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1 Climatic zone effects of non-native plant invasion on CH4 and N2O emissions from natural

2 wetland ecosystems

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18 Abstract

Plant invasion markedly alters carbon and nitrogen cycles, and possibly influences the emission of 19 greenhouse gases from wetlands in different climatic zones. In this study, data pertaining to 207 20 paired observational cases from studies on global ecosystems were retrieved for evaluating the 21 effect of non-native plant invasion on the emission of CH₄ and N₂O from tropical/sub-tropical (TS) 22 and temperate (TE) wetlands. The mean CH₄ emission rate from TS wetlands increased 23 significantly from 337 to 577 kg CH₄ ha⁻¹ yr⁻¹ in sites populated with native and invasive plants. 24 respectively, while that of TE wetlands increased from 211 to 299 kg CH₄ ha⁻¹ yr⁻¹ in sites 25 populated with native and non-native plants, respectively. The increase in CH₄ emissions in 26 invaded sites was possibly attributed to the increases in plant biomass, soil organic carbon (SOC), 27 and soil moisture (SM). Plant invasion did not affect the emission of N₂O from TS wetlands, but 28 reduced the emission of N₂O from TE wetlands, and this was primarily attributed to the depletion 29 of NH₄⁺ and NO₃⁻ in soils and the lower soil temperature in temperate regions. Plant invasion 30 increased the global net CH₄ emissions from natural wetlands by 10.54 Tg CH₄ yr⁻¹, which varied 31 across different climatic zones. The net increase in CH₄ emissions was 9.97 and 0.57 Tg CH₄ yr⁻¹ in 32 TS and TE wetlands, respectively. Our finding not only highlights that plant invasion exhibited 33 strong stimulation effect on CH₄ emission in TS wetland and suppression effect on N₂O emission in 34 TE wetland but also improves our current understanding of major controlling factors, which is vital 35 to producing curving mechanisms. 36

Keywords: Climate zones; plant invasion; CH₄ emission; N₂O emission; wetland ecosystem
 39

40 1. Introduction

Natural wetlands are a major contributor to carbon sequestration, and it is estimated that they play a 41 crucial role in atmospheric CO₂ fixation (Schlesinger and Bernhardt, 2013). However, wetlands are 42 the largest source of CH₄ worldwide, and contribute 100 to 231 Tg CH₄ annually (IPCC, 2007; 43 IPCC, 2013). The proportion of CH_4 emitted from the northern, temperate, and tropical wetlands is 44 estimated to be 34%, 5%, and ~60%, respectively (Wang et al., 1996). Cao et al. (1996) reported 45 that the annual emission of CH₄ from natural wetlands is 92 Tg CH₄, of which the tropical wetlands 46 release 51.4 Tg CH₄. Bartlett and Harriss (1993) estimated that the global CH₄ emission of wetlands 47 is 109 Tg CH₄ yr⁻¹, and tropical and temperate wetlands account for 61% and 5% of the total 48 emission, respectively. Previous studies have reported that the CH₄ fluxes of tropical wetlands are 49 generally higher than those of temperate wetlands (Frank and Hein, 2021), which is possibly 50 51 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 52 with a dramatic increase in global consumption and the proliferation of invasive plants (Pegg et al., 53 2022), which represents a major global challenge in natural ecosystems with the potential to 54 significantly modify greenhouse gas (GHG) emissions (Mantoani et al., 2021). 55

Numerous previous studies have found that plant invasion alters CH₄ and N₂O emissions in
natural ecosystems (Cheng et al., 2007; Gao et al., 2019; Qiu, 2015; Yao et al., 2023). Yuan et al.

58	(2015) reported that the invasion of <i>Spartina alterniflora</i> increased the emission of CH ₄ in a coastal
59	salt marsh in China by 57-505%. The introduction of <i>Phragmites australis</i> into a temperate tidal
60	marsh in Korea populated by the native Suaeda japonica increased the emission of CH4 by up to
61	2000% (Kim et al., 2020). Another study reported that the invasion of Typha \times glauca in a
62	temperate coastal marsh in USA increased the emission of CH ₄ by more than 50-fold compared to
63	that induced by the native species, Carex stricta (Lawrence et al., 2017). Gao et al. (2019) showed
64	that the invasion of S. alterniflora in the mangrove wetlands of China increased the emission of
65	N_2O by 2500%. However, Grand and Gaidos (2010) observed that the emission of CH_4 from a
66	tropical wetland in USA did not increase following plant invasion, and similar observations were
67	reported by Jiang et al. (2009) in a sub-tropical wetland in China. Additionally, some studies have
68	reported that the invasion of plant species reduced the emission of CH4 and N2O in tropical and
69	sub-tropical wetlands (Sheng et al., 2021; Yin et al., 2015; Zhang et al., 2018). Bezabih et al. (2022)
70	estimated that plant invasion increased CH_4 emissions in wetland ecosystems by 68% and $\mathrm{N}_2\mathrm{O}$
71	emissions in grassland ecosystems by 78%. A recent meta-analysis by Yao et al. (2023) found that
72	plant invasion in natural ecosystems enhanced CH_4 and N_2O emissions by 94.6% and 27.3%,
73	respectively. As for regions, the net increase in CH ₄ emissions from S. apetala invaded mangrove
74	wetland in Hainan Island, China, was 0.04 Tg CH_4 yr ⁻¹ and accounts for 2.5% of the global
75	mangrove wetland CH_4 emission (1.6 Tg yr ⁻¹) (He et al., 2019). Gao et al. (2019) estimated that the
76	total N2O emission from invasive Spartina alterniflora wetlands in China covering 55181 ha was

approximately 0.06 Tg N₂O yr⁻¹, and accounts for ~0.60% of the global N₂O emission (9.6–10.8 Tg N₂O yr⁻¹) (IPCC, 2013).

79	Plant invasion altered several biotic and abiotic factors, including soil properties (Stefanowicz
80	et al., 2016; Tong et al., 2012; Xiang et al., 2015; Zhang et al., 2010; Zhou et al., 2015) and plant
81	biomass (Su et al., 2020; Zhang et al., 2010; Zhou et al., 2015). Plant invasion can modify soil
82	properties by increasing the deposition of litter and rhizodeposits (Liao et al., 2008; Ravichandran
83	and Thangavelu, 2017). It has been reported that the quantity and chemical quality of litter and
84	rhizodeposits differ among species (Chen et al., 2015; Zhu et al., 2020). Invading plants can also
85	modify fundamental ecosystem processes, including the decomposition of organic matter and
86	nitrogen fixation (Hawkes et al., 2005; Liao et al., 2008; Rice et al., 2004; Stefanowicz et al., 2016;
87	Tharayil et al., 2013). Invading plants can affect the structure of vegetation by displacing the native
88	species and altering the rates and patterns of nutrient cycling (D'Antonio and Vitousek, 1992;
89	Ravichandran and Thangavelu, 2017), which alter the composition of soil microbes (Windham and
90	Ehrenfeld, 2003). In turn, soil microbes are one of the key components that facilitate or inhibit plant
91	invasion (Beckstead and Parker, 2003; Inderjit and van der Putten, 2010; van der Putten et al.,
92	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)

97	and belowground biomass (BGB) of sites in the temperate coastal wetland of the USA compared to
98	those of sites populated with native sedges, rushes, and bulrushes. In Yancheng Natural Reserve in
99	China, plant carbon storage following S. alterniflora invasion was increased by 16.9 and 1.4-fold
100	compared with native Suaeda salsa and P. australis, respectively (Zhou et al., 2015). The increase
101	in biomass production directly increases the organic carbon input of soils in the form of exudates
102	and root debris for methanogenesis (Christensen et al., 2002). Zhang et al. (2019) reported that the
103	increase in the SOC of a wetland populated with S. alterniflora was 5-fold higher than that of a
104	wetland occupied by the native S. salsa. Xu et al. (2014) and Xiang et al., (2015) estimated that the
105	invasion of S. alterniflora increased the SOC in a coastal wetland in China by 3-fold compared to
106	that of the native plants, S. glauca and Salix glauca, and depended on the time of invasion (Zhang et
107	al., 2010b). The increase in SOC due to an increase in plant biomass also provides more substrates
108	for the production of CH ₄ (Christensen et al., 2002; Zhao et al., 2017).
109	Up to date, however, there has been less work on the net GHG emissions induced by plant
110	invasion at the global climatic zone level. In this study, the emission of CH_4 and N_2O from natural
111	wetlands populated by invasive and native plants in different climatic zones was evaluated at the
112	global level based on published peer-reviewed studies. The present study aimed to evaluate the
113	effect of the invasion of non-native plants on the emission of CH4 and N2O in different climatic
114	zones and identify the key factors that affect the annual emission of CH_4 and N_2O following plant
115	invasion in different climatic zones. The study also aimed to estimate the effects of plant invasion
116	on the net global budgets of CH4. We hypothesized that plant invasion would more efficiently

increase CH₄ emissions in tropical/sub-tropical wetlands than in temperate wetlands due to higher
temperatures and a longer growth season.

119

120 **2. Materials and Methods**

121 *2.1. Data retrieval*

122 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 123 study. The keywords used for the literature searches were "plant invasion" OR, "invasive" AND 124 "non-invasive", "native" AND "non-native plant", "exotic" AND "non-exotic" plant species, 125 "effects" OR "impacts" on "greenhouse gases", and "CH4" OR "N2O". A systematic review was 126 conducted to avoid bias during data retrieval using the criteria described hereafter. Field observation 127 studies not involving field manipulation or experimental studies at sites populated with invasive and 128 native plants were included. Studies in which each of the treatments included at least three 129 130 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 131 warming were excluded. Studies addressing the effects of expanding or colonizing native species, 132 such as woody or shrub encroachment were excluded. The densely invaded sites were considered 133 for studies in which a site populated with native plants was compared to sites populated with 134 varying densities of invasive species. Lastly, if a paper included data from multiple sites, the data 135 from each site was regarded as separate and independent. 136

137	The Web Plot Digitizer tool (version 3.11; https://automeris.io/WebPlotDigitizer) was used to
138	extract the data presented in the figures and plots in the articles. Both manual and automatic
139	data-extraction algorithms were used after calibration with the corresponding values from the plots
140	and images. Alternative descriptive sources, including the global invasive species database (GISD;
141	http://www.issg.org), were used if the study did not specify whether the plants were invasive or
142	native to the case study area. The data pertaining to CH_4 and $\mathrm{N}_2\mathrm{O}$ fluxes were converted to kg ha ⁻¹
143	yr ⁻¹ . Auxiliary information, including the location (longitude, LON and latitude, LAT), climatic
144	data (annual mean air temperature, MAT and mean annual precipitation, MAP), plant biomass,
145	plant height, and soil properties such as soil pH, SOC, total nitrogen (TN), bulk density (BD),
146	contents of NO3 ⁻ and NH4 ⁺ , soil temperature (ST), and soil gravimetric water content (SM), were
147	additionally obtained. The mean values, standard deviation (SD), and sample sizes of all the
148	variables in ecosystems populated with invasive and native species were retrieved. In c cases where
149	the articles reported the standard error (SE) of the variables instead of the SD, the SD was
150	determined using the formula: SE $\times \sqrt{n}$, where <i>n</i> represents the sample size. However, in case where
151	the values of SD or SE were not reported, the SD was calculated as 1/10 th of the mean (Luo et al.,
152	2006). The authors of the relevant studies were contacted to obtain any useful information not
153	published in the articles. If the authors were unable to provide the requested information, the data
154	pertaining to soil properties were retrieved from the Harmonized World Soil Database, version 1.2
155	(FAO, 2012), based on the geographic coordinates of the study location. Data pertaining to the
156	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).

162

163 2.2. Data organization and estimation of net CH_4 and N_2O emissions induced by plant invasion

Owing to spatial variations in the CH₄ and N₂O fluxes across wetland ecosystems in different 164 climatic regions, the dataset was subcategorized into (1) tropical/sub-tropical (TS) wetlands and (2) 165 temperate (TE) wetlands. The datasets obtained from tropical and sub-tropical regions were merged 166 to increase the number of paired observational cases. The net emission of CH₄ induced by plant 167 invasion was estimated for each species by calculating the difference in CH₄ fluxes between 168 wetland sites populated with non-native plants and those occupied by native species. The fluxes 169 170 were subsequently multiplied by the area invaded by each species. The regional and net global CH4 emissions were then summed for each species based on their global distribution and geographic 171 locations. However, net global N₂O emission estimations were not included in our present 172 estimation because of the paucity of data about the area coverage of invasive plants that were 173 considered for N₂O measurements in each region. 174

175

176 *2.3. Data analyses*

The effect size of the CH₄ and N₂O fluxes from wetlands in different climatic regions was estimated 177 using Hedge's d (RRd) method. Hedge's d is a unit-free index that ranges from $-\infty$ to $+\infty$ (Qiu, 178 2015). This index weights cases according to the number of replicates, and the inverse of their 179 variance is calculated as Xt/Xc < 0, where Xt and Xc represent the mean values of GHG fluxes 180 from sites populated with invasive and native species, respectively (Wu et al., 2022). The index is 181 182 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 183 indicate a greater effect size. Additionally, zero d-values indicate no difference, whereas positive 184 and negative d-values indicate a general increase and decrease in the response variable, 185 respectively, following plant invasion (Oiu, 2015). The effect of plant invasion on environmental 186 factors was evaluated using natural logarithm-transformed response ratios (RRs). The RRs for a 187 given case study were calculated using the following formulas: 188

189
$$RR = ln(Xt / Xc)$$
 (1)

190 RRd =
$$\frac{(Xt-Xc) \times J}{\sqrt{\frac{(Nt-1)St^2 + (Nc-1)Sc^2}{Nt+Nc-2}}}$$
 (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; *N*t and *N*c represent the sample sizes obtained from sites populated with invasive and native species, respectively; and *S*t and *S*c 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:

197
$$J = 1 - \frac{3}{4(Nt + Nc - 2) - 1}$$
 (3).

198	The RRs of the environmental factors, plant parameters, soil properties, and RRd of the GHG
199	fluxes were calculated using the rma.mv function in the "metafor" package of R, version 4.2.1
200	(Balduzzi et al, 2019). A random-effects model was preferred because it accounts for the random
201	component of variation in effect sizes among studies besides sampling error (Castro-Díez et al.,
202	2014). The relationships of the environmental factors, plant parameters, and soil properties with the
203	weighted RRd of CH4 and N2O fluxes following plant invasion in different climatic regions were
204	calculated using the OriginPro 2022b software. The violin and box plots of plant biomass and CH4
205	and N ₂ O fluxes in response to plant invasion in wetland ecosystems across different climatic
206	regions were prepared using OriginPro 2022b. The relative importance of the environmental factors,
207	plant parameters, and soil properties that affect the CH4 and N2O fluxes following plant invasion
208	was determined by random forest analysis. The Random Forest algorithm is a machine learning
209	technique that can handle both linear and nonlinear classification and regression problems with
210	non-parametric data. This algorithm is robust to outliers and missing values, enabling the
211	integration of complex data from various sources in high-dimensional spaces without overfitting
212	(Hengl et al., 2015; Guo et al., 2015). For our study, the total number of observations used to
213	predict CH ₄ emissions in TS and TE wetlands was 104 and 82, respectively, while 36 and 10
214	observations were used to predict N ₂ O emissions in TS and TE wetlands, respectively. Any missing
215	values for soil and environmental factors were imputed by using the nearest neighbor algorithm
216	(Beretta and Santaniello, 2016; Troyanskaya et al., 2001; Tang and Ishwaran, 2017). Plant

characteristics, including aboveground biomass, belowground biomass, stem density, and plant 217 height were not included in the random forest model and SEM because of data scarcity. Finally, the 218 predictors were ranked in order of importance according to the percent increase in mean square 219 error (%IncMSE), and negative values of %IncMSE indicated a lack of importance (Liaw and 220 Wiener, 2002). Additionally, structural equation model (SEM) was used to assess the multivariate 221 222 effects of environmental factors and soil properties on regulating the responses of CH₄ and N₂O fluxes to invasive plants in TS and TE wetlands. We conducted a correlation matrix, and then 223 "lavaan" packages of R were used for SEM. Maximum likelihood estimation was used to fit the 224 SEM, and the model was evaluated based on the modification indices and goodness of fit after 225 stepwise exclusion of non-significant paths. Fit indices including the degree of freedom (df), 226 chi-square, probability level (p > 0.05), comparative fit index (CFI) closer to 1.0, and root mean 227 squared error of approximation index (RMSEA < 0.05) were used to evaluate the adequacy of the 228 SEM (Grace et al., 2012; Schermelleh-Engel et al., 2003; Zhou et al., 2022). 229

230

3. Results

232 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 NH₄⁺ content, and soil moisture (SM) content by 68%, 106%, 38%, and 17%, respectively, reduced soil bulk density (BD) and soil NO₃⁻ 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 NO₃⁻ and NH₄⁺ by 114% and 76%, respectively, in TE wetlands. Additionally, plant invasion increased SM in TE wetlands by 5% but decreased BD by 9%.

241

242 3.2. Effect of plant invasion on CH_4 and N_2O fluxes

The findings revealed that plant invasion significantly increased (p < 0.05) CH₄ fluxes by 62% in 243 global wetland ecosystems (Fig. 3). The mean CH₄ flux in TS wetlands populated with native plants 244 was 337 kg CH₄ ha⁻¹ yr⁻¹, which increased significantly by 71% to 577 kg CH₄ ha⁻¹ yr⁻¹ following 245 the invasion of exotic plants (Fig. 4). The invasion of non-native plants in TE wetlands increased 246 CH₄ fluxes from 211 kg CH₄ ha⁻¹ yr⁻¹ in sites populated with native plants to 299 kg CH₄ ha⁻¹ yr⁻¹ 247 in sites occupied by invasive species; however, the differences in CH₄ fluxes were not statistically 248 significant. In contrast, there was no apparent difference in N₂O fluxes following plant invasion in 249 TS wetlands. However, plant invasion significantly reduced N₂O fluxes in TE wetlands from 1.28 250 kg N₂O ha⁻¹ yr⁻¹ in sites populated with native plants to 0.60 kg N₂O ha⁻¹ yr⁻¹ in sites occupied by 251 invasive species (Fig. 4). 252

253

3.3. Factors affecting the difference in CH₄ and N₂O fluxes following plant invasion in different
climatic zones

256 There was a significant positive linear relationship between the weighted response ratios (\overline{RRd}) of CH₄ fluxes and nitrogen deposition (ND), the RR of SOC, the RR of TN, the RR of AGB, the RR 257 of plant height, and the RR of SM in TS wetlands (Fig. 5). However, the \overline{RRd} of CH₄ fluxes 258 exhibited a negative linear relationship with the RR of soil NO₃⁻. The \overline{RRd} of N₂O fluxes exhibited 259 a significant positive linear relationship with the RR of soil pH and the RR of soil NO₃ in TS 260 261 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 CH₄ fluxes in TE wetlands also exhibited a quadratic 262 relationship with the MAT, and RR of SM, and a negative linear relationship with the RR of ST 263 (Fig. 6). 264

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 CH₄ fluxes in TS wetlands (Fig. 7). The MAT, RR of SM, and RR of ST were identified as key factors that regulated the CH₄ fluxes in TE wetlands following plant invasion. Our results demonstrated that the RRd of SOC, RR of NO₃⁻, and RR of SM were the most important factors that affected the N₂O fluxes in TS wetlands. The MAT, RR of SOC, and RR of SM were identified as the most important factors that influenced the N₂O fluxes in TE wetlands following plant invasion.

The structural equation model (SEM) explained 50% and 46% of the variance in the RRd of CH₄ fluxes in TS and TE wetland, respectively, while 61% and 83% of the variance in the RRd of N₂O 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

276	significant role in CH_4 and N_2O fluxes in TS and TE wetlands. The SOC, SM, and TN had the
277	greatest role in regulating the responses of CH ₄ fluxes to plant invasion in TS wetlands, while MAT,
278	ST, and SM had a significant role in CH ₄ fluxes in TE wetlands. For N_2O fluxes, soil NO_3^- , SM,
279	and SOC had the greatest impact on the response of N_2O fluxes in TS wetlands, while MAT and
280	SM had a substantial role in the response of N ₂ O fluxes in TE wetlands.
281	
282	3.4. Plant invasion increased the net CH_4 emission of wetlands
283	Based on the area coverage of 15 key non-native plant species included in our datasets and their mean
284	difference in CH ₄ fluxes with native plant species (Table 1), we estimated plant invasion increased
285	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

287 CH₄.

288

289 **4. Discussion**

290 *4.1. Alterations in CH*₄ *emission from TS wetlands following plant invasion*

The findings revealed that plant invasion significantly increased the annual CH₄ emission of TS wetlands. Banik et al. (1993) and Das and Krishnakumar (2022) reported that the CH₄ 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 CH₄ fluxes by 140–220%. The higher CH₄ fluxes of TS wetlands populated with invasive species are attributed to the followingfactors, which are described hereafter.

Firstly, the present study revealed that the invasion of exotic plants significantly increased the 298 SM by 17%, and the \overline{RRd} of CH₄ emission was correlated to the RR of SM in TS wetlands. 299 However, the increase in SM following plant invasion was contrary to the findings of previous 300 301 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 302 evapotranspiration in invasive grasslands is responsible for the reduction in SM and is primarily 303 attributed to the higher plant biomass and longer duration of persistence (Dar et al., 2019; Wang et 304 al., 2015; Wolf et al., 2004). In contrast, the higher SM of water-rich wetland ecosystems following 305 plant invasion is attributed to the much higher coverage of invasive plants, which reduces the rate of 306 evapotranspiration (Lin et al., 2013), and increased SOC that enhances soil water holding capacities 307 (Bu et al., 2018; Bu et al., 2019). The increase in the SM lowers the diffusivity and concentration of 308 309 oxygen, which favors for the formation of anaerobic environment for CH₄ production, and reduces the activity of aerobic microbes in the soils (Román et al., 2015; Rubol et al., 2013), which in turn 310 increases the dissolved organic carbon and promotes the production of CH₄ by methanogens (Liu et 311 al., 2019a; Liu et al., 2019b). The increase in the SM also alters soil microbial community 312 compositions and increases the copies of methanogenic mcrA genes (Rankin et al., 2018; Yao et al., 313 2023; Zhang et al., 2018; Zhou et al., 2022), causing an increase in CH₄ production rates (McLain et 314 al., 2002; Warner et al., 2017). 315

316	Secondly, the present study revealed a significant correlation between the \overline{RRd} of CH ₄
317	emission and the RRd of AGB. Within our dataset, AGB increased by 3.29-fold following plant
318	invasion in TS wetlands, compared to sites populated with native species. Numerous previous
319	studies reported that invasive plants are more prevalent in TS wetland than TE wetlands, with a
320	rapid reproductive rate, complex root structure, and a very fast doubling capacity of plant biomass
321	within a short period of time (Villamagna and Murphy, 2010; Hu et al., 1998; Owens et al., 1995).
322	This is probably due to the high concentration of nutrients sourced from agricultural runoff,
323	deforestation, insufficient wastewater treatment, and untreated sewage to wetland ecosystems
324	(Villamagna and Murphy, 2010; Sun et al., 2021). In turn, eutrophication processes can exacerbate
325	plant invasiveness (Sepulveda-Jauregui et al., 2018; Wassmann et al., 1992). The increase in AGB
326	resulted in the generation of higher quantities of exudates and debris for methanogenesis (Chanton
327	et al., 1997; Christensen et al., 2002; Repo et al., 2007). Angeloni et al. (2006) reported that the
328	AGB and BGB at sites following the invasion of the cattail species, $Typha \times glauca$, were nearly
329	2-fold the AGB and BGB of sites populated by native sedges, rushes, and bulrushes. Another study
330	demonstrated that invasive plants produce deeper roots, which enhance the distribution of root
331	exudates to deeper layers and increase the number of microsites for the production of CH4 (von
332	Fischer and Hedin, 2007). However, fast-growing invasive plants have lower lignin content (Arthur
333	et al., 2012; Liao et al., 2008), and lower carbon:nitrogen and lignin:nitrogen ratios (Poulette and
334	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 CH₄ emission in TS wetlands was 337 correlated to the RRd of SOC. The SOC increased by 68% on average in TS wetlands populated 338 with invasive species. Gao et al. (2012) also reported that the increase in SOC in the tidal salt 339 marshes of China is attributed to the well-developed rhizomes and increased BGB of the invasive 340 species, S. anglica and S. alterniflora. Interestingly, Liu et al. (2019) found that even though they 341 both have similar BGB, S. alterniflora can release more labile organic carbon in the rhizosphere 342 than *P. australis*. In this study, we are unable to identify whether the increase in SOC was primarily 343 attributed to the litters, rhizomes, or exudates of the invasive plants, and further studies are 344 necessary in this regard. Yuan et al. (2015) reported that the rate of carbon sequestration in 345 marshlands populated with S. alterniflora was 3.16 Mg C ha⁻¹ yr⁻¹ in the top 100 cm of the soil, 346 which was 2.63 and 8.78-fold higher than that of marshlands populated with the native plants, S. 347 348 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 349 the accumulation of SOC. Previous studies have reported that the increase in SOC in TS wetlands 350 351 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 352 on a sulfate-rich salt marsh reported that an increase in the SOC following plant invasion also 353 increased the abundance of methanogenic archaea and caused a shift in the dominant methanogens 354

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 CH₄ emission correlated with the 358 RR of plant height, and this finding was consistent with the results obtained in studies by Ding et al. 359 (1999), Zhou et al. (2016), and Qi et al. (2021). In this study, the height of the invasive plants in TS 360 wetlands was 1.84 times higher than that of the native plants. In general, the tiller number and leaf 361 area increased with an increase in plant height, which increased the formation of aerenchyma and 362 the release of CH₄ into the atmosphere (Bansal et al., 2020; Granse et al., 2022; Schimel, 1995; 363 Struik et al., 2022). The results of these studies agree with the aforementioned finding of the present 364 study, which revealed that the deeper roots of invasive plants are more efficient in releasing the CH₄ 365 produced in the deeper soil layers of wetlands. 366

Fifthly, the present study revealed that the \overline{RRd} of CH₄ emission in TS wetlands was 367 368 positively associated with the ND, and peak CH₄ 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 369 quality by increasing the nitrogen availability of the soil (Iversen et al., 2010; Liao et al., 2008), and 370 stimulates microbial reproduction (Bai et al., 2010; Chen et al., 2011; Le Quéré et al., 2009; 371 Thomas et al., 2012; Treseder, 2008). This in turn enhances the conversion of residues into SOC 372 and substrates for the utilization of methanogens by better optimizing microbial stoichiometries 373 (Brown et al., 2014). In this study, the growth of invasive plants was found to be more effectively 374

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).

380

381 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 CH4 382 from TE wetlands. As discussed above, or AGB although plant invasion also increased plant 383 biomass in TE wetlands, however the increase rate was far lower than that in the TS wetland (142%) 384 vs. 229% for AGB). Previous studies have shown that differences in plant size, leaf area allocation, 385 shoot allocation and growth rate between invasive plants and native plants in TS regions are larger 386 than those in TE regions (Van Kleunen et al., 2010). In the present study, it is likely that the 387 388 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 389 alter the SOC of TE wetlands. These findings indicated that plant invasion did not effectively 390 increase the availability of substrates for methanogens. The results demonstrated that the significant 391 increase in the ABG and BGB was not correlated with the apparent lack of changes in the SOC 392 following plant invasion. This could also be attributed to the fact that the relatively lower 393 temperatures in the temperate region suppress the conversion of plant litter into SOC (Zhang et al., 394

395 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 396 ecosystems. A previous study revealed that the rate of mineralization of lignocellulose in S. 397 alterniflora was positively correlated with temperature (Benner et al., 1986). The phenomenon 398 could also be attributed to the relatively low water tables in TE wetlands such as peatlands, the 399 levels of which generally range from 20 to >50 cm below the surface owing to low precipitation 400 (Amaral and Knowles, 1994). This results in the formation of an aerobic environment near the 401 surface of the soil, which favors the decomposition of exudates and plant litter. Zhang et al. (2023) 402 demonstrated that the microbial necromass in invaded wetlands increases from the temperate region 403 to the tropical region, and in tropical wetland soils, is 1.3–5.0 times greater than that in temperate 404 wetland soils. 405

Another possible explanation for the lack of a significant effect of plant invasion on CH₄ 406 emissions in the TE wetlands might be due to the relatively lower response of the SM. In the 407 408 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 409 also found that the response of CH₄ fluxes in TE wetland was quadratically correlated with MAT, 410 with an optimum value of approximately 10-15°C. In this meta-analysis, however, MAT in 57% of 411 the experimental sites of TE wetlands was higher or lower than the above optimum value, which 412 may partly weaken the response of CH₄ fluxes to plant invasion. Further field measurements are 413

414 necessary for evaluating the effect of invasive plants on the emission of CH₄ in TE wetlands,
415 especially in inundated freshwater TE wetlands.

416

417 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 418 reduced the emission of N₂O from TE wetlands; however, this was not observed in TS wetlands. 419 Several studies have previously demonstrated that the emission of N₂O in wetlands populated with 420 non-native plants is lower than that in wetlands occupied by native species (Bezabih et al., 2022; 421 Wang et al., 2016; Yin et al., 2015; Yuan et al., 2015). This could be attributed to the fact that the 422 concentrations of soil NO3⁻ in TS and TE wetlands are generally below the threshold value 423 necessary for denitrification, which subsequently suppresses the production of N₂O during 424 denitrification (Dobbie and Smith, 2003). The present study demonstrated that plant invasion in TE 425 wetland reduced the RRs of soil NH4⁺ and NO3⁻ and significantly decreased the concentration of 426 NH4⁺ and NO3⁻ in soils by 76% and 114%, respectively, which was primarily attributed to the 427 increased uptake of nitrogen by the invasive plants. Previous studies have demonstrated that the 428 decrease in the production of N₂O is attributed to the depletion of inorganic nitrogen in soils, 429 especially NH4⁺, following plant invasion (Yang and Silver, 2016; Zhu et al., 2013). In contrast, 430 plant invasion increased the SM in this study, which could have accelerated the anaerobic 431 conditions and reduced the production of N₂O during denitrification in the subsurface layer of TE 432 wetlands. Yuan et al. (2015) observed that marshland ecosystems populated by invasive S. 433

alterniflora adsorb atmospheric N₂O primarily due to accelerated denitrification by increased SOC.
Therefore, the findings of the present study suggest that plant invasion can lower the emission of
N₂O from TE wetlands.

437

438 *4.4. Plant invasion increased the net CH*₄ *emission from wetlands*

The net emission of CH₄ was determined based on the 15 key non-native wetland plant species in our 439 dataset and their coverage areas. The summed coverage areas of the non-native exotic species were 440 10.10 and 20.92 Mha in TS and TE wetlands, respectively (Table 1), and the non-native exotic plants 441 covered a total global area of 31.02 Mha. The study by Zedler and Kercher (2005) reported that the 442 total area of TS and TE wetlands is 743 and 536 Mha, respectively. The ratio of the area populated 443 with invasive species to the total area was determined to be 1.36% and 3.90% for TS and TE 444 wetlands, respectively. This finding indicated that plant invasion occurs more frequently in TE 445 wetlands than in TS wetlands. 446

In this study, the global net increase in the emission of CH₄ from wetlands following plant invasion was estimated to be 10.54 Tg CH₄ annually, and varied across different climatic regions, with the annual net increase in the emission of CH₄ from TS and TE wetlands being 9.97 and 0.57 Tg CH₄, respectively. Previous studies have suggested that tropical wetlands are the main source of atmospheric CH₄. Seiler and Conrad (1987) estimated that tropical wetlands release 81% of the total CH₄ 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 CH₄ emission. The 454 present study indicated that plant invasion considerably increased the emission of CH₄ from TS wetlands. Although the findings indicated that the invasion of exotic plants induces the emission of 455 CH₄ on a global scale, the estimates obtained herein have certain limitations, which are described 456 hereafter. The first limitation was the scarcity of data, especially accurate data pertaining to the 457 coverage area of the invasive plants. Therefore, the increase in the emission of CH₄ following plant 458 invasion was possibly underestimated in this study. Secondly, the differences in the sampling times 459 and frequencies of the GHG fluxes may have affected the accuracy of the findings (Godwin et al., 460 2013). Thirdly, the scarcity of field studies in Africa, South America, South Asia, and Southeast 461 Asia may have skewed the results of global estimation. 462

463

464 **5.** Conclusions

Overall, the present study indicated that plant invasion considerably increased the emission of CH₄ 465 from TS wetlands, which was primarily attributed to the increase in the AGB of plants, SOC, and 466 SM. In contrast, plant invasion significantly reduced the emission of N2O from TE wetlands, which 467 was possibly attributed to the reduction in the content of NH_4^+ and NO_3^- in soils. The net increase in 468 the emission of CH₄ following plant invasion was estimated to be 10.54 Tg CH₄ yr⁻¹ in global 469 wetland sites, with the global net increase in CH_4 emissions being 9.97 and 0.57 Tg CH_4 yr⁻¹ for TS 470 and TE wetlands, respectively. The findings suggested that non-native plants efficiently invaded 471 and stimulated the emission of CH₄ in tropical and sub-tropical wetlands, compared to native plant 472

species. Thus, it seems necessary to control the invasion of non-native plants for the mitigation ofCH₄ emissions in TS wetlands.

475

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484

485 **Conflict of interest**

486 The authors declare that the research was conducted in the absence of any commercial or financial

487 relationships that could be construed as a potential conflict of interest.

488

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Climatic zone	Invasive plant	Invaded area	ΔCH_4	Net CH ₄ emission	ם - <i>ב</i>
		(ha)	(kg CH ₄ ha ⁻¹ yr ⁻¹)	(Gg CH ₄ yr ⁻¹)	Kelerence
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	I	10,544.42	
		-			

⁸⁷⁸ Table 1 Net CH₄ emissions of natural wetlands in different climatic zones following plant invasion

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

880 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.
- 883 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 \pm 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; NH₄⁺, soil NH₄⁺; NO₃⁻, soil NO₃⁻; 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 CH₄ and N₂O 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

899	tropical/subtropical (TS) wetlands following the invasion of non-native plants. MAT, mean annual air
900	temperature; MAP, mean annual precipitation; ND, nitrogen deposition; RR-SOC, RR of soil organic
901	carbon; RR-TN, RR of soil total nitrogen; RR-AGB, RR of aboveground biomass; RR-PT, RR of plant
902	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 ⁺ ,
903	RR of soil NH4 ⁺ ; and RR-SM, RR of soil moisture; RR-ST, RR of soil temperature.
904	Figure 6. Relationships between the RRd of CH ₄ (red triangles) and N ₂ O (black triangles) fluxes with
905	the climatic factors, ND, RRs of soil properties, and RRs of AGB in temperate (TE) wetlands following
906	the invasion of exotic plants. MAT, mean annual air temperature; MAP, mean annual precipitation;
907	ND, nitrogen deposition; RR-SOC, RR of soil organic carbon; RR-TN, RR of soil total nitrogen;
908	RR-AGB, RR of plant aboveground biomass; RR-BD, RR of soil bulk density; RR-NO3 ⁻ , RR of soil
909	NO3 ⁻ ; RR-pH, RR of soil pH; RR-SM, RR of soil moisture; and RR-ST, RR of soil temperature.
910	Figure 7. Identification of the main predictors of the RRd of (a) CH ₄ fluxes of tropical/subtropical
911	wetlands, (b) CH_4 fluxes of temperate wetlands, (c) N_2O fluxes of tropical/subtropical wetlands, and
912	(d) N ₂ O fluxes of temperate wetlands by random forest analysis. The %IncMSE represents the
913	importance of the main predictors, and negative values of %IncMSE indicate a lack of importance. The
914	yellow bars depict the key predictors that significantly affected the CH ₄ and N ₂ O fluxes of wetlands in
915	different climatic zones. MAP, mean annual precipitation; MAT, mean annual air temperature; ND, N

nitrogen; RR-pH; RR of soil pH; RR-ST, RR of soil temperature; RR-NO₃⁻, RR of NO₃⁻; RR-BD, RR
of soil bulk density.

916

deposition; RR_SM, RR of soil moisture; RR-SOC, RR of soil organic carbon; RR_TN, RR of total

919	Figure 8. Structural equation models (SEMs) showing the effects of biotic and abiotic factors on the
920	weighted response ratios (RRd) of CH4 fluxes in (a) tropical/sub-tropical regions and (b) temperate
921	regions, and RRd of N ₂ O fluxes in (c) tropical/sub-tropical regions and (d) temperate regions. Dark
922	cyan and black arrows refer to negative and positive correlations, respectively. Dotted lines denote
923	insignificant paths ($p > 0.05$). Path widths are scaled proportionally to the path coefficient. * $p < 0.05$,
924	** $p < 0.01$, *** $p < 0.001$. MAP, mean annual precipitation; MAT, mean annual air temperature; ND,
925	N deposition; RR_SM, RR of soil moisture; RR-SOC, RR of soil organic carbon; RR_TN, RR of total
926	nitrogen; RR-pH; RR of soil pH; RR-ST, RR of soil temperature; RR-NO ₃ ⁻ , RR of NO ₃ ⁻ .
927	



Figure 1

930 Figure 2









Figure 4



939 Figure 5











3

1

%IncMSE

6

4



MAT

RR-NO₃-

RR-SM

RR-SOC

0

Figure 7

945

947

948

949

ND

RR-SOC

RR-SM

MAT

0

2

%IncMSE

