fig. 3). The mean CH_4 flux in TS wetlands populated with native plants was 337 kg CH_4 ha^{-1} yr^{-1}, which increased significantly by 71% to 577 kg CH_4 ha^{-1} yr^{-1} following the invasion of exotic plants (Fig. 4). The invasion of non-native plants in TE wetlands increased CH_4 fluxes from 211 kg CH_4 ha^{-1} yr^{-1} in sites populated with native plants to 299 kg CH_4 ha^{-1} yr^{-1} in sites occupied by invasive species; however, the differences in CH_4 fluxes were not statistically significant. In contrast, there was no apparent difference in N_2O fluxes following plant invasion in TS wetlands. However, plant invasion significantly reduced N_2O fluxes in TE wetlands from 1.28 kg N_2O ha^{-1} yr^{-1} in sites populated with native plants to 0.60 kg N_2O ha^{-1} yr^{-1} in sites occupied by invasive species (Fig. 4).

3.3. Factors affecting the difference in CH_4 and N_2O fluxes following plant invasion in different climatic zones

There was a significant positive linear relationship between the weighted response ratios $(\overline{RRd})$ of CH_4 fluxes and nitrogen deposition (ND), the RR of SOC, the RR of TN, the RR of AGB, the RR of plant height, and the RR of SM in TS wetlands (Fig. 5). However, the $\overline{RRd}$ of CH_4 fluxes exhibited a negative linear relationship with the RR of soil NO_3^-. The $\overline{RRd}$ of N_2O fluxes exhibited a significant positive linear relationship with the RR of soil pH and the RR of soil NO_3^- in TS wetlands, but exhibited a negative linear relationship with the RRd of SOC and a quadratic relationship with the RR of SM. The $\overline{RRd}$ of CH_4 fluxes in TE wetlands also exhibited a quadratic relationship with the MAT, and RR of SM, and a negative linear relationship with the RR of ST (Fig. 6).

The results of random forest analysis revealed that the RR of SM, RR of SOC, and RR of TN were the most important factors that affected the CH_4 fluxes in TS wetlands (Fig. 7). The MAT, RR of SM, and RR of ST were identified as key factors that regulated the CH_4 fluxes in TE wetlands following plant invasion. Our results demonstrated that the RRd of SOC, RR of NO_3^-, and RR of SM were the most important factors that affected the N_2O fluxes in TS wetlands. The MAT, RR of SOC, and RR of SM were identified as the most important factors that influenced the N_2O fluxes in TE wetlands following plant invasion.

The structural equation model (SEM) explained 50% and 46% of the variance in the RRd of CH_4 fluxes in TS and TE wetland, respectively, while 61% and 83% of the variance in the RRd of N_2O fluxes in TS and TE wetlands, respectively (Fig. 8). Our SEM demonstrated that plant invasion-induced changes in soil properties and environmental factors consistently play a significant role in CH_4 and N_2O fluxes in TS and TE wetlands. The SOC, SM, and TN had the greatest role in regulating the responses of CH_4 fluxes to plant invasion in TS wetlands, while MAT, ST, and SM had a significant role in CH_4 fluxes in TE wetlands. For N_2O fluxes, soil NO_3^-, SM, and SOC had the greatest impact on the response of N_2O fluxes in TS wetlands, while MAT and SM had a substantial role in the response of N_2O fluxes in TE wetlands.

3.4. Plant invasion increased the net CH_4 emission of wetlands

Based on the area coverage of 15 key non-native plant species included in our datasets and their mean difference in CH_4 fluxes with native plant species (Table 1), we estimated plant invasion increased the net emission of CH_4 from TS and TE wetlands by 9.97 and 0.57 Tg CH_4 yr^{-1}, respectively. The annual increase in global net CH_4 emissions due to plant invasion was estimated to be 10.54 Tg CH_4.

4. Discussion

4.1. Alterations in CH_4 emission from TS wetlands following plant invasion

The findings revealed that plant invasion significantly increased the annual CH_4 emission of TS wetlands. Banik et al. (1993) and Das and Krishnakumar (2022) reported that the CH_4 emissions of tropical wetlands with invasive exotic plants exhibit considerable variations and are higher than those of wetlands populated with native plants. Zhou et al. (2022) found that plant invasion in sub-tropical wetlands of the Yangtze River in China increased CH_4 fluxes by 140–220%. The higher CH_4 fluxes of TS wetlands populated with invasive species are attributed to the following factors, which are described hereafter.

Firstly, the present study revealed that the invasion of exotic plants significantly increased the SM by 17%, and the $\overline{RRd}$ of CH_4 emission was correlated to the RR of SM in TS wetlands. However, the increase in SM following plant invasion was contrary to the findings of previous studies, which reported that plant invasion reduces SM in a coastal grassland ecosystem in California (Ehrenfeld, 2010; Potts et al., 2008). Wolf et al. (2004) suggested that the rapid rate of evapotranspiration in invasive grasslands is responsible for the reduction in SM and is primarily attributed to the higher plant biomass and longer duration of persistence (Dar et al., 2019; Wang et al., 2015; Wolf et al., 2004). In contrast, the higher SM of water-rich wetland ecosystems following plant invasion is attributed to the much higher coverage of invasive plants, which reduces the rate of evapotranspiration (Lin et al., 2013), and increased SOC that enhances soil water holding capacities (Bu et al., 2018; Bu et al., 2019). The increase in the SM lowers the diffusivity and concentration of oxygen, which favors for the formation of anaerobic environment for CH_4 production, and reduces the activity of aerobic microbes in the soils (Román et al., 2015; Rubol et al., 2013), which in turn increases the dissolved organic carbon and promotes the production of CH_4 by methanogens (Liu et al., 2019a; Liu et al., 2019b). The increase in the SM also alters soil microbial community compositions and increases the copies of methanogenic mcrA genes (Rankin et al., 2018; Yao et al., 2023; Zhang et al., 2018; Zhou et al., 2022), causing an increase in CH_4 production rates (McLain et al., 2002; Warner et al., 2017).

Secondly, the present study revealed a significant correlation between the $\overline{RRd}$ of CH_4 emission and the RRd of AGB. Within our dataset, AGB increased by 3.29-fold following plant invasion in TS wetlands, compared to sites populated with native species. Numerous previous studies reported that invasive plants are more prevalent in TS wetland than TE wetlands, with a rapid reproductive rate, complex root structure, and a very fast doubling capacity of plant biomass within a short period of time (Villamagna and Murphy, 2010; Hu et al., 1998; Owens et al., 1995). This is probably due to the high concentration of nutrients sourced from agricultural runoff, deforestation, insufficient wastewater treatment, and untreated sewage to wetland ecosystems (Villamagna and Murphy, 2010; Sun et al., 2021). In turn, eutrophication processes can exacerbate plant invasiveness (Sepulveda-Jauregui et al., 2018; Wassmann et al., 1992). The increase in AGB resulted in the generation of higher quantities of exudates and debris for methanogenesis (Chanton et al., 1997; Christensen et al., 2002; Repo et al., 2007). Angeloni et al. (2006) reported that the AGB and BGB at sites following the invasion of the cattail species, *Typha* × *glauca*, were nearly 2-fold the AGB and BGB of sites populated by native sedges, rushes, and bulrushes. Another study demonstrated that invasive plants produce deeper roots, which enhance the distribution of root exudates to deeper layers and increase the number of microsites for the production of CH_4 (von Fischer and Hedin, 2007). However, fast-growing invasive plants have lower lignin content (Arthur et al., 2012; Liao et al., 2008), and lower carbon:nitrogen and lignin:nitrogen ratios (Poulette and Arthur, 2012), which indicates that the litter produced by invasive plants tends to have fewer recalcitrant carbon compounds and is more efficiently converted into methanogenic substrates (Chanda et al., 2016).

Thirdly, the present study revealed that the $\overline{RRd}$ of CH_4 emission in TS wetlands was correlated to the RRd of SOC. The SOC increased by 68% on average in TS wetlands populated with invasive species. Gao et al. (2012) also reported that the increase in SOC in the tidal salt marshes of China is attributed to the well-developed rhizomes and increased BGB of the invasive species, *S. anglica* and *S. alterniflora*. Interestingly, Liu et al. (2019) found that even though they both have similar BGB, *S. alterniflora* can release more labile organic carbon in the rhizosphere than *P. australis*. In this study, we are unable to identify whether the increase in SOC was primarily attributed to the litters, rhizomes, or exudates of the invasive plants, and further studies are necessary in this regard. Yuan et al. (2015) reported that the rate of carbon sequestration in marshlands populated with *S. alterniflora* was 3.16 Mg C ha^{-1} yr^{-1} in the top 100 cm of the soil, which was 2.63 and 8.78-fold higher than that of marshlands populated with the native plants, *S. salsa* and *P. australis*, respectively. Liu et al. (2022) and Xia et al. (2021) observed that the increase in SM and net photosynthetic rate following the invasion of *S. alterniflora* in marshlands favored the accumulation of SOC. Previous studies have reported that the increase in SOC in TS wetlands accelerates the formation of an anaerobic environment and induces the generation of substrates for methanogenic archaea (Ajwang et al., 2021; Were et al., 2021; Zhao et al., 2017). Previous studies on a sulfate-rich salt marsh reported that an increase in the SOC following plant invasion also increased the abundance of methanogenic archaea and caused a shift in the dominant methanogens from the acetotrophic Methanosaetaceae in the bare tidal mudflat to Methanosarcinaceae that utilize methylated amines, which was possibly attributed to an increase in the concentration of trimethylamine (Yuan et al., 2014; Yuan et al., 2019).

Fourthly, the present study demonstrated that the $\overline{RRd}$ of CH_4 emission correlated with the RR of plant height, and this finding was consistent with the results obtained in studies by Ding et al. (1999), Zhou et al. (2016), and Qi et al. (2021). In this study, the height of the invasive plants in TS wetlands was 1.84 times higher than that of the native plants. In general, the tiller number and leaf area increased with an increase in plant height, which increased the formation of aerenchyma and the release of CH_4 into the atmosphere (Bansal et al., 2020; Granse et al., 2022; Schimel, 1995; Struik et al., 2022). The results of these studies agree with the aforementioned finding of the present study, which revealed that the deeper roots of invasive plants are more efficient in releasing the CH_4 produced in the deeper soil layers of wetlands.

Fifthly, the present study revealed that the $\overline{RRd}$ of CH_4 emission in TS wetlands was positively associated with the ND, and peak CH_4 emission was determined to be approximately 15 kg N ha^{-1} yr^{-1}. It has been reported that the deposition of nitrogen improves plant growth and litter quality by increasing the nitrogen availability of the soil (Iversen et al., 2010; Liao et al., 2008), and stimulates microbial reproduction (Bai et al., 2010; Chen et al., 2011; Le Quéré et al., 2009; Thomas et al., 2012; Treseder, 2008). This in turn enhances the conversion of residues into SOC and substrates for the utilization of methanogens by better optimizing microbial stoichiometries (Brown et al., 2014). In this study, the growth of invasive plants was found to be more effectively stimulated by the ND, and this could be attributed to the increase in the root biomass of invasive plants, which resulted in the uptake of nitrogen from the deeper layers of the soil where the roots of native species are unable to reach (Luo et al., 2006). Additionally, it has been reported that an increase in microbial biomass can increase net nitrogen bio-fixation and the accumulation of nitrogen in soils (Knops et al., 2002).

4.2. Response of CH_4 emissions to plant invasion in TE wetlands

Unexpectedly, the present study revealed that plant invasion did not increase the emission of CH_4 from TE wetlands. As discussed above, or AGB although plant invasion also increased plant biomass in TE wetlands, however the increase rate was far lower than that in the TS wetland (142% vs. 229% for AGB). Previous studies have shown that differences in plant size, leaf area allocation, shoot allocation and growth rate between invasive plants and native plants in TS regions are larger than those in TE regions (Van Kleunen et al., 2010). In the present study, it is likely that the reduced soil inorganic N availability in invaded sites as well as short growth season in the temperate region limits invasive plant growth. The study further revealed that increased plant biomass did not alter the SOC of TE wetlands. These findings indicated that plant invasion did not effectively increase the availability of substrates for methanogens. The results demonstrated that the significant increase in the ABG and BGB was not correlated with the apparent lack of changes in the SOC following plant invasion. This could also be attributed to the fact that the relatively lower temperatures in the temperate region suppress the conversion of plant litter into SOC (Zhang et al., 2023). The meta-analysis study by Ouyang et al. (2017) demonstrated that the rate of decomposition of plant roots decreases with increasing latitudes and decreasing temperatures in saltmarsh ecosystems. A previous study revealed that the rate of mineralization of lignocellulose in *S. alterniflora* was positively correlated with temperature (Benner et al., 1986). The phenomenon could also be attributed to the relatively low water tables in TE wetlands such as peatlands, the levels of which generally range from 20 to >50 cm below the surface owing to low precipitation (Amaral and Knowles, 1994). This results in the formation of an aerobic environment near the surface of the soil, which favors the decomposition of exudates and plant litter. Zhang et al. (2023) demonstrated that the microbial necromass in invaded wetlands increases from the temperate region to the tropical region, and in tropical wetland soils, is 1.3–5.0 times greater than that in temperate wetland soils.

Another possible explanation for the lack of a significant effect of plant invasion on CH_4 emissions in the TE wetlands might be due to the relatively lower response of the SM. In the present study, plant invasion increased SM by 17% in the TS wetland and only by 5% in TE wetland. This indicated that plant invasion did not efficiently alter the SM in the TE wetland. We also found that the response of CH_4 fluxes in TE wetland was quadratically correlated with MAT, with an optimum value of approximately 10–15°C. In this meta-analysis, however, MAT in 57% of the experimental sites of TE wetlands was higher or lower than the above optimum value, which may partly weaken the response of CH_4 fluxes to plant invasion. Further field measurements are necessary for evaluating the effect of invasive plants on the emission of CH_4 in TE wetlands, especially in inundated freshwater TE wetlands.

4.3. Effect of plant invasion on the emission of N_2O from wetlands in different climatic zones

Unexpectedly, the findings of the present study demonstrated that plant invasion significantly reduced the emission of N_2O from TE wetlands; however, this was not observed in TS wetlands. Several studies have previously demonstrated that the emission of N_2O in wetlands populated with non-native plants is lower than that in wetlands occupied by native species (Bezabih et al., 2022; Wang et al., 2016; Yin et al., 2015; Yuan et al., 2015). This could be attributed to the fact that the concentrations of soil NO_3^- in TS and TE wetlands are generally below the threshold value necessary for denitrification, which subsequently suppresses the production of N_2O during denitrification (Dobbie and Smith, 2003). The present study demonstrated that plant invasion in TE wetland reduced the RRs of soil NH_4^+ and NO_3^- and significantly decreased the concentration of NH_4^+ and NO_3^- in soils by 76% and 114%, respectively, which was primarily attributed to the increased uptake of nitrogen by the invasive plants. Previous studies have demonstrated that the decrease in the production of N_2O is attributed to the depletion of inorganic nitrogen in soils, especially NH_4^+, following plant invasion (Yang and Silver, 2016; Zhu et al., 2013). In contrast, plant invasion increased the SM in this study, which could have accelerated the anaerobic conditions and reduced the production of N_2O during denitrification in the subsurface layer of TE wetlands. Yuan et al. (2015) observed that marshland ecosystems populated by invasive *S.*

alterniflora adsorb atmospheric N_2O primarily due to accelerated denitrification by increased SOC. Therefore, the findings of the present study suggest that plant invasion can lower the emission of N_2O from TE wetlands.

4.4. Plant invasion increased the net CH_4 emission from wetlands

The net emission of CH_4 was determined based on the 15 key non-native wetland plant species in our dataset and their coverage areas. The summed coverage areas of the non-native exotic species were 10.10 and 20.92 Mha in TS and TE wetlands, respectively (Table 1), and the non-native exotic plants covered a total global area of 31.02 Mha. The study by Zedler and Kercher (2005) reported that the total area of TS and TE wetlands is 743 and 536 Mha, respectively. The ratio of the area populated with invasive species to the total area was determined to be 1.36% and 3.90% for TS and TE wetlands, respectively. This finding indicated that plant invasion occurs more frequently in TE wetlands than in TS wetlands.

In this study, the global net increase in the emission of CH_4 from wetlands following plant invasion was estimated to be 10.54 Tg CH_4 annually, and varied across different climatic regions, with the annual net increase in the emission of CH_4 from TS and TE wetlands being 9.97 and 0.57 Tg CH_4, respectively. Previous studies have suggested that tropical wetlands are the main source of atmospheric CH_4. Seiler and Conrad (1987) estimated that tropical wetlands release 81% of the total CH_4 emission of global wetlands, while Cao et al. (1996) and Masamba et al. (2015) reported that tropical wetlands contribute 56% and 50–60%, respectively, of the total global CH_4 emission. The present study indicated that plant invasion considerably increased the emission of CH_4 from TS wetlands. Although the findings indicated that the invasion of exotic plants induces the emission of CH_4 on a global scale, the estimates obtained herein have certain limitations, which are described hereafter. The first limitation was the scarcity of data, especially accurate data pertaining to the coverage area of the invasive plants. Therefore, the increase in the emission of CH_4 following plant invasion was possibly underestimated in this study. Secondly, the differences in the sampling times and frequencies of the GHG fluxes may have affected the accuracy of the findings (Godwin et al., 2013). Thirdly, the scarcity of field studies in Africa, South America, South Asia, and Southeast Asia may have skewed the results of global estimation.

5. Conclusions

Overall, the present study indicated that plant invasion considerably increased the emission of CH_4 from TS wetlands, which was primarily attributed to the increase in the AGB of plants, SOC, and SM. In contrast, plant invasion significantly reduced the emission of N2O from TE wetlands, which was possibly attributed to the reduction in the content of NH_4^+ and NO_3^- in soils. The net increase in the emission of CH_4 following plant invasion was estimated to be 10.54 Tg CH_4 yr^{-1} in global wetland sites, with the global net increase in CH_4 emissions being 9.97 and 0.57 Tg CH_4 yr^{-1} for TS and TE wetlands, respectively. The findings suggested that non-native plants efficiently invaded and stimulated the emission of CH_4 in tropical and sub-tropical wetlands, compared to native plant species. Thus, it seems necessary to control the invasion of non-native plants for the mitigation of CH_4 emissions in TS wetlands.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Table 1 Net CH_4 emissions of natural wetlands in different climatic zones following plant invasion

Climatic zone	Invasive plant	Invaded area (ha)	ΔCH_4 (kg CH_4 ha^{-1} yr^{-1})	Net CH_4 emission (Gg CH_4 yr^{-1})	Reference
Tropical	*Psidium cattleianum*	384,000	-223.87	-85.97	Barbosa et al. (2016)
Tropical	*Eichhornia crassipes*	4,000,000	2534.97	100,139.88	Zimdahl (2018)
Tropical	*Nelumbo nucifera*	308	173.45	0.05	Das and Krishnakumar (2022)
Tropical	*Cyperus papyrus*	4,000,000	11.00	44.00	PROTA4U database
Tropical	*Typha domingensis*	692	1816.51	1.26	Trama et al. (2009)
Sub-tropical	*Spartina alterniflora*	465,214	206.31	95.98	Li et al. (2022)
Sub-tropical	*Sonneratia apetala*	3,800	143.31	0.00	Jiang et al. (2019)
Sub-tropical	*Laguncularia racemosa*	1,145	-248.79	-0.28	Wang et al. (2020)
Sub-tropical	*Deyeuxia angustifolia*	1,240,000	-179.17	-0.22	Li et al. (2011)
Sub-total		10,095,158		9,973.29	
Temperate	*Betula papyrifera*	1,910,000	-24.09	-46.01	Shahzad et al. (2022)
Temperate	*Phragmites australis*	10,000,000	179.05	1790.50	Baibagyssov et al. (2020)
Temperate	*Typha species*	38,648	577.61	22.32	Svedarsky (2014)
Temperate	*Phalaris arundinacea*	201,634.60	-1139.42	-229.75	Greenstein et al. (2021)
Temperate	*Phragmites australis*	20,000	90.80	1.82	Baibagyssov et al. (2020)
Temperate	*Sasa* sp.	8,750,000	-110.61	-967.84	Agata (1980)
Sub-total		20,920,282	-	571.04	
Total		31,015,440	-	10,544.42	

ΔCH_4, difference in CH_4 fluxes of wetlands populated by non-native and native plants.

Figure captions

Figure 1: Violin and box plots depicting the AGB and BGB in tropical/subtropical (TS) and temperate (TS) wetlands populated with native and non-native plants. The white boxes represent the mean values. The black and white dots represent 95% confidence intervals (CIs).

Figure 2. Effect of the invasion of non-native plants on soil properties and plant biomass in tropical/subtropical (TS) and temperate (TS) wetlands. The values represent the mean ± 95% CI of the weighted RRs between wetlands populated by non-native plants and those occupied by native species. The number of paired observations is depicted beside the properties, and the asterisks indicate significant differences at $p < 0.05$. SOC, soil organic carbon; TN, total soil nitrogen; BD, soil bulk density; NH_4^+, soil NH_4^+; NO_3^-, soil NO_3^-; pH, soil pH; and SM, soil moisture; AGB, aboveground biomass; BGB, belowground biomass; PT, plant height.

Figure 3. Violin and box plots depicting the RRd of CH_4 and N_2O fluxes following the invasion of non-native plants in natural wetlands. The white boxes represent the mean values. The black dots represent the 95% CIs, and the numbers within the brackets represent the number of samples.

Figure 4. Violin plots of the CH_4 and N_2O fluxes in wetlands populated by native and non-native plants. The white boxes represent the mean values. The black dots represent the 95% CIs, and the numbers within the brackets represent the number of samples.

Figure 5. Relationships between the RRd of CH_4 (red triangles) and N_2O (black triangles) fluxes with the climatic factors, ND, RRs of soil properties, and RRs of AGB and plant height in

tropical/subtropical (TS) wetlands following the invasion of non-native plants. MAT, mean annual air temperature; MAP, mean annual precipitation; ND, nitrogen deposition; RR-SOC, RR of soil organic carbon; RR-TN, RR of soil total nitrogen; RR-AGB, RR of aboveground biomass; RR-PT, RR of plant height; RR-pH, RR of soil pH; RR-BD, RR of soil bulk density; RR-NO_3^-, RR of soil NO_3^-; RR-NH_4^+, RR of soil NH_4^+; and RR-SM, RR of soil moisture; RR-ST, RR of soil temperature.

Figure 6. Relationships between the RRd of CH_4 (red triangles) and N_2O (black triangles) fluxes with the climatic factors, ND, RRs of soil properties, and RRs of AGB in temperate (TE) wetlands following the invasion of exotic plants. MAT, mean annual air temperature; MAP, mean annual precipitation; ND, nitrogen deposition; RR-SOC, RR of soil organic carbon; RR-TN, RR of soil total nitrogen; RR-AGB, RR of plant aboveground biomass; RR-BD, RR of soil bulk density; RR-NO_3^-, RR of soil NO_3^-; RR-pH, RR of soil pH; RR-SM, RR of soil moisture; and RR-ST, RR of soil temperature.

Figure 7. Identification of the main predictors of the RRd of (a) CH_4 fluxes of tropical/subtropical wetlands, (b) CH_4 fluxes of temperate wetlands, (c) N_2O fluxes of tropical/subtropical wetlands, and (d) N_2O fluxes of temperate wetlands by random forest analysis. The %IncMSE represents the importance of the main predictors, and negative values of %IncMSE indicate a lack of importance. The yellow bars depict the key predictors that significantly affected the CH_4 and N_2O fluxes of wetlands in different climatic zones. MAP, mean annual precipitation; MAT, mean annual air temperature; ND, N deposition; RR_SM, RR of soil moisture; RR-SOC, RR of soil organic carbon; RR_TN, RR of total nitrogen; RR-pH; RR of soil pH; RR-ST, RR of soil temperature; RR-NO_3^-, RR of NO_3^-; RR-BD, RR of soil bulk density.

Figure 8. Structural equation models (SEMs) showing the effects of biotic and abiotic factors on the weighted response ratios (RRd) of CH_4 fluxes in (a) tropical/sub-tropical regions and (b) temperate regions, and RRd of N_2O fluxes in (c) tropical/sub-tropical regions and (d) temperate regions. Dark cyan and black arrows refer to negative and positive correlations, respectively. Dotted lines denote insignificant paths ($p > 0.05$). Path widths are scaled proportionally to the path coefficient. $*p < 0.05$, $**p < 0.01$, $***p < 0.001$. MAP, mean annual precipitation; MAT, mean annual air temperature; ND, N deposition; RR_SM, RR of soil moisture; RR-SOC, RR of soil organic carbon; RR_TN, RR of total nitrogen; RR-pH; RR of soil pH; RR-ST, RR of soil temperature; RR-NO_3^-, RR of NO_3^-.

Figure 1

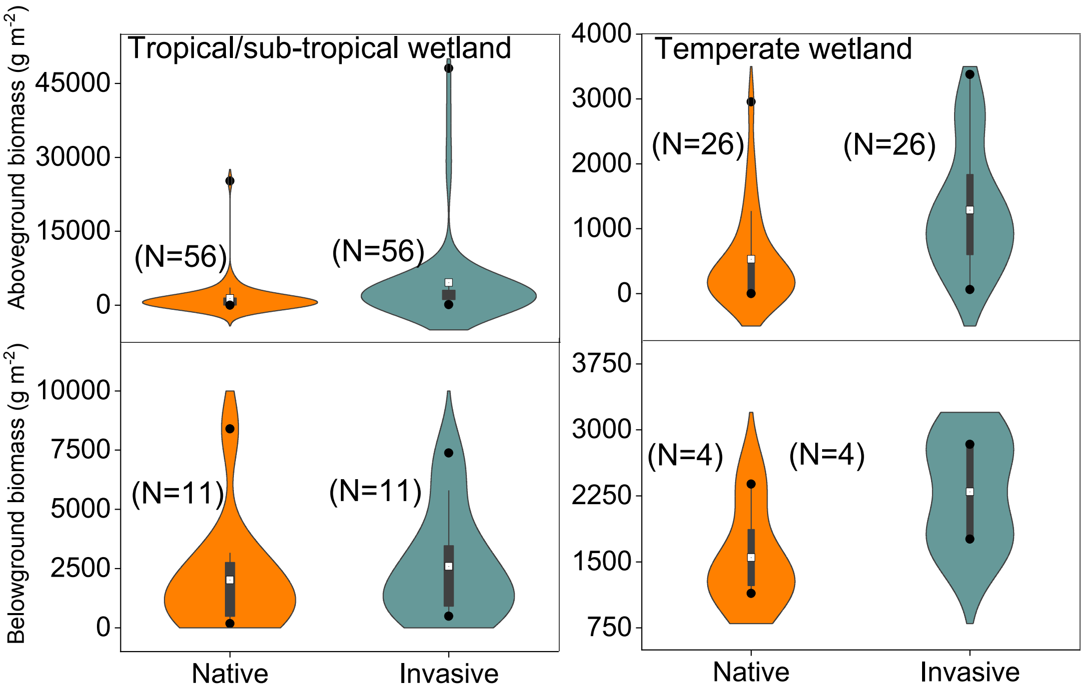

Tropical/sub-tropical wetland
Temperate wetland
Aboveground biomass (g m-2)
Belowground biomass (g m-2)
(N=56)
(N=56)
(N=26)
(N=26)
(N=11)
(N=11)
(N=4)
(N=4)
45000
30000
15000
0
4000
3000
2000
1000
0
10000
7500
5000
2500
0
3750
3000
2250
1500
750
Native
Invasive
Native
Invasive

Figure 2

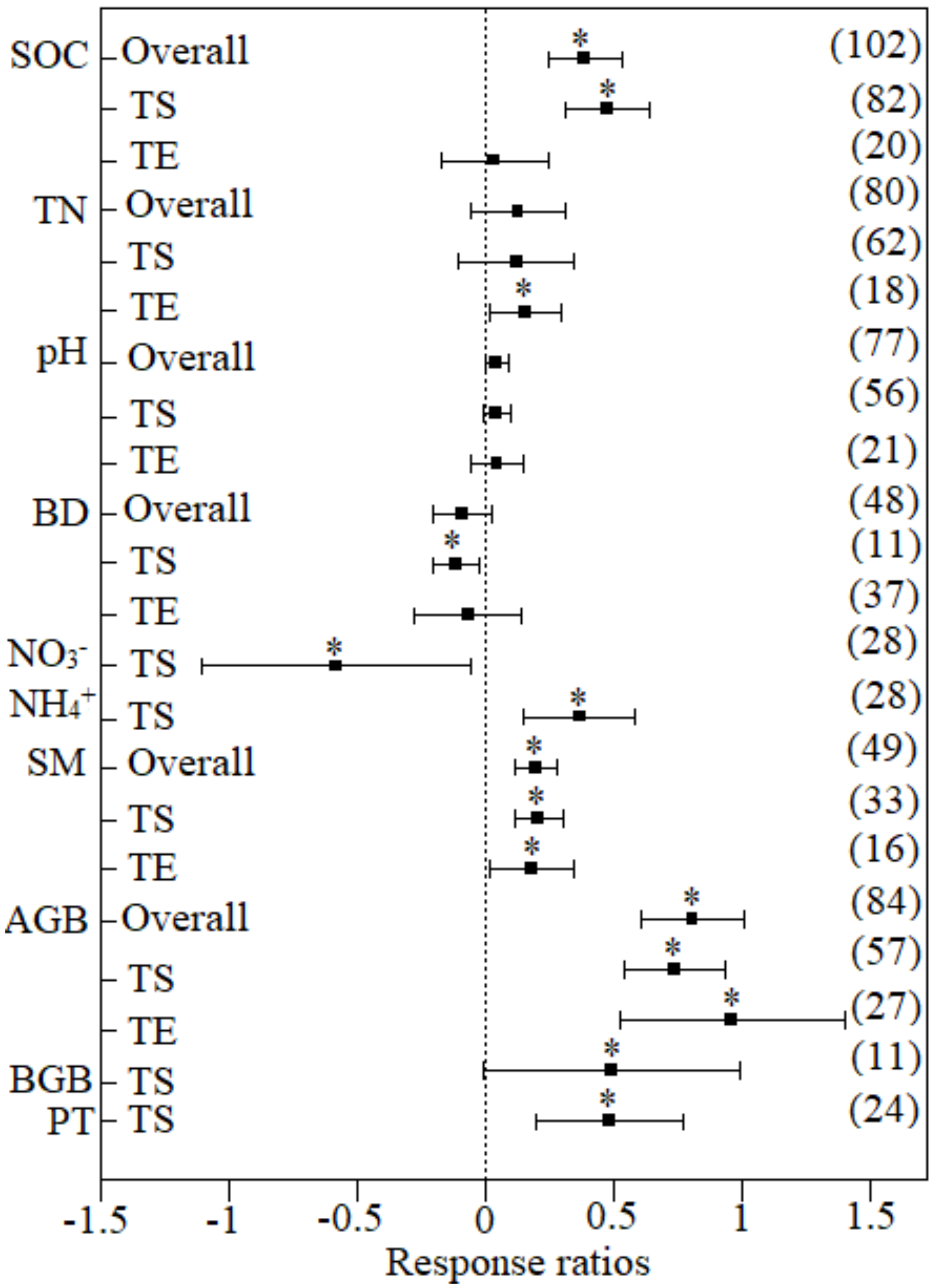

SOC
TN
pH
BD
NO3-
NH4+
SM
AGB
BGB
PT
Overall
TS
TE
(102)
(82)
(20)
(80)
(62)
(18)
(77)
(56)
(21)
(48)
(11)
(37)
(28)
(28)
(49)
(33)
(16)
(84)
(57)
(27)
(11)
(24)
-1.5
-1
-0.5
0
0.5
1
1.5
Response ratios

Figure 3

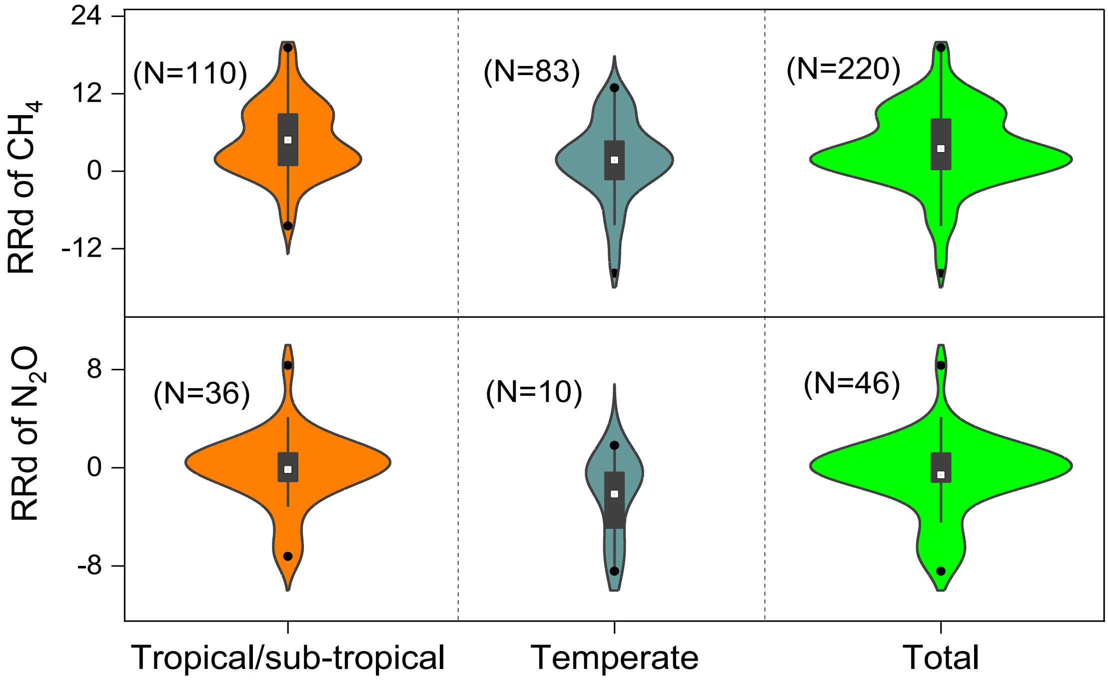

24
12
0
-12
8
0
-8
RRd of CH_4
RRd of N_2O
(N=110)
(N=83)
(N=220)
(N=36)
(N=10)
(N=46)
Tropical/sub-tropical
Temperate
Total

Figure 4

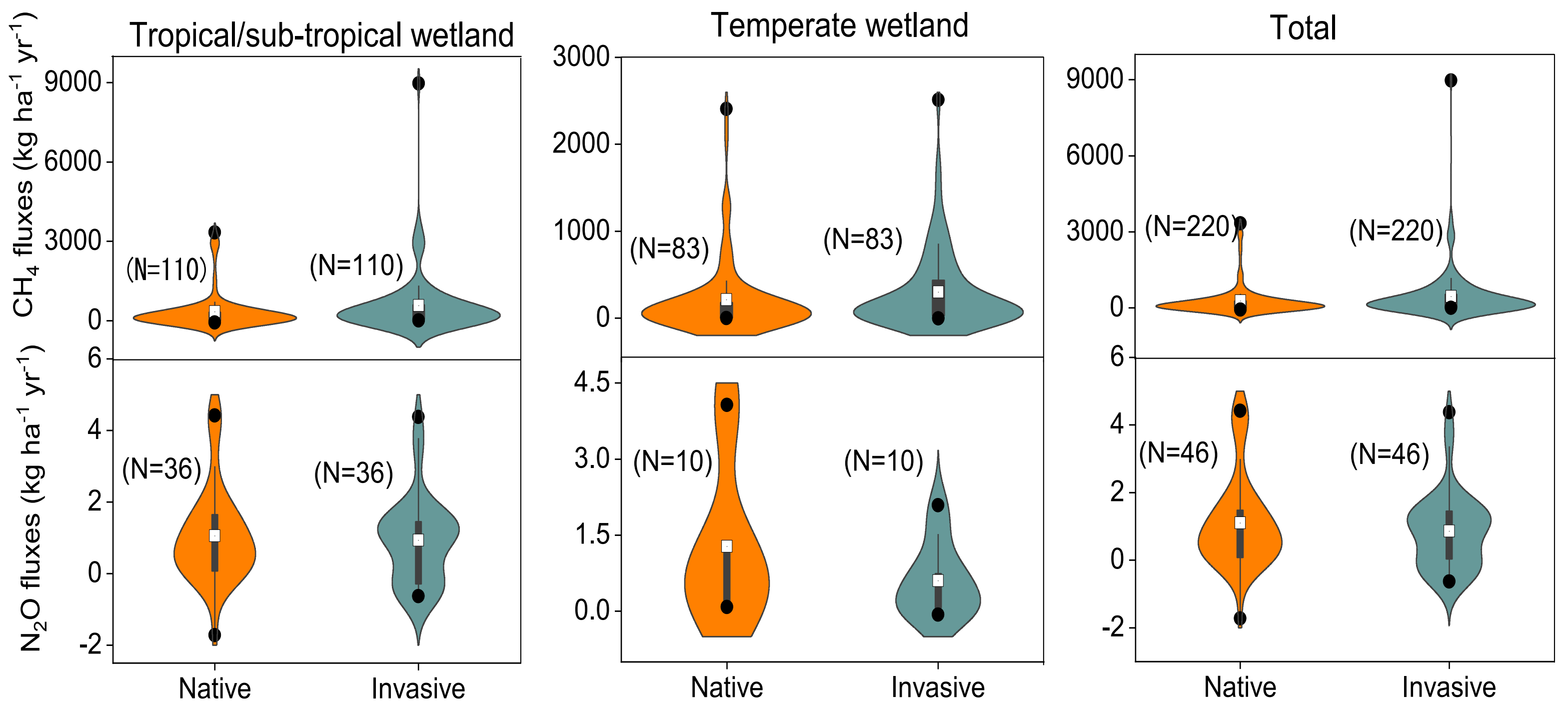
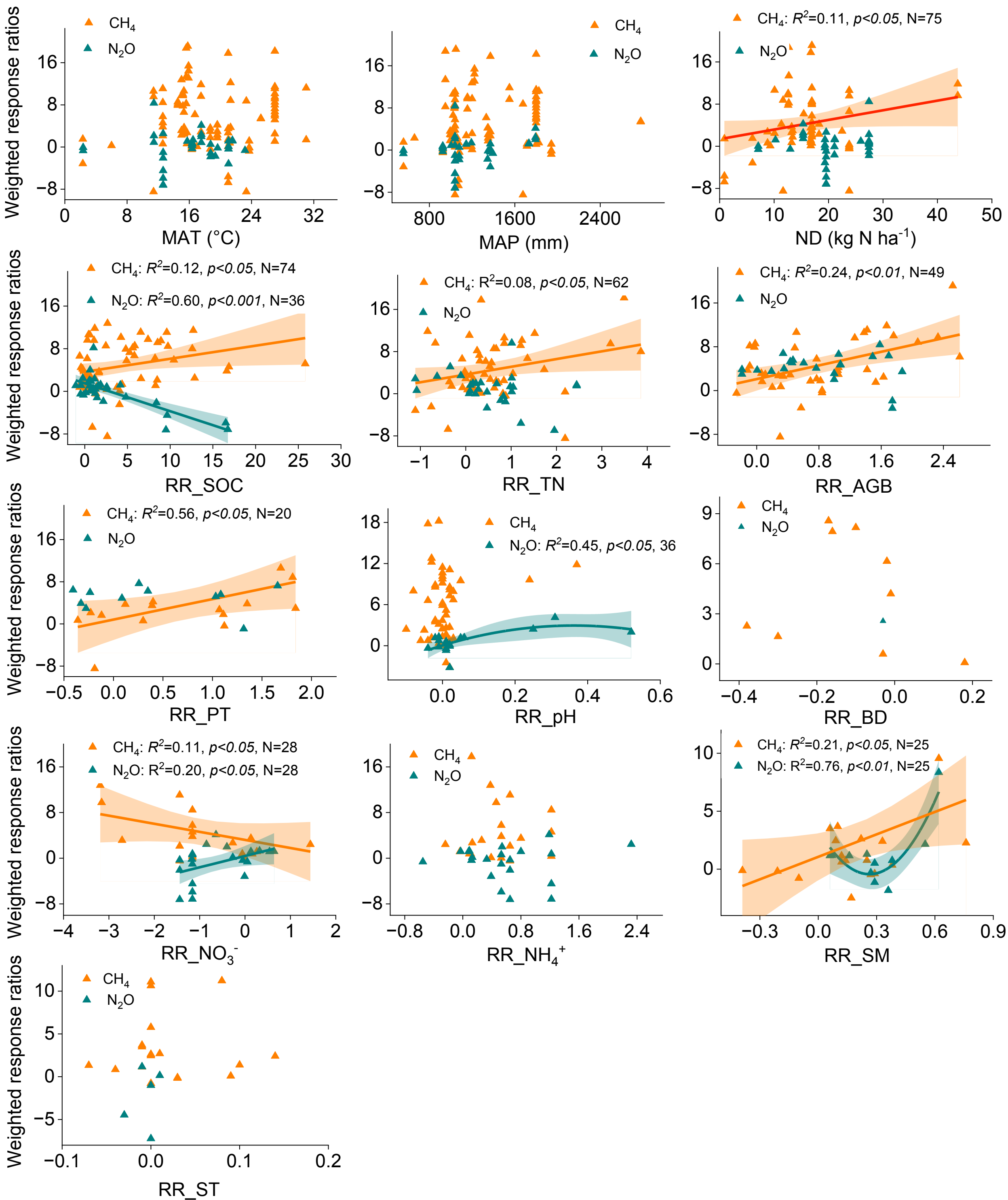
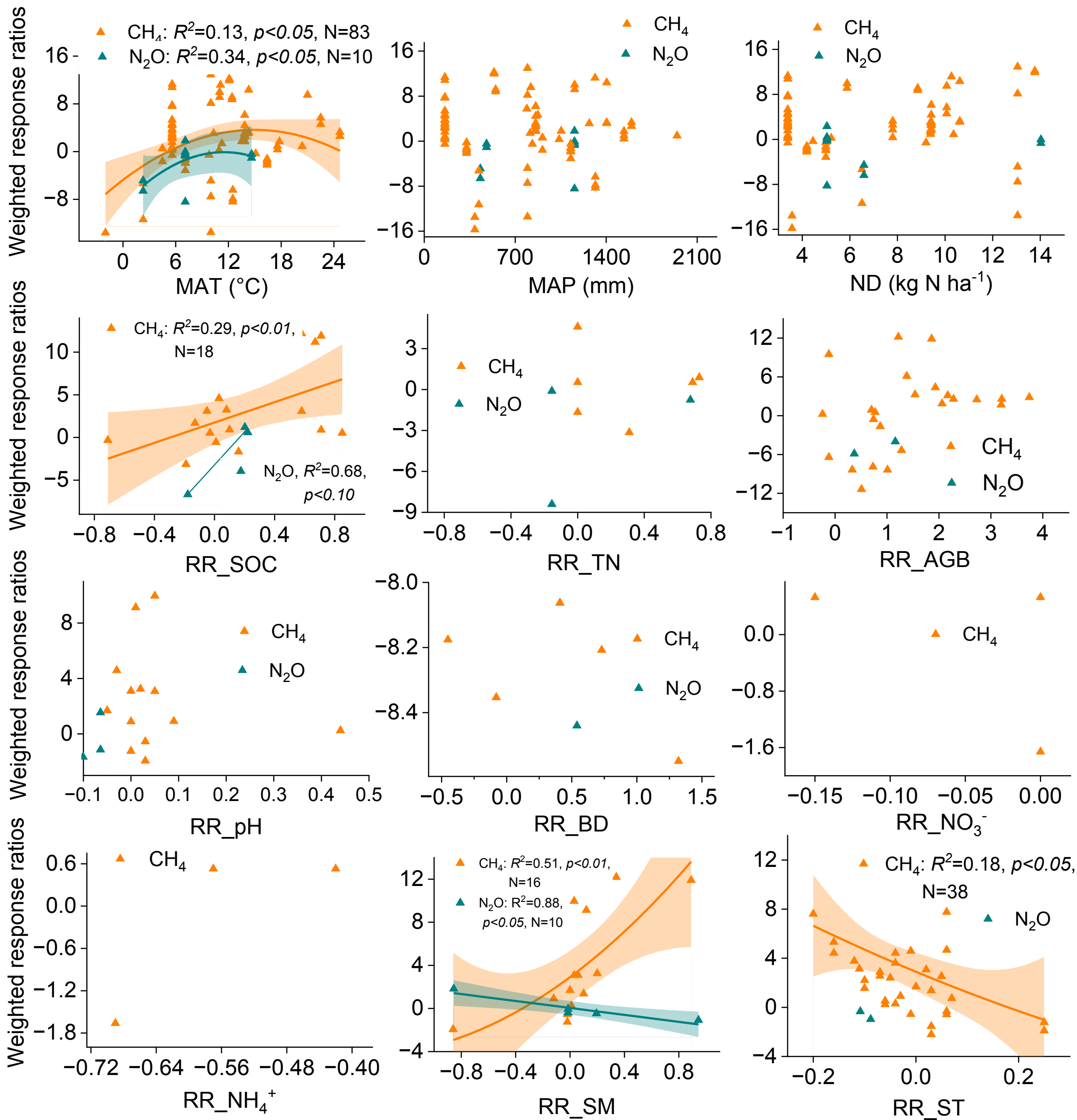

Tropical/sub-tropical wetland
Temperate wetland
Total
CH4 fluxes (kg ha-1 yr-1)
N2O fluxes (kg ha-1 yr-1)
9000
6000
3000
0
3000
2000
1000
0
6
4
2
0
-2
4.5
3.0
1.5
0.0
(N=110)
(N=110)
(N=83)
(N=83)
(N=220)
(N=220)
(N=36)
(N=36)
(N=10)
(N=10)
(N=46)
(N=46)
Native
Invasive

Figure 5


Weighted response ratios
CH$_4$
N$_2$O
MAT (°C)
MAP (mm)
CH$_4$: R^2=0.11, p<0.05, N=75
ND (kg N ha^{-1})
CH$_4$: R^2=0.12, p<0.05, N=74
N$_2$O: R^2=0.60, p<0.001, N=36
RR_SOC
CH$_4$: R^2=0.08, p<0.05, N=62
RR_TN
CH$_4$: R^2=0.24, p<0.01, N=49
RR_AGB
CH$_4$: R^2=0.56, p<0.05, N=20
RR_PT
N$_2$O: R^2=0.45, p<0.05, 36
RR_pH
RR_BD
CH$_4$: R^2=0.11, p<0.05, N=28
N$_2$O: R^2=0.20, p<0.05, N=28
RR_NO$_3^-$
RR_NH$_4^+$
CH$_4$: R^2=0.21, p<0.05, N=25
N$_2$O: R^2=0.76, p<0.01, N=25
RR_SM
RR_ST

942 **Figure 6**



943
944

Figure 7

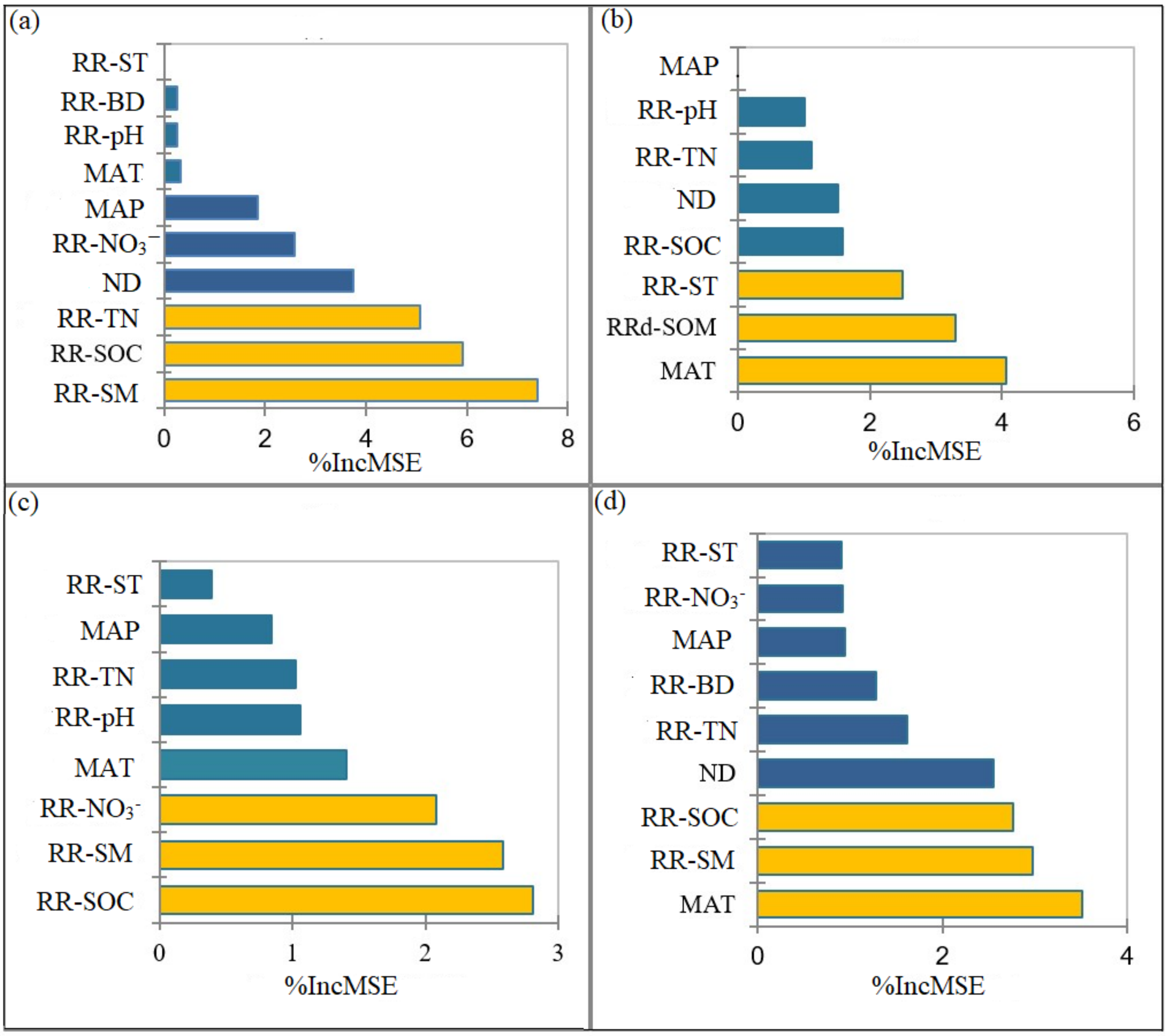
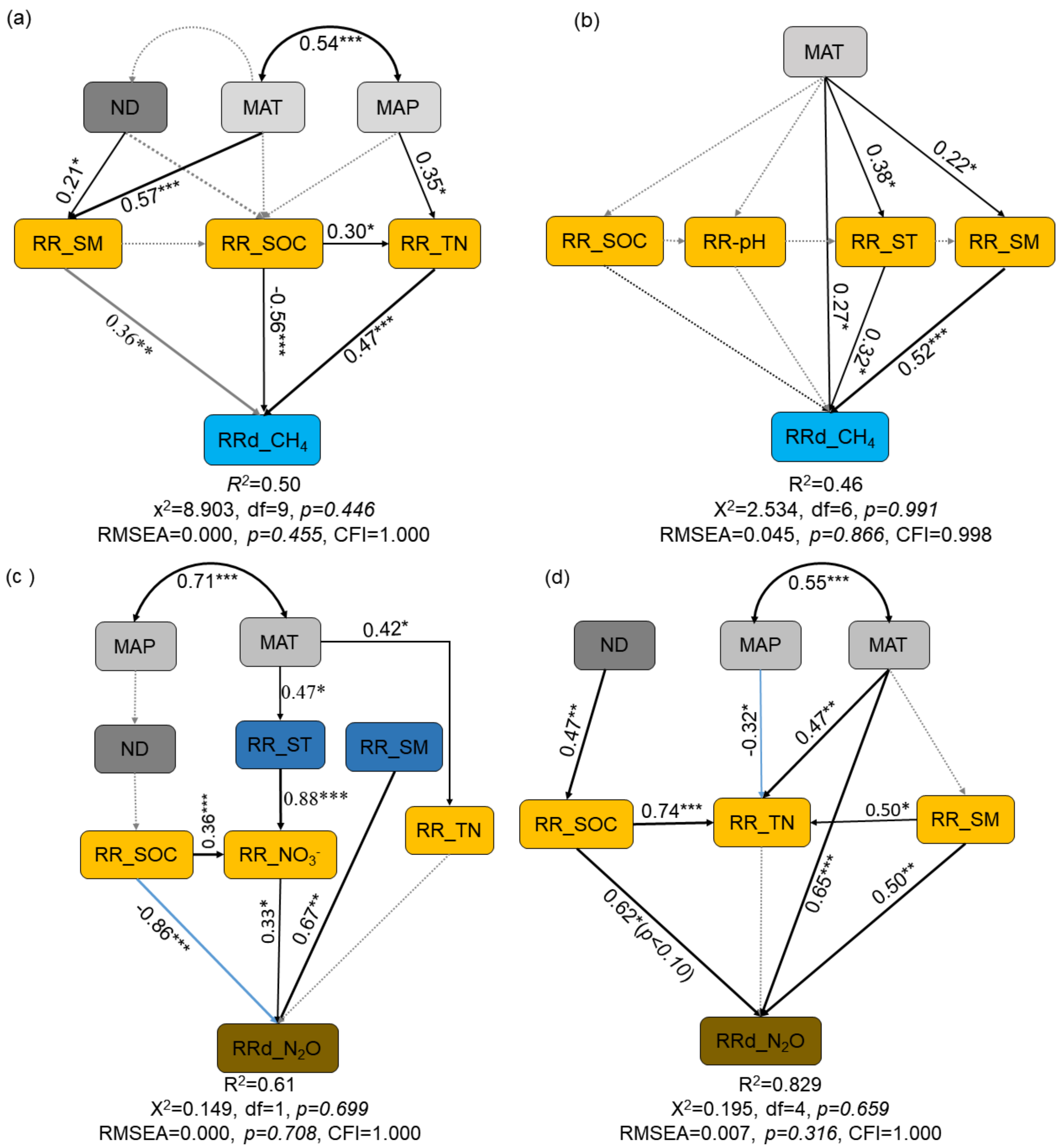

(a)
RR-ST
RR-BD
RR-pH
MAT
MAP
RR-NO3⁻
ND
RR-TN
RR-SOC
RR-SM
0
2
4
6
8
%IncMSE
(b)
MAP
RR-pH
RR-TN
ND
RR-SOC
RR-ST
RRd-SOM
MAT
0
2
4
6
%IncMSE
(c)
RR-ST
MAP
RR-TN
RR-pH
MAT
RR-NO3⁻
RR-SM
RR-SOC
0
1
2
3
%IncMSE
(d)
RR-ST
RR-NO3⁻
MAP
RR-BD
RR-TN
ND
RR-SOC
RR-SM
MAT
0
2
4
%IncMSE

Figure 8


(a)
0.54***
ND
MAT
MAP
0.21*
0.57***
0.35*
RR_SM
RR_SOC
0.30*
RR_TN
0.36**
-0.56***
0.47***
RRd_CH4
R2=0.50
x2=8.903, df=9, p=0.446
RMSEA=0.000, p=0.455, CFI=1.000
(b)
MAT
0.38*
0.22*
RR_SOC
RR-pH
RR_ST
RR_SM
0.27*
0.32*
0.52***
RRd_CH4
R2=0.46
X2=2.534, df=6, p=0.991
RMSEA=0.045, p=0.866, CFI=0.998
(c)
0.71***
MAP
MAT
0.42*
0.47*
ND
RR_ST
RR_SM
0.88***
0.36***
RR_TN
RR_SOC
RR_NO3-
-0.86***
0.33*
0.67**
RRd_N2O
R2=0.61
X2=0.149, df=1, p=0.699
RMSEA=0.000, p=0.708, CFI=1.000
(d)
0.55***
ND
MAP
MAT
0.47**
-0.32*
0.47**
RR_SOC
0.74***
RR_TN
0.50*
RR_SM
0.65***
0.62*(p<0.10)
0.50**
RRd_N2O
R2=0.829
X2=0.195, df=4, p=0.659
RMSEA=0.007, p=0.316, CFI=1.000