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Non-native plant invasion can accelerate global climate change by increasing wetland methane and terrestrial nitrous oxide emissions

Running head: Plant invasion affects CH₄ and N₂O emissions

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Abstract

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Approximately 17% of the land worldwide is considered highly vulnerable to non-native plant invasion, which can dramatically alter nutrient cycles and influence greenhouse gas (GHG) emissions in terrestrial and wetland ecosystems. However, a systematic investigation of the impact of non-native plant invasion on GHG dynamics at a global scale has not yet been conducted, making it impossible to predict the exact biological feedback of non-native plant invasion to global climate change. Here, we compiled 273 paired observational cases from 94 peer-reviewed articles to evaluate the effects of plant invasion on GHG emissions and to identify the associated key drivers. Non-native plant invasion significantly increased methane (CH₄) emissions from 129 kg CH₄ ha⁻¹ yr⁻¹ in natural wetlands to 217 kg CH₄ ha⁻¹ yr⁻¹ in invaded wetlands. Plant invasion showed a significant tendency to increase CH₄ uptakes from 2.95 to 3.64 kg CH₄ ha⁻¹ yr⁻¹ in terrestrial ecosystems. Invasive plant species also significantly increased nitrous oxide (N₂O) emissions in grasslands from an average of 0.76 kg N₂O ha⁻¹ yr⁻¹ in native sites to 1.35 kg N₂O ha⁻¹ yr⁻¹ but did not affect N₂O emissions in forests or wetlands. Soil organic carbon, mean annual air temperature (MAT), and nitrogenous deposition (N_DEP) were the key factors responsible for the changes in wetland CH₄ emissions due to plant invasion. The responses of terrestrial CH₄ uptake rates to plant invasion were mainly driven by MAT, soil NH₄⁺, and soil moisture. Soil NO₃⁻, mean annual precipitation, and N_DEP affected terrestrial N₂O emissions in response to plant invasion. Our meta-analysis not only sheds light on the stimulatory effects of plant invasion on GHG emissions from wetland and terrestrial ecosystems but also improves our current understanding of the mechanisms underlying the responses of GHG emissions to plant invasion.

Keywords: invasive species, native plants, methane, nitrous oxide, wetland ecosystem, terrestrial ecosystem

1 Introduction

Invasion by non-native plants is a critical ecological threat (Jackson et al., 2001; van Kleunen et al., 2015; Walker & Smith, 1997) because of its widespread occurrence across diverse habitats (Catford et al., 2009; van Kleunen et al., 2015). Invasive (non-native) plants can dominate or even completely displace native plant communities (Ehrenfeld, 2003; Liao et al., 2008), and their rapid growth can form dense canopies (Stiers et al., 2011). However, the rate of expansion and magnitude of space occupied by invasive plants vary with time and space (Theoharides & Dukes, 2007). For example, a species native to the east coast of North America, *Spartina alterniflora*, covered 260 ha of coastal China in 1985, but it had spread to more than 54,580 ha by 2015 (An et al., 2007; Mao et al., 2019). In the United States, 4% of the land surface, which is equivalent to 40.5 Mha, has been infested by invasive plant species, with an increase of 0.305% per year (Bhowmik, 2005). Globally, approximately 17% of the land area (excluding Antarctica and glaciated Greenland) is highly vulnerable to invasive plants (Early et al., 2016).

Invasive plants tend to absorb soil nutrients faster, modify the quantity and quality of litter, and create heterogeneous microclimates and change the biological communities within them, thereby creating invasive monoculture (Castro-Díez et al., 2011; Yelenik et al., 2004). These characteristics allow invasive plants to accelerate the turnover and availability of soil nutrients, enhance productivity, and reduce geomorphological disturbances such as erosion (Mack & D'Antonio, 1998; McLeod et al., 2016; Zhang & Feng, 2004). Therefore, displacement of native plant communities by non-native plants can alter the functions and disrupt the sustainability of ecosystems (Ehrenfeld, 2003; Liu et al., 2018). Although invasion by non-native plants has mostly been studied in the context of biodiversity loss and species extinction, it also poses a substantial threat to the

biogeochemical climate service and economy (Anderson-Teixeira et al., 2012; Qiu, 2015; Shiferaw et al., 2018). Exotic plant invasion can accelerate global climate change by enhancing the emissions of volatile organic compounds such as isoprene and greenhouse gases (GHGs) (Bansal et al., 2019; Charles & Dukes, 2008). Moreover, invasive plant species have huge economic costs; for instance, the total economic cost of ragweed and water primrose invasion in Europe was USD 19.62 billion (Haubrock et al., 2021).

Wetland ecosystems are considered to be more susceptible to, and affected by, invasive plants (Zedler & Kercher, 2004). In that context, wetlands draw a lot of attention as they are the single largest contributor to atmospheric methane (CH₄), accounting for 53% of annual emissions globally (Rosentreter et al., 2021). In contrast, soils in terrestrial ecosystems, including forests and grasslands, are responsible for 5–8% of the total atmospheric CH₄ sink (Curry, 2009). However, grasslands and forests are also substantial sources of atmospheric nitrous oxide (N₂O), accounting for 9–20% and 15–55% of global annual emissions, respectively (Tian et al., 2013; Xu & Prentice, 2008; Zhuang et al., 2012). Hall & Asner (2007) found that invasion by *Morella faya*, a dinitrogen-fixing tree species, increased N₂O emissions by 435% when compared with the native evergreen *Metrosideros polymorpha*, likely because of increased soil N pools. In China, replacement of *Eragrostis pilosa* with *Alternanthera philoxeroides* and *Sesbania cannabina* with *Solidago canadensis* increased N₂O emissions by 109% (Zhang et al., 2018). In the US grasslands, invasion of *Pueraria montana* doubled N₂O and nitric oxide emissions when compared with sites where only native species were present (Hickman et al., 2010). Conversely, Yuan et al. (2015) found that invasion of *S. alterniflora* increased CH₄ emissions but decreased N₂O emissions in the coastal salt marshes of China. Mou et al. (2019) reported no apparent effects of *S. alterniflora* invasion on

N₂O emissions at the Min River Estuary in China. Although a number of studies have focused on the impacts of invasive plants on GHG emissions at local or regional levels, their impacts at the global scale have not yet been elucidated (Qiu, 2015). This is of great importance for the accurate estimation of biological feedback to global climate change, which is one of the areas in which our scientific understanding is severely limited. Here, we evaluated the influence of invasive plants on CH₄ and N₂O emissions on the basis of findings from peer-reviewed articles published by reputable scientific journals. Our objectives were to (1) understand the effects of invasive plants on CH₄ and N₂O emissions within wetland and terrestrial ecosystems, (2) identify key factors that affect annual CH₄ and N₂O emission rates in the presence of invasive plants, and (3) improve current understanding of the response mechanisms of GHG emissions to plant invasion across wetland and terrestrial ecosystems.

2 Materials and Methods

2.1 Characteristics of the database

The dataset used in this study included 273 paired measured cases from 94 peer-reviewed articles (Figures S1 and S2). A literature search of published journal articles and scientific reports was conducted using the following databases: Web of Science, Google Scholar, and the China National Knowledge Infrastructure. The search results were filtered to include articles published between December 1999 and May 2020. Keywords included “invasive” OR “non-native” OR “exotic” OR “alien” OR “non-indigenous” AND “non-invasive” OR “native” OR “non-exotic” OR “non-alien” OR “indigenous” plant species, “effects” OR “impacts” on “greenhouse gases” OR “CH₄” OR “N₂O”. A systematic review was conducted to avoid bias during data selection by using the

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following inclusion and exclusion criteria: (1) selection required either (a) field observational cases from invaded and native sites without field manipulation or (b) experimentally manipulated cases; (2) each treatment was required to have at least three replicates; (3) the measurement covered at least one growing season; (4) additional treatments such as fertilization, burning, and warming were excluded; (5) studies that addressed the effects of native woody plants encroachment were excluded; (6) if authors compared a non-invaded scenario with those of varying invader density, only data from the most densely invaded scenario was used for the analysis; and (7) if a paper included data from multiple sites, each site was considered as separate and independent.

Web Plot Digitizer (version 3.11; <https://automeris.io/WebPlotDigitizer>) was used to extract the data presented as figures and plots. Both manual and automatic data-extraction algorithms were used after calibration with corresponding values from plots and images. All data were classified into natural wetland ecosystem, which was subdivided into coastal wetlands and freshwater wetlands, and terrestrial ecosystem, which was subdivided into grasslands and forests. If the authors did not mention the plant species were invasive or native to the case study area in wetland and terrestrial ecosystems, alternative descriptive sources, such as the global invasive species database (GISD; <http://www.issg.org>), were used. All CH₄ and N₂O emission data were converted to kg ha⁻¹ yr⁻¹. Additionally, location (longitude, LON and latitude, LAT); climatic data (mean annual air temperature, MAT, and mean annual precipitation, MAP); plant biomass; and soil properties such as soil pH, soil organic carbon (SOC), total nitrogen (TN), bulk density (BD), NO₃⁻, NH₄⁺, soil temperature (ST), and soil gravimetric water content (SM) were collected. The means, standard deviation (SD), and sample sizes for all variables in both invaded and native ecosystems were collected. If some studies reported standard error (SE) of the variables instead of SD, the SD was

determined using the formula $SE \times \sqrt{n}$, where n is the sample size. When studies did not include SD or SE values, SD was assigned as 1/10 of the mean (Luo et al., 2006). Moreover, plant biomass collected from the wetland ecosystems was aboveground biomass (AGB), whereas that collected from the terrestrial ecosystems included litter biomass. The original authors of relevant studies were contacted to obtain any useful information missing from the articles. If the authors were unable to provide the requested information, information regarding soil properties was obtained from the Harmonized World Soil Database version 1.2 (FAO/IIASA/ISRIC/ISS-CAS/JRC, 2012) by using the geographic coordinates of the study location. MAP and MAT were available from the Department of Geography and Spatial Sciences at the University of Delaware (http://climate.geog.udel.edu/~climate/html_pages). Soil temperature (0–20 cm) was obtained from the study by van den Hoogen et al. (2021). Global soil temperature maps were generated by calculating the offset between *in situ* soil temperature measurements, based on 8519 time series from over 1200 1-km² pixels across the world's major terrestrial biomes, and coarse-grained air temperature estimates from ERA5-Land (Lembrechts et al., 2022). Soil volumetric moisture content was acquired from the Land-Atmosphere Interaction Research Group at Sun Yat-sen University (<http://globalchange.bnu.edu.cn/research/soilw>) and converted to SM by dividing with BD. Atmospheric N deposition was obtained using global N deposition maps (Ackerman et al., 2018). Furthermore, environmental factors can also be extracted from published studies with the same experimental sites in which the CH₄ and/or N₂O fluxes were measured in our dataset. All the GHG fluxes and environmental variables mentioned previously were subjected to outlier detection by using a simple empirically based method that excluded values more than $2 \times SD$ above or below mean values (Williams & Baker, 2012).

2.2 Data analysis

We used meta-analysis to assess the response of GHGs (CH₄ and N₂O) and environmental factors to plant invasion. For GHG fluxes, Hedges' *d* (*RRd*) was used to estimate the weighted response ratios because it is suitable for $X_t/X_c < 0$, where X_t and X_c are the means of GHG fluxes in invaded and native sites, respectively (Wu et al., 2022). The effect of plant invasion on environmental factors was evaluated by natural logarithm-transformed response ratios (*RR*). The two response ratios for a given case study were calculated as follows:

$$RR = \ln(X_t / X_c) \quad (1)$$

$$RRd = \frac{(X_t - X_c) \times J}{\sqrt{\frac{(N_t - 1)S_t^2 + (N_c - 1)S_c^2}{N_t + N_c - 2}}} \quad (2)$$

where X_t and X_c are the mean values of the selected GHG fluxes or environmental variables in invaded and native ecosystems, respectively; N_t and N_c are the sample sizes of the invaded and native sites, respectively; and S_t and S_c are the corresponding SDs. In addition, J is a bias correction factor that used to remove the small-sample-size bias of the standardized differences of means. J was calculated as follows:

$$J = 1 - \frac{3}{4(N_t + N_c - 2) - 1} \quad (3)$$

The variances (v and vd) of *RR* and *RRd* were calculated as follows:

$$v = \frac{S_t^2}{N_t^2 X_t^2} + \frac{S_c^2}{N_c^2 X_c^2} \quad (4)$$

$$vd = \frac{N_t + N_c}{N_t N_c} + \frac{d^2}{2(N_t + N_c)} \quad (5)$$

The weighted response ratios (\overline{RR} and \overline{RRd}) were calculated from the *RR* and *RRd* of individual

paired comparison between the invaded and native ecosystems:

$$\overline{RR} = \frac{\sum_{i=1}^n w_i(RR_i)}{\sum_{i=1}^n w_i} \quad \text{or} \quad \overline{RRd} = \frac{\sum_{i=1}^n w_i(RRd_i)}{\sum_{i=1}^n w_i} \quad (6)$$

where n is the number of paired comparisons. The weighting factor (w_i) was calculated as follows:

$$w_i = \frac{1}{v_i} \quad \text{or} \quad w_i = \frac{1}{vd_i} \quad (7)$$

The 95% confidence interval (CI) and standard error of \overline{RR} (\overline{RRd}) were calculated as follows:

$$95\% \text{ CI} = \overline{RR} \pm 1.96s(\overline{RR}) \quad \text{or} \quad 95\% \text{ CI} = \overline{RRd} \pm 1.96s(\overline{RRd}) \quad (8)$$

$$s(\overline{RR}) \quad \text{or} \quad s(\overline{RRd}) = \sqrt{\frac{1}{\sum_{i=1}^n w_i}} \quad (9)$$

\overline{RR} was also transformed to effect size, but this was not suitable for \overline{RRd} :

$$\text{Effect size (\%)} = (e^{\overline{RR}} - 1) \times 100\% \quad (10)$$

The random-effects model was used to calculate the \overline{RR} of environmental factors and \overline{RRd} of GHG fluxes with the *rma.mv* function of “metafor” package of R (Viechtbauer, 2010).

Across wetland and terrestrial ecosystems, linear mixed-effect models were used to examine whether the response of CH₄ and N₂O fluxes to plant invasion changed with LAT, climate factors, N_DEP, and RR of plant biomass and soil properties. The linear mixed-effect model was performed using the restricted maximum likelihood estimation with the “lme4” package of R. Furthermore, random-forest analysis was conducted to determine the relative importance of environmental factors in affecting the response of CH₄ and N₂O fluxes to plant invasion. We used percent increase in mean square error (%IncMSE) to rank the predictors in order of importance, and negative values of %IncMSE, which indicate lack of importance (Liaw & Wiener, 2002). Finally, the structural equation model (SEM) was used to evaluate the standardized direct, indirect, and total effects of

MAT, MAP, N_DEP, RR of AGB, and RR of soil properties on the CH₄ and N₂O fluxes in response to plant invasion. Because of no significant relationships of RR of pH and ST with RR of CH₄ and N₂O fluxes, pH and ST were not included in our SEM. Given that the variables of the soil properties were strongly correlated, we conducted the principal component analysis to create soil chemical/physical properties before establishing SEM, where soil chemical properties included SOC and TN and soil physical properties included BD and SM. Notably, binominal and exponential relationships may not be identified using SEM, which would additionally be revealed by linear mixed-effect models (Figures S3 and S4). The optimal SEM was evaluated using the following criteria: p -value (χ^2) > 0.05, RMSEA < 0.08, and CFI > 0.90. Random-forest analysis and SEM were performed using the “randomforest” and “lavaan” packages of R, respectively. Additionally, plant biomass was not included in the linear mixed-effect analysis, random-forest model, and SEM across terrestrial ecosystems because of data paucity. Similarly, mineral N was not included in the random-forest analysis and SEM across wetland ecosystems because of data paucity.

3 Results

3.1 Effects of plant invasion on plant biomass and soil properties

Within our dataset, non-native plant invasion significantly increased plant biomass by 131% (95% CI: 86.2–187%; $p < 0.05$) in wetland ecosystems and by 50.6% (95% CI: 10.6–105%; $p < 0.05$) in terrestrial ecosystems (Figure 1). When considering differences between the wetland subclasses, exotic plant invasion significantly increased plant biomass by 132% (95% CI: 81.7–195%; $p < 0.05$) in coastal wetlands and by 131% (95% CI: 45.2–268%; $p < 0.05$) in freshwater wetlands. Among

terrestrial ecosystems, plant invasion significantly increased plant biomass by 27.2% (95% CI: 1.92–58.7%; $p < 0.05$) in forests and by 158% (95% CI: 58.0–322%; $p < 0.05$) in grasslands.

Exotic plant invasion significantly increased SOC by 25.9% ($p < 0.05$) and marginally increased soil NH_4^+ by 33.0% ($p = 0.056$) (Figure 2). Conversely, exotic plant invasion marginally decreased ST by 1.97% ($p = 0.078$). Non-native plant invasion in wetlands significantly increased SOC by 44.8%, TN by 25.1%, NH_4^+ by 62.3%, and SM by 23.0%, but significantly decreased NO_3^- by 35.9% ($p < 0.05$); such changes were more pronounced in coastal wetlands (Figure S5). With respect to terrestrial ecosystems, non-native plant invasion significantly decreased SM by 17.6% and TN by 14.5% ($p < 0.05$) and marginally decreased ST by 3.06% ($p = 0.079$).

3.2 Effects of plant invasion on CH_4 fluxes

Overall, CH_4 fluxes significantly increased after plant invasion (\overline{RRd} : 1.85; 95% CI: 0.90–2.80; $p < 0.05$) (Figure 3). However, the effects of exotic plant invasion on CH_4 fluxes varied on the basis of the ecosystem. The \overline{RRd} of CH_4 fluxes was 3.09 (95% CI: 2.06–4.12) in wetland ecosystems and, conversely, -1.75 (95% CI: -3.47 to -0.04) in terrestrial ecosystems, indicating that CH_4 emissions in wetland ecosystems and CH_4 uptakes in terrestrial ecosystems significantly increased after exotic plant invasion ($p < 0.05$). On average, CH_4 fluxes increased from 129 $\text{kg CH}_4 \text{ ha}^{-1} \text{ yr}^{-1}$ in wetlands with native plants to 217 $\text{kg CH}_4 \text{ ha}^{-1} \text{ yr}^{-1}$ after plant invasion, whereas CH_4 uptake rates increased from 2.95 (native sites) to 3.64 $\text{kg CH}_4 \text{ ha}^{-1} \text{ yr}^{-1}$ (invaded sites) in terrestrial ecosystems (Figure 4). Among wetlands, plant invasion had a greater stimulatory effect on CH_4 emission in coastal wetlands (\overline{RRd} : 3.50; 95% CI: 2.47–4.53; $p < 0.05$), with mean CH_4 fluxes increasing from 111 $\text{kg CH}_4 \text{ ha}^{-1} \text{ yr}^{-1}$ in native wetlands to 255 $\text{kg CH}_4 \text{ ha}^{-1} \text{ yr}^{-1}$ in invaded wetlands. In contrast, no

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significant changes in CH₄ fluxes were observed in freshwater wetlands after plant invasion (\overline{RRd} : 1.22; 95% CI: -0.71 to 3.17). Within terrestrial ecosystems, exotic plant invasion significantly increased CH₄ uptake rates from 1.58 kg CH₄ ha⁻¹ yr⁻¹ in native grasslands to 2.48 kg CH₄ ha⁻¹ yr⁻¹ in invaded grasslands (\overline{RRd} : -2.23; 95% CI: -3.72 to -0.75; $p < 0.05$), but it did not alter CH₄ uptake rates in forests (\overline{RRd} : -1.55; 95% CI: -4.78 to 1.68).

3.3 Effects of plant invasion on N₂O fluxes

With respect to N₂O fluxes, the 95% CI of \overline{RRd} overlapped zero, indicating no significant changes in N₂O fluxes in the overall dataset after plant invasion (Figure 3). Similarly, no significant differences in N₂O fluxes were observed in wetland ecosystems and wetland subclasses, coastal and freshwater wetlands, after plant invasion. In contrast, exotic plant invasion significantly increased N₂O fluxes in terrestrial ecosystems (\overline{RRd} : 1.64; 95% CI: 0.52–2.76; $p < 0.05$). Among terrestrial ecosystems, N₂O fluxes significantly increased in grasslands after plant invasion (\overline{RRd} : 3.01; 95% CI: 0.83–5.20; $p < 0.05$), from 0.76 kg N₂O ha⁻¹ yr⁻¹ in native grasslands to 1.35 kg N₂O ha⁻¹ yr⁻¹ in invaded grasslands (Figure 5); exotic plant invasion did not affect N₂O fluxes in forests (Figure 3).

3.4 Relationships between environmental factors and responses of CH₄ and N₂O fluxes to plant invasion

The linear mixed-effect analysis suggested that the RRd of CH₄ fluxes in wetland ecosystems was positively correlated with the RR of AGB and RR of SOC and negatively correlated with the RR of BD ($p < 0.05$) (Figure 6). The RRd of wetland CH₄ fluxes showed convex correlations with LAT,

MAT, and N_DEP. The *RRd* of wetland N₂O fluxes exhibited convex relationships with the *RR* of SOC, *RR* of TN and *RR* of NH₄⁺:NO₃⁻, and was negatively correlated with the *RR* of BD.

The *RRd* of CH₄ fluxes in terrestrial ecosystems was positively correlated with LAT, *RR* of BD, and *RR* of NH₄⁺ and negatively correlated with MAT ($p < 0.05$) (Figure 7). In addition, the *RRd* of terrestrial CH₄ fluxes was correlated with the *RR* of SM in a logarithmic relationship. Within terrestrial ecosystems, the *RRd* of N₂O fluxes showed exponential decay relations to N_DEP and natural log of MAP (ln_MAP), and it was positively correlated with the *RR* of NO₃⁻.

3.5 Dominant factors that regulate the responses of CH₄ and N₂O fluxes to plant invasion

The random-forest analysis suggested that the most important factors associated with the effects of plant invasion on CH₄ fluxes in wetland ecosystems were MAT, N_DEP, *RR* of SOC, and *RR* of AGB (Figure 8). The *RR* of SOC, *RR* of TN, and *RR* of BD were key factors that controlled the response of wetland N₂O fluxes to plant invasion. MAT, *RR* of NH₄⁺, *RR* of soil BD, and *RR* of SM played more important roles in regulating the response of terrestrial CH₄ fluxes to plant invasion. MAP, N_DEP, and *RR* of NO₃⁻ significantly drove terrestrial N₂O fluxes in response to plant invasion.

Our SEMs explained 58.2%, 70.2%, 57.9%, and 46.8% of the variance in the *RRd* of wetland CH₄ fluxes, wetland N₂O fluxes, terrestrial CH₄ fluxes, and terrestrial N₂O fluxes, respectively (Figures 9 and 10). The SEM demonstrated that the *RR* of soil properties consistently played a remarkable role in the effects of plant invasion on wetland CH₄ and N₂O fluxes. MAT and N_DEP also have great significance in regulating the responses of wetland CH₄ fluxes to plant invasion directly and indirectly by altering the *RR* of soil properties and *RR* of AGB (Figure S3). In terrestrial

ecosystems, the *RRd* of CH₄ fluxes depended largely on MAT, *RR* of soil physical properties, and *RR* of NH₄⁺, whereas N_DEP and MAP regulated the responses of terrestrial CH₄ fluxes to plant invasion by affecting the *RR* of NH₄⁺ (Figure S4a). For the *RRd* of terrestrial N₂O fluxes, N_DEP, MAP, and *RR* of NO₃⁻ were identified as the key factors, whereas MAT and *RR* of soil chemical properties also increased the *RRd* of terrestrial N₂O fluxes via enhancing the *RR* of NO₃⁻.

4 Discussion

4.1 Effects of invasive plants on wetland CH₄ emissions

We found that plant invasion significantly increased annual CH₄ emission in wetland ecosystems (average, 68.2%), with coastal wetland as the most-affected wetland subclass. Interestingly, the *RRd* of wetland CH₄ fluxes showed hump-shaped relationships with LAT and MAT, and the maximum values for the effects of plant invasion were detected at around latitude 32° and MAT of 15°C, respectively. It is likely that latitudinal variation in the *RRd* of wetland CH₄ fluxes was controlled by MAT. Our result indicates that natural wetlands located at around latitude 32° with MAT of 15°C are probably optimal habitats for invasive plants to stimulate CH₄ emissions.

Previous studies have reported that physiological processes (e.g., methanogenesis) and enzymatic reactions relative to nutrient cycles are generally faster at higher temperatures, particularly if there are no other constraints such as water availability (Castro-Díez et al., 2014; Wallenstein et al., 2010). The increasing temperature can accelerate the decomposition of SOC and increase the activities of methanogens, thereby stimulating CH₄ emissions (Bridgham et al., 2013; Chen et al., 2021; Dean et al., 2018; Leroy et al., 2017). CH₄ fluxes have been reported to linearly increase with temperature between 0°C and 30°C across microbial and ecosystem scales

(Yvon-Durocher et al., 2014). We found that the optimal MAT for the *RRd* of wetland CH₄ fluxes was approximately 15°C, indicating that other factors also control the response of wetland CH₄ emissions to invasive plants. The SEM results revealed that the *RRd* of wetland CH₄ fluxes linearly increased with the *RR* of AGB and *RR* of SOC; a hump-shaped relationship was detected for *RR* of AGB and *RR* of soil properties with MAT, with the peak values for *RR* of AGB and *RR* of soil properties observed at around 15°C (Figure S3). Liu et al. (2020) also found that the aboveground biomass of invasive *S. alterniflora* displayed hump-shaped relationships with LAT and MAT in China, with the biomass in coastal wetlands peaking at around latitude 31°N. Thus, we can infer that natural wetlands located at around latitude 32° with MAT of 15°C are more favorable for the growth of invasive plants and improvement of soil properties such as SOC in wetlands, resulting in high *RRd* of wetland CH₄ fluxes.

Previous studies have demonstrated that invasive plants show higher nutrient use efficiency and net primary productivity than native plants (Ehrenfeld, 2003; Liao et al., 2008). In our meta-analysis, the aboveground biomass of invasive plants was 2.31-fold higher than that of native species, which in turn delivered more organic C directly into the soil in the form of exudates and debris for methanogenesis (Christensen et al., 2002). Approximately 30–60% of plant photosynthates are delivered into the underground, of which as much as 40–90% enters the soil (Lynch & Whipps, 1990; Whipps, 1990). Fast-growing invasive plants have lower C:N and lignin:N ratios as well as higher nutrient contents than native plants (Poulette & Arthur, 2012). Ravit et al. (2003) found that the decomposer population was higher in a brackish wetland vegetated with invasive *Phragmites australis* than in a native *S. alterniflora* wetland in the US, and the microbial community structure and function in the invaded wetland were altered by the increased bacteria-to-fungi ratio and

saprophytic fungi (Kourtev et al., 2002). The decomposition rates of invasive plant litters were higher than that of native plant litters by an average of 117% (Liao et al., 2008). Apparently, invasive plant residues in wetlands are more efficiently mineralized and become methanogenic substrates, thereby accelerating CH₄ production and emission (Duke et al., 2015).

The greater photosynthetic capacity and reproduction of exotic plants increase plant coverage and stem density (Ehrenfeld, 2003; Mozdzer & Megonigal, 2013). A mesocosm study revealed that the stem density of *S. alterniflora* was correlated with CH₄ fluxes because of the stem's function as a conduit for CH₄ emissions (Cheng et al., 2007; Zhang et al., 2010). Invasive plants like *S. alterniflora* provide more conduits for CH₄ transport via the aerenchyma system, preventing CH₄ from oxidizing when it passes through aerobic surface layers of sediments (Bansal et al., 2020; Granse et al., 2022). Likewise, invasive *Phalaris arundinacea* and *Telimeia domingensis* are found to have highly developed aerenchyma for CH₄ emission when compared with native plants (Chabbi et al., 2000). Cheng et al. (2007) and Tong et al. (2010) attributed higher CH₄ emissions in invasive *S. alterniflora* wetlands to both higher primary productivity and transporting capacity.

Interestingly, the *RRd* of wetland CH₄ fluxes was binomially correlated with N_{DEP}, with an optimal N_{DEP} of approximately 15 kg N ha⁻¹. This indicates that N_{DEP} boosts the effect of plant invasion on wetland CH₄ emissions. We noted a consistent hump-shaped relationship between N_{DEP} and *RR* of AGB, suggesting that N_{DEP} impacts the *RRd* of wetland CH₄ fluxes via regulating the responses of AGB and associated changes in soil properties. As the exogenous N input increases, fierce competition for N between microbes and plants can be partly alleviated in N-limited wetlands, especially coastal wetlands invaded by *S. alterniflora* with higher N demands (Mou et al., 2019; Zhang et al., 2007; 2013). As mentioned previously, invasive plants with a more

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efficiently increased biomass than native plants under N_DEP provided more substrates for methanogenesis and conduits for CH₄ transport via the aerenchyma system (Bansal et al., 2020; Christensen et al., 2002; Zhang et al., 2013). N_DEP also improved plant litter quality, thereby increasing the conversion rate of residues into SOC and substrates by better matching microbe and optimizing substrate stoichiometries (Brown et al., 2014). However, when the N_DEP exceeds 15 kg N ha⁻¹, the response of the invasive plant biomass gradually decreased with increasing N_DEP in the wetlands (Figure S3d). In Canadian peatlands, the apparent increase in plant aboveground biomass gradually disappeared when N_DEP was higher than 6 kg N ha⁻¹ (Granath et al., 2009; Turunen et al., 2004). Similar hump-shaped relationships between N_DEP and the response of AGB were observed across terrestrial and aquatic ecosystems (Xu et al., 2019). Thus, it is likely that a long-term high dose of N_DEP improves wetland N availability, thereby minimizing the stimulation effect of N_DEP on plant growth and, consequently, weakening the response of wetland CH₄ emissions to plant invasion.

4.2 Effects of invasive plants on terrestrial CH₄ uptakes

Plant invasion significantly increased the CH₄ uptake in grasslands by 57.0%, whereas no significant differences were observed between invaded and native forests. Previous studies have shown that plant invasion enhances soil microbial activity and promotes soil nutrient turnover and utilization (Bell et al., 2020; Ehrenfeld et al., 2001; Xu et al., 2021; Zou et al., 2006). We found that MAT had the greatest effects on the response of CH₄ uptakes to plant invasion, and it showed a linear relationship with the *RRd* of CH₄ uptake rates in terrestrial ecosystems, especially those with MAT > 13°C. This was consistent with the results of previous studies in which terrestrial CH₄

uptakes increased with increasing temperature, with optimal CH₄ consumption in soils occurring at temperatures between 20°C and 30°C (Butterbach-Bahl & Papen, 2002; Cai & Yan, 1999; Castro et al., 1995; Ishizuka et al., 2000; Shrestha et al., 2012). Moreover, we noted that plant invasion increased the temperature sensitivity of atmospheric CH₄ uptake, thereby increasing the stimulation effect of the temperature rise on CH₄ uptakes in low latitude grasslands. This indicates enhancement of the activities of soil microbes (e.g., methanotrophs) and associated enzymatic reactions during plant invasion would be more efficient at high temperatures (Castro-Díez et al., 2014; Täumer et al., 2021).

Soil moisture was the next key factor that affected the response of terrestrial CH₄ uptakes to plant invasion, mainly by altering the diffusion of CH₄ and O₂ between the soil and atmosphere (D'Imperio et al., 2017; Price et al., 2004; Smith et al., 2000). Castro et al. (1995) observed a sharp decrease in annual CH₄ uptake rates, from 11.7 kg CH₄ ha⁻¹ to nearly zero, as the soil moisture increased from 42% to 70% w/w or from 60% to 100% water-filled pore space (WFPS). In a Swiss forest vegetated with Norway spruce, soil CH₄ uptake rates were negatively correlated with soil moisture and decreased from 5.24 μmol m⁻² h⁻¹ to nearly zero as the soil moisture increased from 18.4% to 50.7% w/w (20.3% to 56.0% WFPS) (Hiltbrunner et al., 2012). Across our dataset, soil moisture in the native sites was, on average, 28.2% w/w (49.8% WFPS) and significantly decreased to 23.8% w/w (43.4% WFPS) in the invaded sites, probably because of higher evapotranspiration and interception of invasive plant species (Giambelluca et al., 2008; Takahashi et al., 2011). The reduction in soil moisture caused by plant invasion provides more aerobic conditions for CH₄ oxidation and facilitates the diffusion of CH₄ and O₂ from the atmosphere to soil, thereby stimulating terrestrial CH₄ uptakes.

Soil NH_4^+ also substantially regulated the response of terrestrial CH_4 uptake rates to plant invasion. The negative relationship between the *RRd* of terrestrial CH_4 uptake rates and *RR* of NH_4^+ indicated that higher, albeit not significantly, soil NH_4^+ concentration in the invaded terrestrial ecosystem decreased the stimulation effect of plant invasion on CH_4 uptakes. Two reasons have been suggested. First, a high NH_4^+ concentration may decrease CH_4 oxidation (Bédard & Knowles, 1989) because methane monooxygenase can also oxidize ammonia into NO_3^- in a concentration-dependent way (Bodelier & Laanbroek, 2004). Second, the intermediates and end products (especially NO_2^-) of NH_4^+ oxidation can suppress the activity of methanotrophic bacteria (Dunfield & Knowles, 1995).

When compared with grasslands, forests, especially old-growth forests, tend to be resistant to exotic plant invasion because of their high species diversity (Byun et al., 2018; Kennedy et al., 2002; Kier et al., 2005; Levine, 2000), thereby minimizing the effect of invasive plants on CH_4 uptakes. Pyšek et al. (2012) found that the ecological impacts of plant invasion would be more significant at a global scale if the invasive species was an annual grass, whereas invasive species taller than 4.8 m (mostly trees) primarily exerted significance in a few regions. However, the ecological effects of invasive plants (especially annual grass) generally become weaker in forests, probably because of the low shade tolerance of invasive plant species (Flory & Clay, 2006; Martin et al., 2009; Valladares & Niinemets, 2008). The higher plant densities and closer interactions between native plants in forests reduced the ecological impacts of invasive plants (Thapa et al., 2017). Therefore, it is likely that the relatively weak extent of plant invasion lowered the response of CH_4 uptakes in forests.

4.3 Effects of invasive plants on wetland and terrestrial N₂O fluxes

Although N₂O fluxes in N-limited native wetlands were low, plant invasion overall reduced wetland N₂O fluxes, albeit not significantly. Plant invasion significantly decreased soil NO₃⁻, whereas the *RRd* of wetland N₂O fluxes decreased with increasing *RR* of NH₄⁺:NO₃⁻; this indicated that the deficiency of substrate NO₃⁻ decreased N₂O fluxes. In natural wetlands, we found that plant invasion increased soil moisture by 23.0%, probably because the increased plant coverage reduced evaporation by blocking solar radiation from reaching the soil surface (Kim et al., 2020; Song & Liu, 2016). Lower or even negative N₂O fluxes have been observed after the invasion of wetlands by non-native plants (Wang et al., 2016; Yin et al., 2015; Yuan et al., 2015). This is likely because the more anaerobic conditions and depletion of NO₃⁻ caused by plant invasion were unfavorable for N₂O production, and even consuming atmospheric N₂O (Chapuis-Lardy et al., 2007; Yang & Silver, 2016; Zhu et al., 2013).

Plant invasion significantly increased N₂O emissions from terrestrial ecosystems, with especially grasslands showing an increase of 77.6%; this is different from wetlands. We noted that the *RRd* of terrestrial N₂O emissions showed an exponential decay relation to MAP (Figure 7c), which suggested that a stronger response of N₂O emission to plant invasion occurred at low MAP. As mentioned previously, plant invasion decreased soil moisture from 49.8% to 43.4% WFPS in terrestrial ecosystems and from 47.3% to 39.5% WFPS in grasslands. In general, N₂O is predominantly produced through nitrification, when the soil moisture is less than 60% WFPS (Linn & Doran, 1984). In this study, although the invasion of non-native plants reduced TN, it had stimulatory effects on soil NH₄⁺ concentrations, albeit not significantly. McLeod et al. (2016) found that exotic grasses increased the abundance of ammonia-oxidizing bacteria and N availability in

North American grasslands, which in turn increased soil nitrification rates and N₂O emissions. Norton et al. (2008) performed incubation in the laboratory and reported that drying-wetting cycles (with a range of 9.6% to 37.5% WFPS) more efficiently increased N₂O emission via nitrification from invasive *Bromus tectorum* steppes than from native *Pascopyrum smithii*, primarily because of greater soil mineralization and microbial activity in the invaded sites. A pulse of N₂O in a single summer rainfall event primarily due to nitrification contributed 30% of total N₂O emission in a dry grassland (Mummey et al., 1994). Du et al. (2006) and Xu et al. (2003) found that 64–88% of annual N₂O emission was derived from heterotrophic nitrification in the Inner Mongolian semi-arid grassland. The *RRd* of terrestrial N₂O fluxes was positively correlated with the *RR* of NO₃⁻. We found that plant invasion slightly increased soil NO₃⁻ concentration from 4.54 to 4.96 mg N kg⁻¹ in grassland ecosystems, which was close to but lower than the threshold value of 5.00 mg N kg⁻¹ for denitrification (Dobbie & Smith, 2003). Parker & Schimel (2011) pointed out that denitrification occurred under heavy continuous rainfall in invasive *Bromus hordeaceus*, *Bromus madritensis*, and *Hordeum murinum* grasslands. Thus, it is likely that the increased soil NO₃⁻ was mainly attributable to enhanced nitrification, and the higher N₂O emission was primarily due to the elevated net N mineralization rates and nitrification.

According to the linear mixed-effect analysis, the *RRd* of terrestrial N₂O fluxes showed an exponential decay relation with N_DEP, which indicated that increasing N_DEP reduced the response of N₂O fluxes to plant invasion. As mentioned previously, invasive plants accelerate the turnover and availability of soil N, thus enhancing N₂O emission from grassland ecosystems. However, as exogenous N input increases, the impacts of plant invasion on N availability are weakened and even masked, especially under high N_DEP conditions (Scherer-Lorenzen et al.,

2008). For instance, the *RR* of mineral N decreased to nearly zero when N_DEP was higher than 8.0 kg N ha⁻¹ (Figure S4c). Therefore, the response of N₂O emissions to plant invasion will be weakened by increasing N deposition.

Plant invasion did not greatly affect N₂O emission rates in forest ecosystems when compared with grasslands. Zhang et al. (2011) found that N₂O was mainly sourced from denitrification in subtropical acid forest soils. Zou et al. (2006) also suggested that the higher N₂O emissions of the invasive Chinese tallow tree (*Sapium sebiferum*) ecotype were primarily associated with increased denitrification rates. In this study, however, invasion of plants into forestlands did not change both soil NH₄⁺ and NO₃⁻ concentrations, whereas averaged NO₃⁻ concentrations were lower than the suggested threshold value for denitrification (Dobbie & Smith, 2003). It is therefore likely that the limited extent of plant invasion in forest ecosystems restricted the cascade impacts on CH₄ and N₂O emissions to relatively low levels (Byun et al., 2018; Kier et al., 2005; Martin et al., 2009). Further studies are required to evaluate the extensive impacts of plant invasion on CH₄ uptakes and N₂O emissions in forest ecosystems.

5 Conclusions

We used a meta-analytical approach and found the highest increase in annual CH₄ emission rates in invaded coastal wetlands and the highest increase in annual CH₄ uptake rate in invaded grasslands. Plant invasion increased annual N₂O emission rates in grasslands but not in forests. With a continual increase in the number of cases of plant invasion, greater CH₄ emissions from wetland ecosystems and greater N₂O emissions from grassland ecosystems can be anticipated. In addition, we found the heterogeneity of plant invasion that impacts GHG emissions from different ecosystems can be

explained by climate factors, exogenous N deposition, soil properties, and plant biomass. This knowledge may help to improve our understanding of how plant invasion affects GHG emissions from wetland and terrestrial ecosystems.

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Conflicts of interest

The authors declare no conflict of interests.

Data availability statement

The data that supports the findings of this study are available at Dryad via <https://doi.org/10.5061/dryad.pvmevdnpd>.

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Figure Captions

Figure 1. Violin plots of the response ratio (RR) of plant biomass to non-native plant invasion across different ecosystem types. Red dots represent mean values. Dark cyan, orange, and gray dots indicate the weighted response ratios (\overline{RR}), and error bars of the dots represent 95% confidence intervals (CIs). The numbers within the brackets represent sample sizes.

Figure 2. Effects of non-native plant invasion on soil properties across different ecosystem types. SOC, soil organic C; TN, total N; BD, bulk density; SM, soil moisture; ST, soil temperature. Values are means \pm 95% CIs of the weighted response ratios (\overline{RR}) between the invaded and native ecosystems. The asterisk and closed symbols indicate significant effects, and the open symbols indicate insignificant effects. The number of paired observations is shown beside each soil property.

Figure 3. Effects of non-native plant invasion on CH_4 and N_2O fluxes across the different wetland and terrestrial ecosystem categories. Values are means \pm 95% CIs of the weighted response ratios (\overline{RRd}) between the invaded and native ecosystems. The asterisk and closed symbols indicate significant effects, and the open symbols indicate insignificant effects. The number of paired observations is shown beside each plant species.

Figure 4. Violin plots of CH_4 fluxes with and without non-native plant invasion across the different wetland and terrestrial ecosystem categories. Red dots represent mean values.

Figure 5. Violin plots of N_2O fluxes with and without non-native plant invasion across the different wetland and terrestrial ecosystem categories. Red dots represent mean values.

Figure 6. Relationships between the response ratios (RRd) of CH_4 (dark cyan dots) and N_2O (orange dots) fluxes and latitude, climate factors, N deposition, and response ratios (RR) of soil properties and aboveground biomass after wetland ecosystems were invaded by exotic plants. MAT, mean annual air temperature; \ln_MAP , natural log of mean annual precipitation; RR_SM , RR of soil

moisture; RR_ST, *RR* of soil temperature; RR_AGB, *RR* of aboveground biomass; RR_SOC, *RR* of soil organic C; RR_TN, *RR* of total N; RR_BD, *RR* of bulk density; RR_pH, *RR* of pH; RR_NH₄⁺:NO₃⁻, *RR* of NH₄⁺:NO₃⁻. The colored area around the regression line represents the 95% confidence interval, where *N* is the number of paired observations.

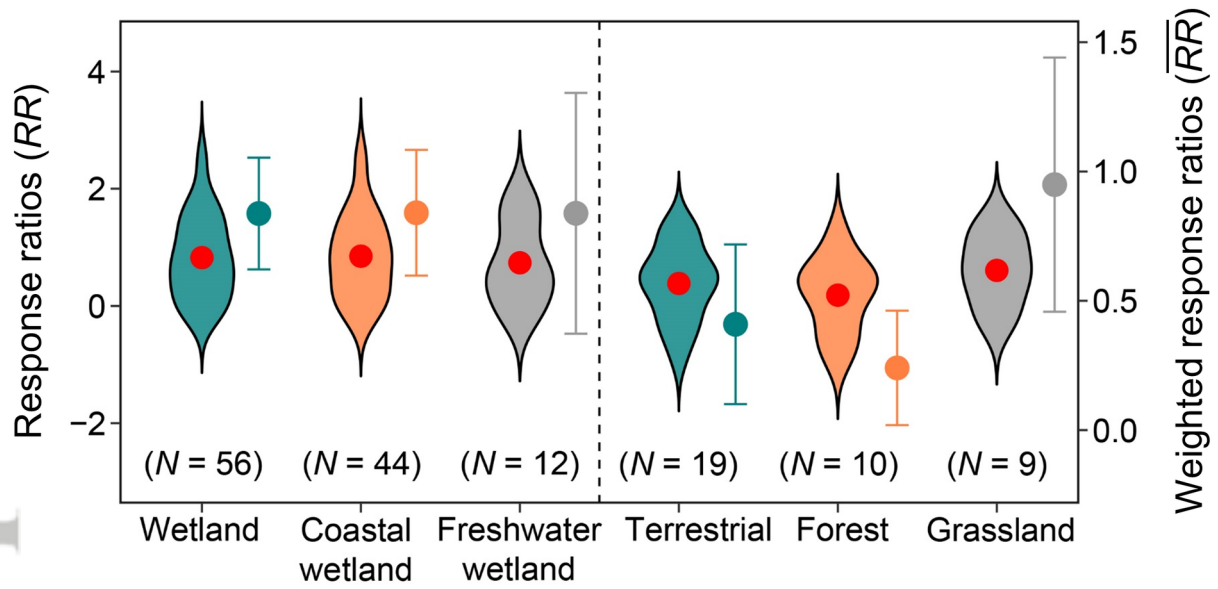
Figure 7. Relationships between the response ratios (*RRd*) of CH₄ (dark cyan dots) and N₂O (orange dots) fluxes and latitude, climate factors, N deposition, and response ratios (*RR*) of soil properties after terrestrial ecosystems were invaded by exotic plants. MAT, mean annual air temperature; ln_MAP, natural log of mean annual precipitation; RR_SM, *RR* of soil moisture; RR_ST, *RR* of soil temperature; RR_SOC, *RR* of soil organic C; RR_TN, *RR* of total N; RR_BD, *RR* of bulk density; RR_pH, *RR* of pH; RR_NO₃⁻, *RR* of NO₃⁻; RR_NH₄⁺, *RR* of NH₄⁺. The colored area around the regression line represents the 95% confidence interval, where *N* is the number of paired observations.

Figure 8. Random forest analysis to identify the main predictors of the response ratios (*RRd*) of wetland CH₄/N₂O fluxes (a, b) and terrestrial CH₄/N₂O fluxes (c, d). The percent increase in mean squared errors (%IncMSE) represents the importance of main predictors, and negative values of %IncMSE, which indicate lack of importance, are not shown. The darker bars reflect key predictors that significantly affect each greenhouse gas flux in wetland and terrestrial ecosystems. MAT, mean annual air temperature; MAP, mean annual precipitation; N_DEP, N deposition; RR_SM, *RR* of soil moisture; RR_ST, *RR* of soil temperature; RR_AGB, *RR* of aboveground biomass; RR_SOC, *RR* of soil organic C; RR_TN, *RR* of total N; RR_BD, *RR* of bulk density; RR_pH, *RR* of pH; RR_NH₄⁺, *RR* of NH₄⁺; RR_NO₃⁻, *RR* of NO₃⁻.

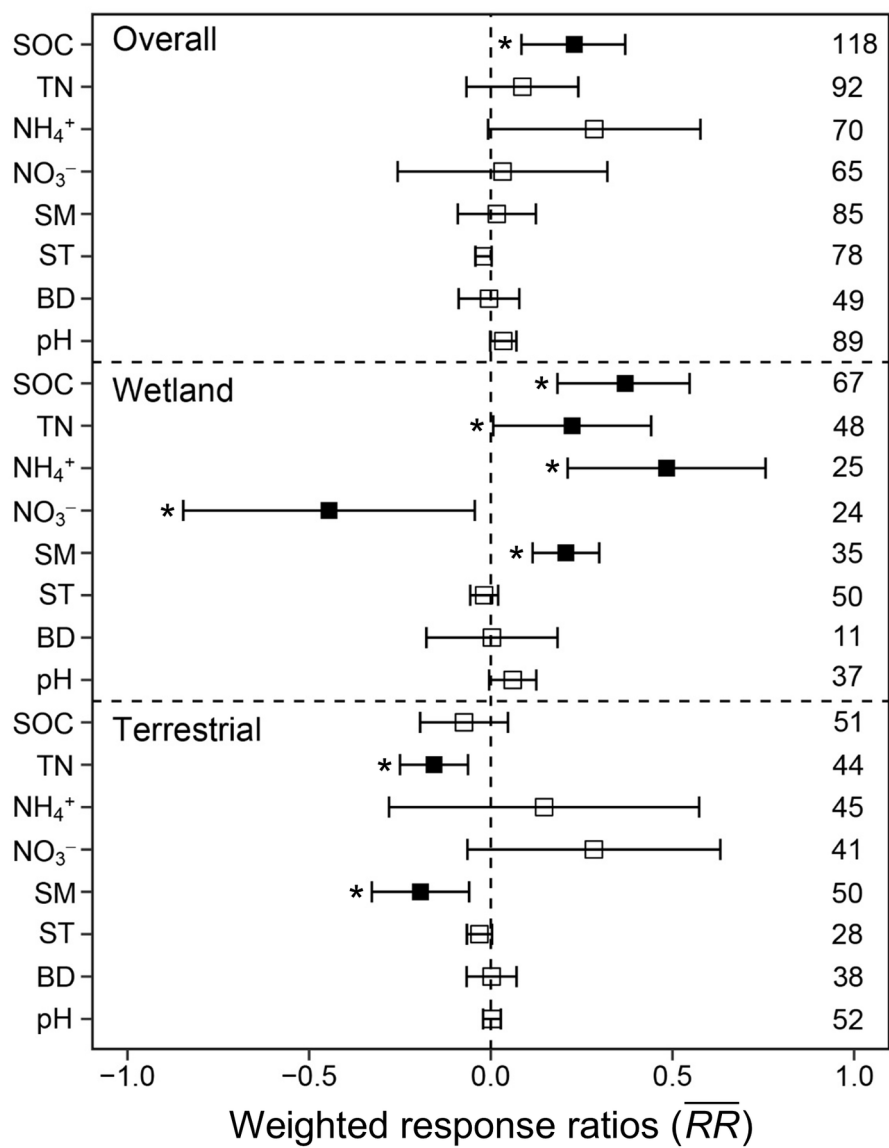
Figure 9. Structural equation models (SEMs) showing the effects of biotic and abiotic factors on the response ratios (*RRd*) of wetland CH₄ (a) and N₂O (b) fluxes. Dark cyan and orange arrows refer

to negative and positive relationships, respectively. Dotted lines denote insignificant paths ($p > 0.05$). The path widths are scaled proportionally to the path coefficient. $*p < 0.05$, $**p < 0.01$, $***p < 0.001$. The letter B within parentheses indicates that the path is a binominal relationship. MAT, mean annual air temperature; MAP, mean annual precipitation; N_DEP, N deposition; RR_AGB, *RR* of aboveground biomass; SOC, soil organic C; TN, total N; BD, bulk density; SM, soil moisture.

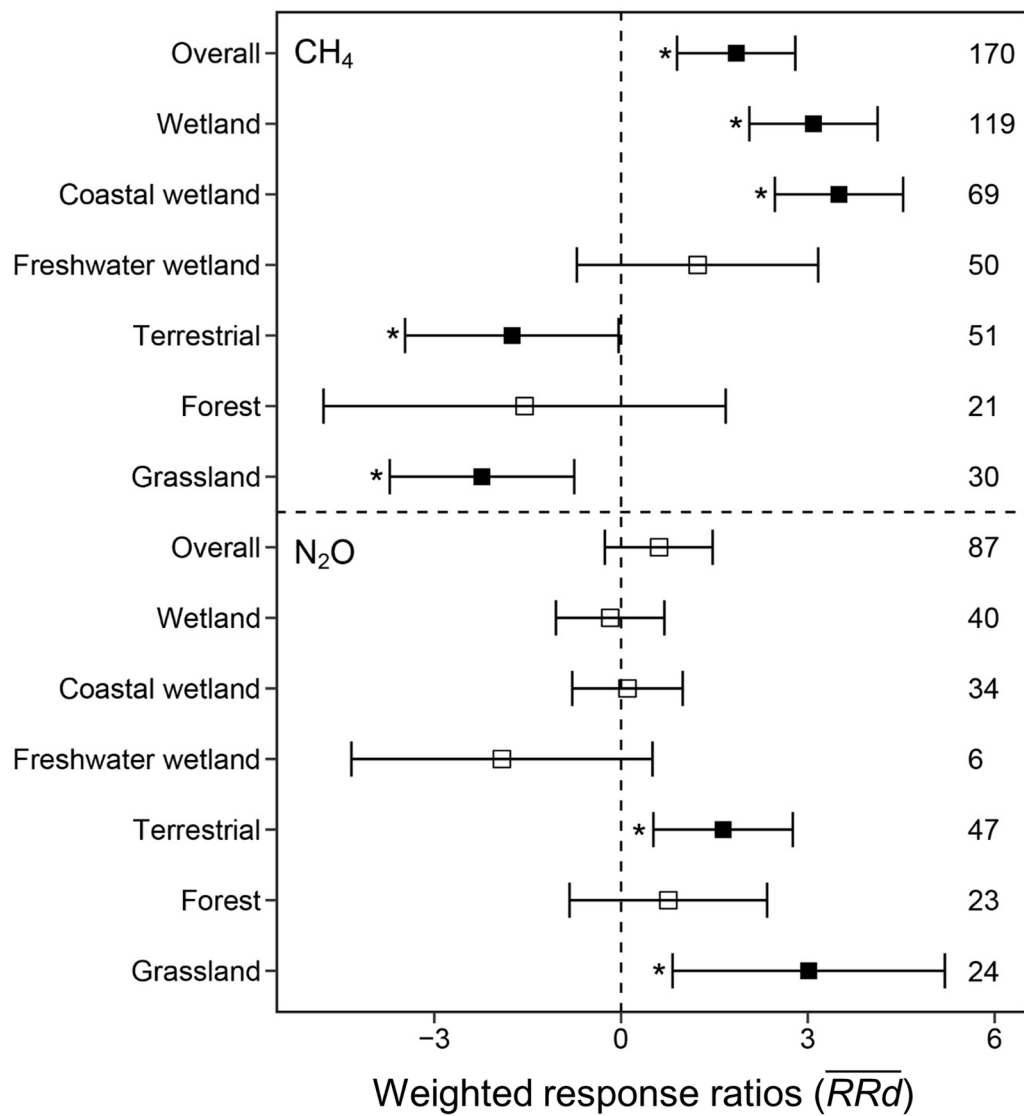
Figure 10. Structural equation models (SEMs) showing the effects of biotic and abiotic factors on the response ratios (*RRd*) of terrestrial CH₄ (a) and N₂O (b) fluxes. Dark cyan and orange arrows refer to negative and positive relationships, respectively. Dotted lines denote insignificant paths ($p > 0.05$). The path widths are scaled proportionally to the path coefficient. $*p < 0.05$, $**p < 0.01$, $***p < 0.001$. MAT, mean annual air temperature; MAP, mean annual precipitation; N_DEP, N deposition; RR_NH₄⁺, *RR* of NH₄⁺; RR_NO₃⁻, *RR* of NO₃⁻; SOC, soil organic C; TN, total N; BD, bulk density; SM, soil moisture.



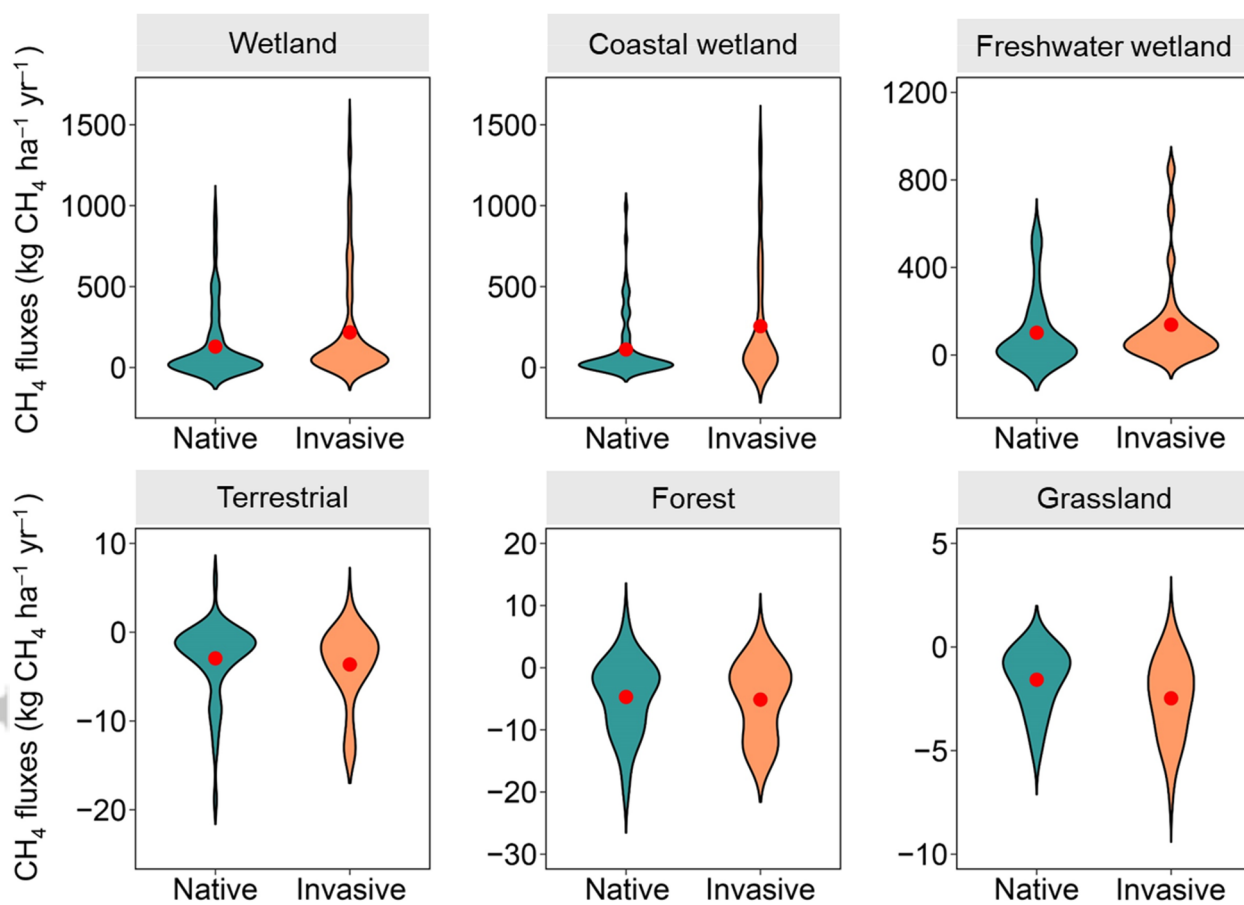
GCB_16290_Figure 1.tif



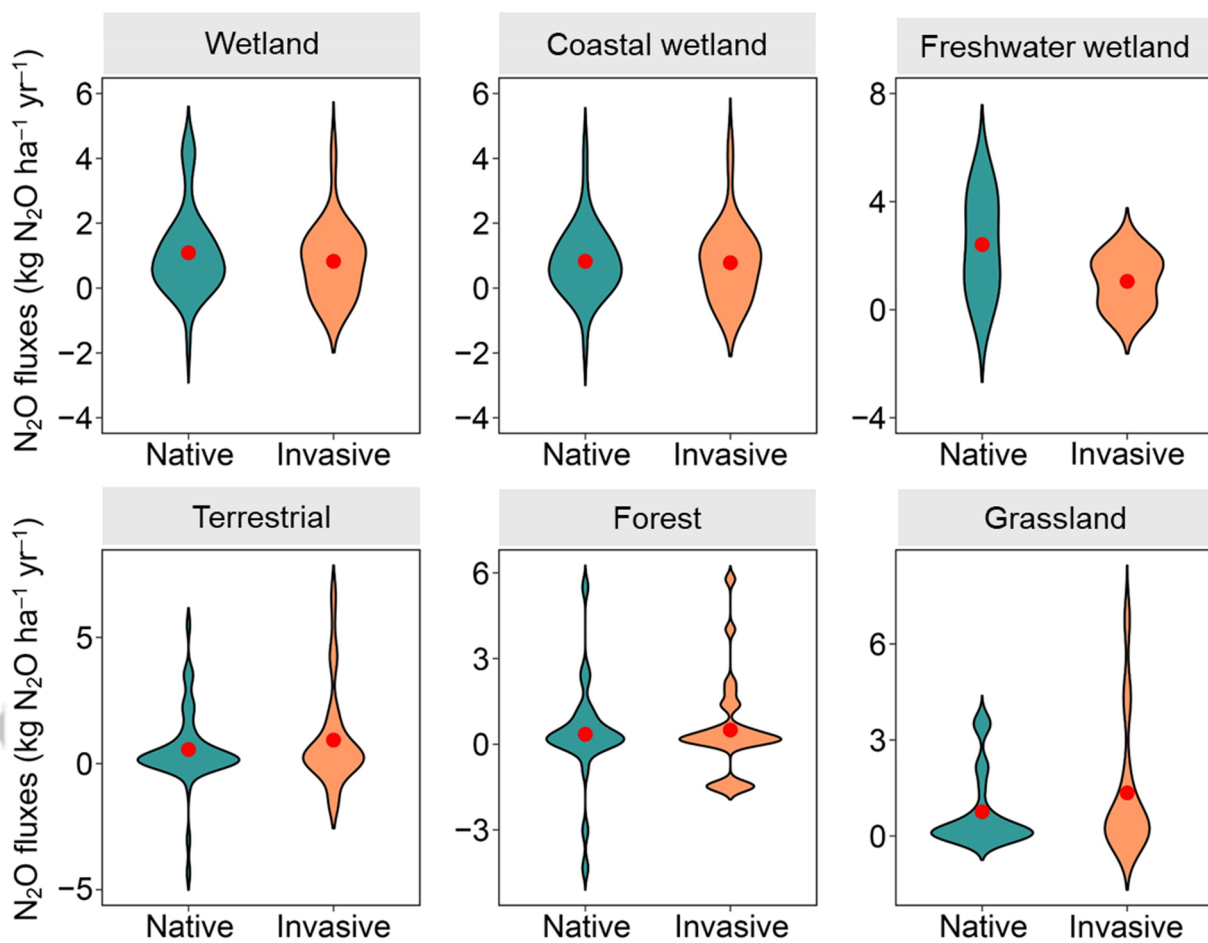
GCB_16290_Figure 2.tif



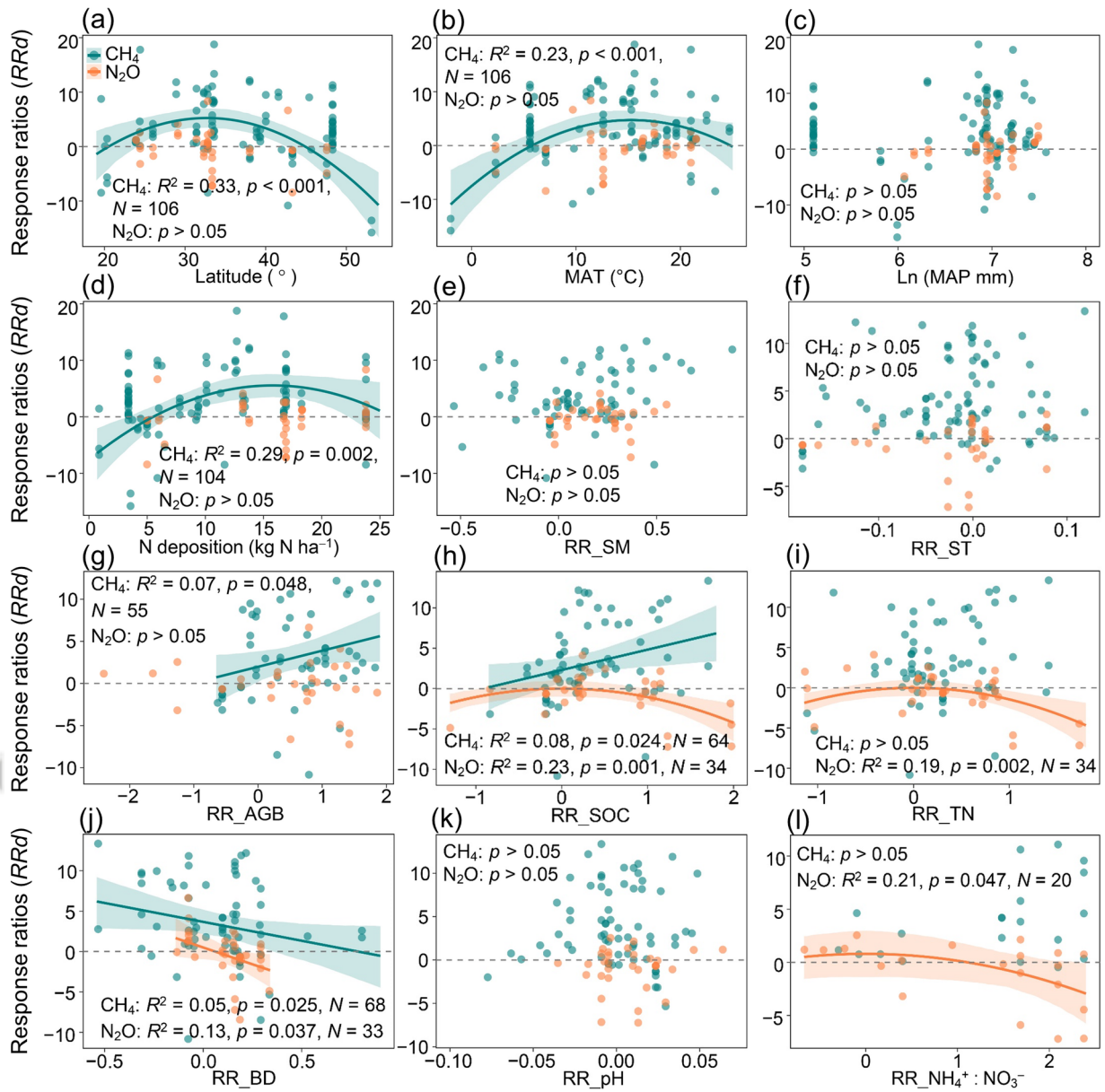
GCB_16290_Figure 3.tif



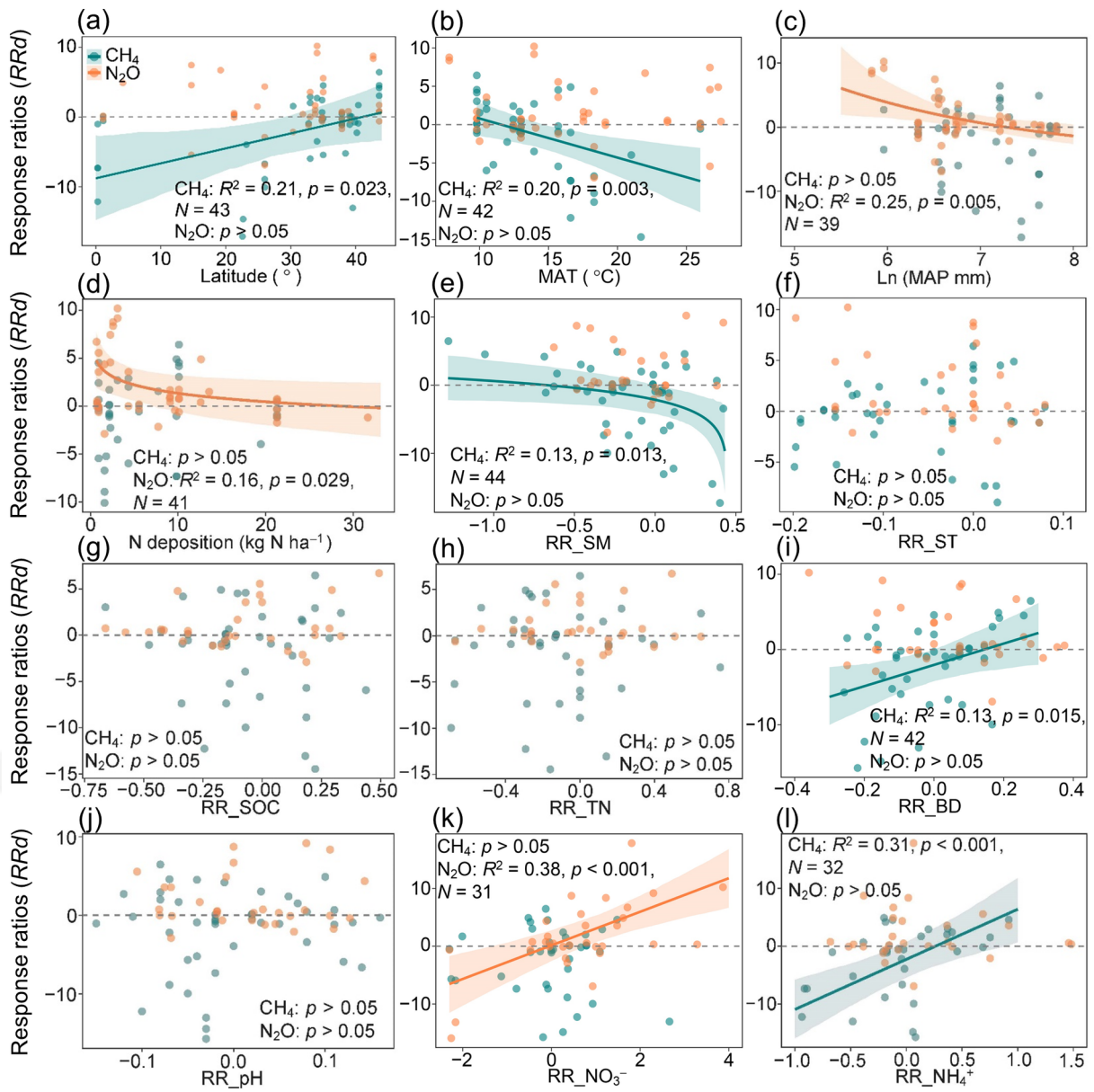
GCB_16290_Figure 4.tif



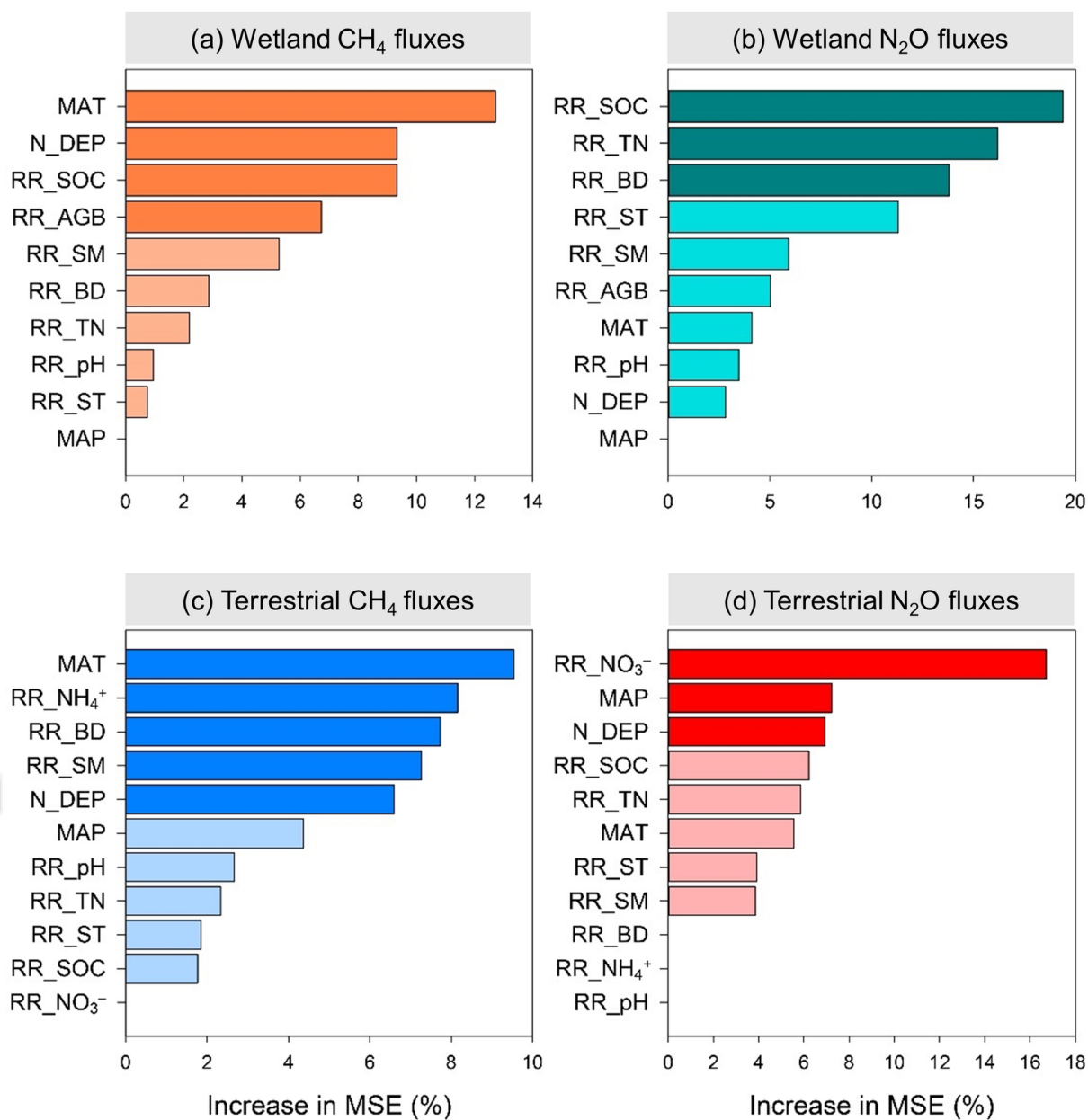
GCB_16290_Figure 5.tif



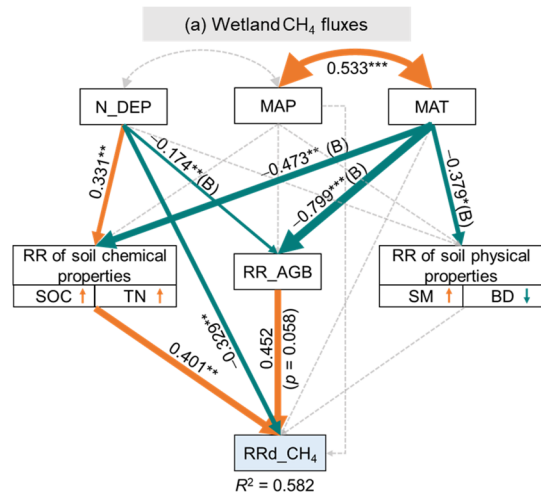
GCB_16290_Figure 6.tif



GCB_16290_Figure 7.tif

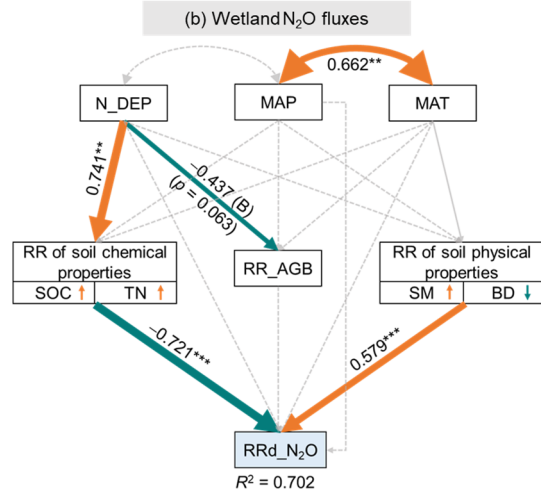


GCB_16290_Figure 8.tif



$$\chi^2 = 3.989, df = 5, p = 0.551,$$

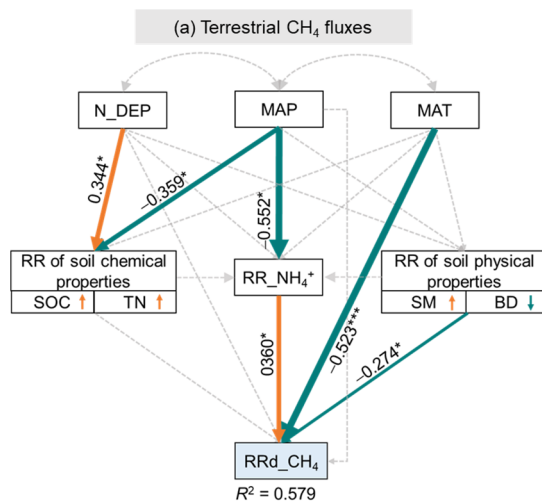
$$RMSEA = 0.000, p = 0.647, CFI = 1.000$$



$$\chi^2 = 6.549, df = 6, p = 0.365,$$

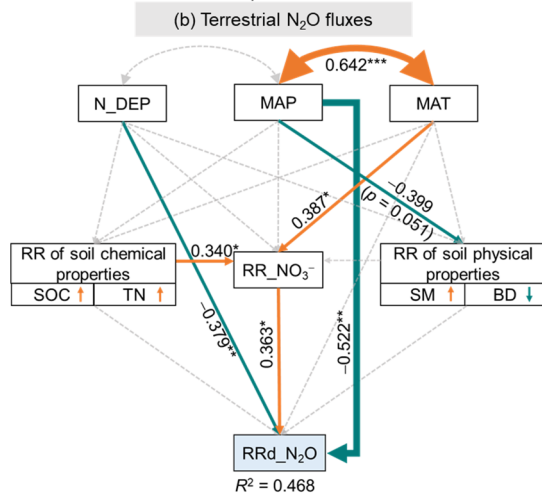
$$RMSEA = 0.048, p = 0.428, CFI = 0.988$$

GCB_16290_Figure 9.tif



$\chi^2 = 3.474, df = 4, p = 0.482,$

RMSEA = 0.000, $p = 0.539$, CFI = 1.000



$\chi^2 = 3.501, df = 4, p = 0.478,$

RMSEA = 0.000, $p = 0.524$, CFI = 1.000

GCB_16290_Figure 10.tif