Received: 15 March 2024 | Revised: 30 August 2024 | Accepted: 30 August 2024

DOI: 10.1002/ppp3.10578

Plants People Planet PPP Open Access

REVIEW

Stronger increase of methane emissions from coastal wetlands by non-native *Spartina alterniflora* than non-native *Phragmites australis*

Andrea Fuchs[1] | Ian C. Davidson[2] | J. Patrick Megonigal[3] | John L. Devaney[4] | Christina Simkanin[5] | Genevieve L. Noyce[3] | Meng Lu[6] | Grace M. Cott[1]

[1]School of Biology and Environmental Sciences, University College Dublin, Dublin 4, Ireland

[2]Cawthron Institute, Nelson, New Zealand

[3]Smithsonian Environmental Research Center, Edgewater, Maryland, USA

[4]Department of Biology, Maynooth University, Kildare, Ireland

[5]The Nelson Tasman Climate Forum, Nelson, New Zealand

[6]Key Laboratory of Soil Ecology and Health in Universities of Yunnan Province, School of Ecology and Environmental Sciences, Yunnan University, Kunming, China

Correspondence

Grace M. Cott, University College Dublin, School of Biology and Environmental Sciences, Belfield, Dublin 4, Ireland.

Email: grace.cott@ucd.ie

Funding information

National Natural Science Foundation of China - State Grid Corporation Joint Fund for Smart Grid, Grant/Award Number: 32160288; National Science Foundation Long-Term Research in Environmental Biology Program, Grant/Award Numbers: DEB-0950080, DEB-1457100, DEB-1557009, DEB-2051343; Science Foundation Ireland, Grant/Award Number: 18/SIRG/5614; Smithsonian Institution

Societal Impact Statement

The invasive species *S. alterniflora* and *P. australis* are fast growing coastal wetland plants sequestering large amounts of carbon in the soil and protect coastlines against erosion and storm surges. In this global analysis, we found that *Spartina* and *Phragmites* increase methane but not nitrous oxide emissions, with *Phragmites* having a lesser effect. The impact of the invasive species on emissions differed greatly among different types of native plant groups, providing valuable information to managers and policymakers during coastal wetland planning and restoration efforts. Further, our estimated net emissions per wetland plant group facilitate regional and national blue carbon estimates.

Summary

- Globally, *Spartina alterniflora* and *Phragmites australis* are among the most pervasive invasive plants in coastal wetland ecosystems. Both species sequester large amounts of atmospheric carbon dioxide (CO_2) and biogenic carbon in soils but also support production and emission of methane (CH_4). In this study, we investigated the magnitude of their net greenhouse gas (GHG) release from invaded and non-invaded habitats.
- We conducted a meta-analysis of GHG fluxes associated with these two species and related soil carbon content and plant biomass in invaded coastal wetlands.
- Our results show that both invasive species increase CH_4 fluxes compared to uninvaded coastal wetlands, but they do not significantly affect CO_2 and N_2O fluxes. The magnitude of emissions from *Spartina* and *Phragmites* differs among native habitats. GHG fluxes, soil carbon and plant biomass of *Spartina*-invaded habitats were highest compared to uninvaded mudflats and succulent forb-dominated wetlands, while being lower compared to uninvaded mangroves (except for CH_4).
- This meta-analysis highlights the important role of individual plant traits as drivers of change by invasive species on plant-mediated carbon cycles.

KEYWORDS
blue carbon, coastal wetlands, greenhouse gas emissions, invasive species, *Phragmites australis*, plant traits, *Spartina alterniflora*

1 | INTRODUCTION

Vegetated coastal wetlands (mangrove forests, tidal saltmarshes and seagrass beds—collectively termed 'blue carbon' habitats) cover only ~0.24% of global land area (Murray et al., 2022) but provide highly valued ecosystem services, such as coastal protection from storm surges, erosion prevention along shorelines, nutrient cycling and habitat provision (Duarte et al., 2013; Temmerman et al., 2013). Plants in these habitats have high production rates, low rates of decomposition in seawater-inundated soils and a unique ability to trap and accrete sediments (Duarte et al., 2005). Blue carbon habitats are valued for sequestering and storing carbon for centuries to millennia, placing them among the most carbon-rich ecosystems on the globe (Kirwan & Megonigal, 2013), with an estimated net CO_2 uptake of 102 Tg C year^{-1} (Lu et al., 2017).

Coastal wetlands can emit substantial quantities of the greenhouse gases (GHG) methane (CH_4) and nitrous oxide (N_2O), which have warming potentials 30–45 and 263–270 times greater than CO_2, respectively (Neubauer & Megonigal, 2015). CH_4 is produced by methanogenic archaea in the anoxic, organic matter-rich conditions found in the soils of vegetated wetlands (Kolb & Horn, 2012; Liikanen et al., 2009), while N_2O production is controlled by microbial nitrogen transformations, such as aerobic nitrification and anaerobic denitrification (Hamersley & Howes, 2005; Qiu, 2015). Other microbial activities mitigate the production of these GHGs. Microbes that use more energy-efficient electron acceptors outcompete methanogens for electron donors (Abram & Nedwell, 1978; Lovley & Klug, 1983), while dihydrogen sulphide (H_2S) produced by sulphate-reducing bacteria inhibits N_2O reduction (Senga et al., 2006; Sørensen et al., 1980) and denitrifiers can consume N_2O (Emery & Fulweiler, 2014; Foster & Fulweiler, 2016; Gao et al., 2022). Further, these microbial processes are influenced by the traits of coastal wetland plants. Plants are the largest source of electron donors supporting microbial metabolism in soils through primary productivity and exudation of dissolved organic compounds (Brix et al., 2001). Simultaneously, plants release oxygen via their aerenchyma (Armstrong & Wright, 1975), creating oxygen microzones (Koop-Jakobsen & Wenzhöfer, 2015). Aerenchyma are spaces that form after cell death, which develop in the shoots, roots and rhizomes of vascular plants in waterlogged soils and allow bidirectional gas transport through the plant (Ni et al., 2019). The oxygen regenerates ferric iron and sulphate, which inhibit methanogenesis when re-reduced (Laanbroek, 2010), and facilitates aerobic methanotrophy (Conrad, 2009), which may oxidise >90% of the methane in the root zone (Laanbroek, 2010; Megonigal & Schlesinger, 2002).

Emission and uptake of GHG in coastal wetlands differ among plant species (Mueller et al., 2020). For example, the invasive *S. alterniflora* (hereafter *Spartina*) and *P. australis* (hereafter *Phragmites*) have been reported to increase CH_4 fluxes compared to native vegetation (Gao et al., 2018; Mozdzer & Megonigal, 2013; Tong et al., 2012). CH_4 emissions from *Phragmites* are enhanced due to convective flow. Diel stomata opening induces a pressurised convective gas flow through the plant towards the rhizomes, which contain aerenchyma filled with CH_4 diffusing in from the surrounding soil. Subsequently, gases are transported with the mass flow to the efflux culms and released into the atmosphere (Armstrong et al., 1996). Both *Phragmites* and *Spartina* belong to the grass family (Poaceae) but are structurally similar to native sedges (Cyperaceae) and can have higher CH_4 concentrations in the lacunae (aerenchyma) of their culms than other grasses in their native ranges (Tong et al., 2012). Their aerenchyma facilitate the release of oxygen and exudates into deep soil layers, as well as transport of GHG from those deep layers (Bertness, 1992; Moseman-Valtierra et al., 2016). Root biomass can affect CH_4 fluxes in opposite ways, (1) by supplying labile carbon substrates via root exudates, which will stimulate fermentation processes and subsequent methanogenesis, (2) by releasing oxygen to the rhizosphere, thereby limiting anaerobic decomposition processes and stimulating aerobic methane oxidation and nitrification and (3) by providing a conduit for GHG formed in the surrounding soil and transporting them through the plant. Henneberg et al. (2012) demonstrated that lateral roots and root tips are the most important plant features affecting CH_4 transport through the plant (*Juncus effusus*).

Blue carbon ecosystems are susceptible to invasion by exotic plant species (Davidson et al., 2018; Zedler & Kercher, 2004), and the increasing threat of climate-induced sea-level rise, erosion and storm surges have prompted purposeful introductions of exotic plant species to coastal wetlands to help elevate, stabilise and protect the coast. *Spartina* and *Phragmites* are rapid colonisers, with the former being introduced intentionally to China in 1979/1980 (An et al., 2007; Qin & Chung, 1992) and the latter incidentally to North America in the 19th century (Bart et al., 2006; Saltonstall, 2002). Invasive *Spartina* and *Phragmites* grow and spread quickly, form large monocultures and replace native species (Chen et al., 2018; Riddin et al., 2016). Both species form tall, densely distributed stems with long leaves (Chen et al., 2015; Riddin et al., 2016), and have deep and dense rooting systems, thereby providing high above- and belowground biomass (BGB) and altering soil conditions (Li et al., 2009; Srivastava et al., 2014). Globally, *Spartina* and *Phragmites* are among the most pervasive invasive plants in coastal wetland ecosystems.

Previous meta-analyses on the impact of invasive species on coastal wetlands focused on comparisons of GHG emission to freshwater wetlands and terrestrial habitats, including multiple invasive species (Beyene et al., 2022), or on impacts of *Spartina* and *Phragmites* invasion combined with management impacts on ecosystem structure and function (Wails et al., 2021). In contrast, this study focused specifically on the impact of invasive *Spartina* and *Phragmites* on blue carbon parameters (GHG fluxes, soil carbon and plant biomass) in coastal wetlands, with emphasis on GHG emissions and the role of plant species diversity. Information on the impact of the different traits of invasive and native plant species on blue carbon potential and GHG emissions is scarce. While many studies have investigated correlations between plant biomass and CH_4 emissions, there is little evidence on the bioavailability of the decomposing organic matter and released exudates, photosynthesis rates and gas transport mechanisms.

Biological invasions alter carbon and nitrogen cycles in a variety of ecosystems (Ehrenfeld, 2003; Liao et al., 2008) and have a net positive effect on carbon pools in coastal vegetated habitats (Davidson et al., 2018). High soil organic carbon (OC) is a key factor correlated to CH_4 emissions from freshwater and coastal wetlands affected by invasive species (Beyene et al., 2022). The effect of invasive species on GHG emissions is complex, and a consensus in the literature remains elusive. An improved understanding of GHG fluxes and the overall carbon balance in invaded blue carbon habitats will inform decisions on coastal wetland management. We present a meta-analytical investigation of GHG emissions affected by *Spartina* and *Phragmites* invasions in blue carbon systems. We focused in addition on differences in impact based on plant traits within different groups of native vegetation (mudflats, succulent forbs, fine grasses, large graminoids and mangroves). Our aim was to determine the direction and magnitude of the effects and to discuss the long-term climate impact of biological invasions on coastal wetland habitats.

2 | MATERIALS AND METHODS

The meta-analysis was performed following the steps outlined by a flow diagram in Figure S1, based on recommendations by Koricheva and Gurevitch (2014).

2.1 | Study selection

A literature search was performed in February 2021 to identify peer-reviewed publications quantifying the effects of the invasive species *Spartina* and *Phragmites* on GHG emissions from blue carbon habitats. This included pairwise studies (invasion vs. non-invasion) as well as repeated studies (before and after invasion). The ISI Web of Science database was screened using the following terms:

- (Spartina OR Phragmites) AND (invasi* OR non-native OR non native OR nonnative OR exotic* OR non-indigenous OR non indigenous OR introduced) AND (Methane OR CH4 OR carbon dioxide OR CO2 OR Nitrous Oxide OR N2O).

One hundred forty-nine publications were found to match the criteria of this search. To relate the data to carbon stocks, literature from a previous meta-analysis by Davidson et al. (2018) was selected for invasive *P. australis* and *S. alterniflora* (28 studies, from March 2, 1864 to November 30,2017). The blue carbon pool literature was updated for the period of November 30, 2017 until February 18, 2021 by an additional search for.

- (Spartina OR Phragmites) AND (invasi* OR non-native OR non native OR nonnative OR exotic* OR non-indigenous OR non indigenous OR introduced)

This second search resulted in 501 publications since November 2017 (in addition to the 28 relevant studies from 1864 to 2017).

Abstracts of the identified literature were screened for inclusion criteria, which were as follows: (a) relevant title and/or text and (b) experiments and/or observations conducted outdoors (not solely within a laboratory or greenhouse) and within a saltmarsh, mangrove or seagrass habitat.

Full texts of the remaining articles were examined for eligibility, that is, for containing appropriate data. Each included study had to have a measure of GHG flux, soil carbon parameters or plant biomass (Table S1) in an invaded (treatment) and uninvaded (control) condition. Dominant native species in uninvaded habitats are listed in Table 1. If a paper included data from multiple sites, each site was considered as separate and independent data. This resulted in 2119 lines of data from 123 articles. Study sites are shown in the map of Figure 1.

2.2 | Data treatments

Several data treatments were applied to account for missing information. If articles did not display their data in numeric form in tables or within the text, the online tool WebPlotDigitizer (https://apps.automeris.io/wpd/) was used to retrieve values from graphs (60 studies, 1389 lines of data). If articles did not contain information on sample size, standard deviation, standard error or confidence intervals (CI), missing values were estimated (details described in Methods S1.1). If an article reported responses over time (40 studies, 969 lines of data [46.4%]), such as seasonal or annual measurements, unweighted random-effects models were performed on each set of time series to collapse the data to one independent entry (Koricheva et al., 2013). The model outcomes of this time-series collapse, that is, estimated effect size (ES) and standard error, were treated as equal to Hedges' *d* and variance in the subsequent meta-analysis. If an article reported responses in different depth layers of the soil (22 studies, 731 data lines [35.0%]), the same approach was applied as for time series. The impact of estimated missing values on the ES was assessed by comparing the results of random-effects models of imputed data to those of complete data (Table S2). In addition, uncollapsed data were analysed separately by time and depth, to determine long-term effects on GHG fluxes and impacts on carbon parameters in different soil depths. These data did not only include time- and depth-series, but all studies that identified the time (33 studies for GHG fluxes, 476 data lines; 58 studies for plant biomass, 571 data lines) or depth

TABLE 1 Grouping of native plant species and their contribution to each analysed parameter category (GHG = greenhouse gases) per invader.

	Native	GHG	Soils	Plants
Spartina	**Succulent forbs**	*Suaeda glauca,* *Suaeda salsa*	*S. glauca,* *S. salsa*	*Salicornia ramosissima,* *Salicornia virginica,* *S. salsa*
	Fine grasses	*Aeluropus littoralis,* "Native"	"Native"	*A. littoralis,* "Native"
	Large graminoids	*Cyperus malaccensis,* *Phragmites australis,* *Scirpus mariqueter*	*C. malaccensis,* *P. australis,* *Phragmites communis,* *S. mariqueter*	*C. malaccensis,* *P. australis,* *S. mariqueter,* *Spartina foliosa,* *Spartina maritima*
	Mangroves	*Avicennia marina,* *Kandelia obovata*	*Aegiceras corniculatum,* *Aricennia marina,* *A. marina,* *K. obovata,* *Kenaelia candel,* "Mangrove"	*A. marina,* *K. obovata,* "Mangrove," *Rhizophora stylosa*
Phragmites	**Succulent forbs**	*Suaeda japonica*	*S. japonica*	-
	Fine grasses	"Native," *Distichlis spicata,* *Spartina patens*	"Native," *D. spicata,* *S. patens*	*Leersia oryzoides, S. patens,* "native"
	Large graminoids	*Spartina alterniflora*	*Cyperus malaccensis,* *P. australis, S. alterniflora,* *Spartina* spp.	*P. australis, S. alterniflora,* *Spartina* spp., *Typha augustifolia*
	Mangroves	-	-	-

(73 studies for soil carbon parameters, 908 data lines) of sampling. For temporal analyses, information on sampling times was recorded as season. All studies were performed on the Northern hemisphere and have similar time-of-year seasonal patterns. For analyses by depth, four main depth layers were defined, as top (0–20 cm), mid (20–50 cm), deep (50–75 cm) and very deep (75–100 cm). For studies that investigated larger portions of soil, or overlapping depth fractions, such as 0–50 cm, the average value was used.

After the initial data treatments, parameters measured in only one or two studies, such as particulate organic carbon (POC) or seagrass species, were eliminated and resulted in a final dataset of 709 lines from 116 studies. The parameters plant height (23 studies, 44 lines of data) and plant density (23 studies, 47 lines of data) were excluded from most analyses, as the ES disproportionally affected the outcome of the analyses (e.g., mangroves being far less dense and fine grasses being far smaller than the invasive species).

2.3 | ES

The effect of invasive species on native coastal wetlands was calculated using Hedges' *d* (*d*, Equation 1) for each case study, based on the sample means (*Y*) of treatment (*T*) and control (*C*) groups. This index weights cases by their number of replicates (*n*) and the inverse of the pooled variance (*S*, Equation 2; Lajeunesse, 2013) and is not biased by small sample sizes and unequal variances (Koricheva et al., 2013). It is also the most appropriate metric for flux data, which are often negative, rendering log response ratios unsuitable. *J* is a small sample size bias correction factor (Equation 3), and v_d is the variance of the ES (Equation 4 Shen & Zhu, 2021).

$$d = \frac{Y_T - Y_C}{S} J \tag{1}$$

$$S = \sqrt{\frac{(n_T - 1)s_T^2 + (n_C - 1)s_C^2}{n_T + n_C - 2}} \tag{2}$$

$$J = 1 - \frac{3}{4(n_T + n_C - 2) - 1} \tag{3}$$

$$v_d = \frac{n_T + n_C}{n_T n_C} + \frac{d^2}{2(n_T + n_C)} \tag{4}$$

The Hedges' *d* values and variances of each case study were entered into unweighted random-effects models to estimate the true ES (see Methods S1.2 for details). The 95% bootstrap CI of Hedges' *d* was used to assess whether *d* differed significantly from zero (i.e., no effect of invasions). In contrast to log response ratios, it is not possible to calculate percentages of change from Hedges' *d* values.

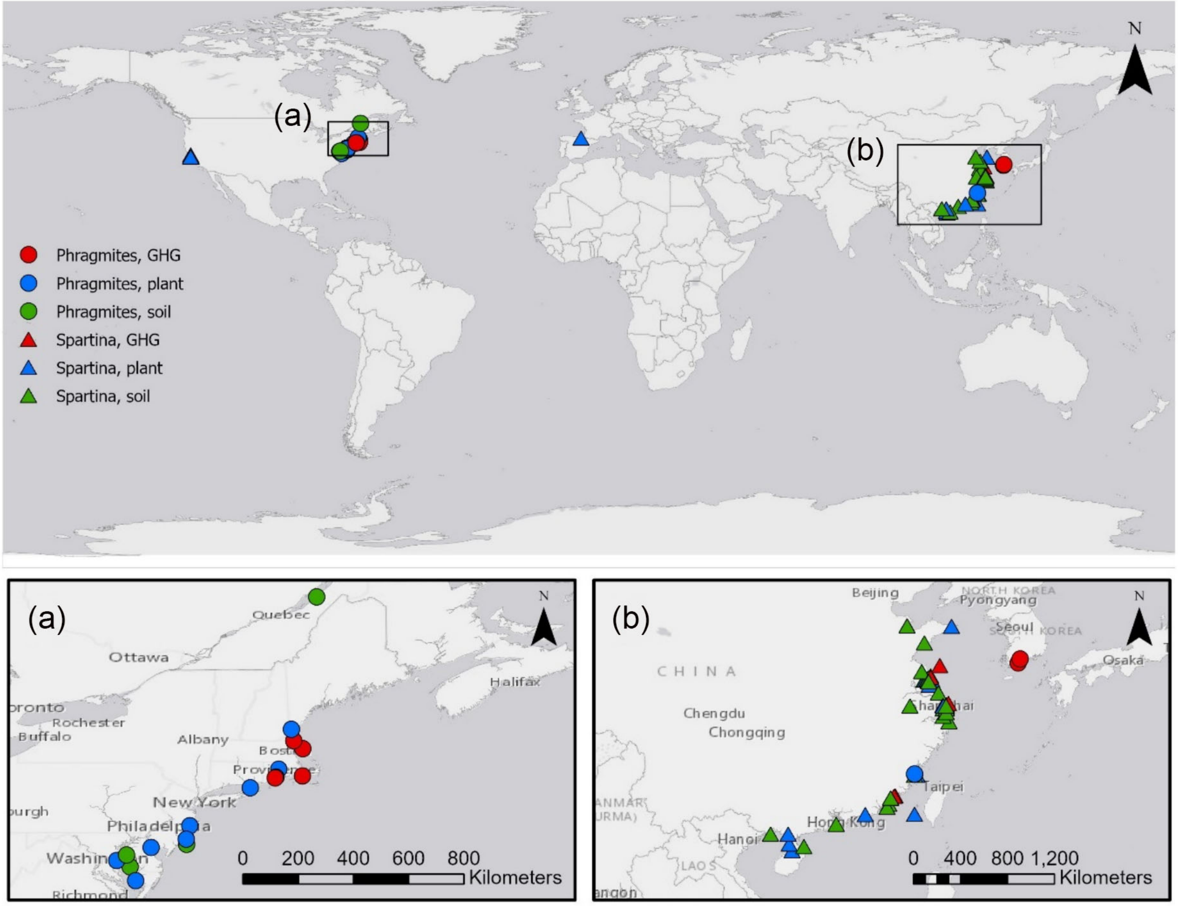

FIGURE 1 Coastal wetland sites investigated by studies on greenhouse gas emissions (red), plant biomass (blue) and soil parameters (green). Main study areas in the US east coast being invaded by *Phragmites* (circles, box A), and the US west coast and China (box B) being invaded by *Spartina* (triangles).

2.4 | CO_2-equivalent fluxes

CH_4 and N_2O have higher sustained-flux global warming potentials than CO_2 (45 and 270 times, respectively, Neubauer & Megonigal, 2015); therefore, relatively small changes in emissions of these gases have the potential to offset large changes in carbon sequestration within the same habitat. For this meta-analysis, literature reporting gross primary production, respiration or net ecosystem exchange was not used due to lack of sufficient data for robust analysis. To demonstrate the potential impact of each invasive species on GHG fluxes from native vegetation groups, average annual fluxes were calculated for each GHG (Table 2). Only data presented in a unit that could be transformed into kg ha^{-1} $year^{-1}$ were included in that calculation. As the number of studies on CO_2, CH_4 and N_2O fluxes vary widely and are predominantly performed in summer, only studies performing measurements in more than one season were used here, resulting in more moderate estimates. Due to this approach, results for *Phragmites* were limited to the native groups fine grasses and large graminoids. The calculated mean flux rates in Table 2 are not suitable to show invader effects on GHG emissions from uninvaded habitats, which need to be calculated for each study individually and are best presented by Hedges' *d*, and merely demonstrate differences in flux ranges per habitat. Average CH_4 and N_2O fluxes were calculated in CO_2-equivalents for each group of invaded and native vegetation and summarised as potential net CO_2-equivalent flux (CO_2e; Table 2). Previous studies show that CO_2 is the dominant GHG emitted from coastal wetlands, and the inclusion of short-term daytime CO_2 fluxes from chamber measurements increases the CO_2-equivalent emission by 81%–96% (Chen et al., 2015; Xu et al., 2014). However, the lack of diurnal and nighttime CO_2 data might result in poor estimates. For the purpose of this analysis, we assumed equal CO_2 uptake and release from each wetland type. Based on the terminology described in detail by Neubauer (2021), these figures do not represent the radiative balance. An accurate calculation of the net CO_2-equivalent GHG flux between ecosystem and atmosphere requires annual data for each GHG emitted as well as annual changes in carbon stocks. In this meta-analysis, we considered a variety of studies that do not fully meet these criteria and therefore present an estimate of the *potential* net CO_2-equivalent flux from each wetland type.

TABLE 2 Annual CH_4 and N_2O fluxes (mean ± sd, in kg ha^{-1} $year^{-1}$) and CO_2-equivalent fluxes (mean ± sd, in t ha^{-1} $year^{-1}$) from uninvaded and invaded coastal wetlands per habitat and invasive species.

			Annual fluxes (kg ha^{-1} $year^{-1}$)				CO_2e (t ha^{-1} $year^{-1}$)	
Invasive species	Habitat	Status	n	CH_4 Mean ± sd	n	N_2O Mean ± sd	n	($CH_4 + N_2O$) Mean ± sd
Spartina	Mudflats	Uninvaded	66	45.5 ± 70.7	35	0.70 ± 1.21	101	2.2 ± 1.3
		Invaded	66	212.8 ± 338.1	35	0.94 ± 1.50	101	9.8 ± 6.6
	Succulent forbs	Uninvaded	25	14.4 ± 32.1	15	0.76 ± 0.93	40	0.9 ± 0.3
		Invaded	25	44.9 ± 54.2	15	1.38 ± 1.36	40	2.4 ± 1.2
	Fine grasses	Uninvaded	21	56.9 ± 102.4	15	1.39 ± 0.84	36	2.9 ± 1.5
		Invaded	21	37.6 ± 49.0	15	1.38 ± 1.36	36	2.1 ± 0.9
	Large graminoids	Uninvaded	34	187.9 ± 287.3	21	1.29 ± 1.98	55	8.8 ± 5.7
		Invaded	34	478.4 ± 622.4	21	1.24 ± 2.00	55	21.9 ± 15.0
	Mangrove	Uninvaded	12	483.8 ± 873.7	12	1.73 ± 1.20	24	22.2 ± 15.1
		Invaded	12	449.4 ± 725.0	12	2.51 ± 2.08	24	20.9 ± 13.8
	All	Uninvaded	158	106.0 ± 299.9	98	1.1 ± 1.4	256	37.1 ± 6.8
		Invaded	158	238.1 ± 440.3	98	1.3 ± 1.7	256	57.1 ± 8.5
	Vegetated	Uninvaded	92	149.4 ± 383.5	63	1.3 ± 1.4	155	34.8 ± 7.6
		Invaded	92	284.3 ± 287.9	63	1.5 ± 1.8	155	47.2 ± 9.3
Phragmites	Fine grasses	Uninvaded	20	19.5 ± 40.0			20	0.9 ± n.a.
		Invaded	20	550.2 ± 792.9			20	24.8 ± n.a.
	Large graminoids	Uninvaded	12	742.7 ± 2,462.0	8	−0.14 ± 0.36	20	33.4 ± 23.7
		Invaded	12	96.1 ± 140.3	8	−0.04 ± 1.01	20	4.3 ± 3.1
	Vegetated	Uninvaded	32	290.7 ± 1,509.5	8	−0.14 ± 0.36	40	34.1 ± 34.3
		Invaded	32	379.9 ± 665.0	8	−0.04 ± 1.01	40	29.1 ± 13.2

2.5 | Quality checks

The impact of data treatments on ESs was assessed (Table S2). Unweighted random-effects models were performed on each subset of data containing estimated standard deviation, and/or estimated sample sizes, as well as on data that were fully available and did not require any treatments ("complete, ungrouped data"). Models were performed on data containing time- and/or depth-series and compared before and after collapsing them to single data entries. The treated data subsets were combined with the "complete, ungrouped" data to assess the change of the overall ES. The robustness of the overall ES was tested by removing outliers per parameter category (GHG, soil carbon, plant biomass).

Different options for weighting the models are compared in Table S3. ESs were compared using (a) unweighted fixed-effects models, which calculate the ES purely on the observed effects and do not take heterogeneity into account, (b) unweighted random-effect models, which considers within-study results as equally independent as between-study results, (c) random-effects models using v_{ssb}, (d) random-effects models weighted by study ID and (e) random-effects models using the *rma.mv* function of the *metafor*-package to include study ID as random factor. Based on the assessments of Buck et al. (2022), we decided that unweighted random-effects models provide the least biased results. The robustness of our analyses was verified by applying various effects models to the data set as well as to data subsets (Tables S2 and S3).

Methodological heterogeneity (i.e., whether variance may be attributed to between-study differences in methods or to some predictor variables) was examined using I^2 statistics (Table S3). Publication bias (i.e., selective publication of articles with significant findings over those with nonsignificant results) was tested using funnel plots (Figure S2), which include regression test results from the function *regtest* of the *metafor*-package in the software R (R Core Team, 2021).

Moderator analyses were performed to determine if specific parameters were dominantly responsible for the estimated ES (Table S4). Tested moderators included publication year, habitat, country of study, invasive species, native vegetation groups and parameter groups (GHG, soil carbon parameters, plant biomass).

2.6 | Data analysis

The results of the meta-analysis on the impact of *Spartina* and *Phragmites* on blue carbon ecosystems were analysed by groups and subgroups to disentangle the roles of different response variables and habitat types. A previous meta-analysis demonstrated that the effect of introduced species varies among blue carbon habitats (Davidson et al., 2018); thus, we ran random-effects models by groups of native vegetation: (a) unvegetated mudflats, (b) succulent forbs, (c) fine grasses (relatively short stature, soft, thin lamina), (d) large graminoids (tall, large lamina, and tough stems—including reeds, cordgrasses, sedges and *Typha*) and (e) mangroves (Table 1). Native vegetation described as "native" or consisting of a mix of species was added to the group of fine grasses. The plant groups were not assigned with regard to phylogenetic relatedness but rather their growth form, size and the plants' contribution to biomass, soil carbon parameters and GHG emission potential. Further, effects were grouped by the type of measured parameters, such as (a) GHG fluxes, (b) soil carbon parameters and (c) plant biomass, and sub-groups of parameters within each of these groups (Table S1).

A principal component analysis (PCA) was performed on the ESs resulting from *Spartina* invasion on succulent forbs, large graminoids, mangroves and unvegetated mudflats using the package *FactoMineR* (Lê et al., 2008). The ESs of CO_2, CH_4 and N_2O were selected as quantitative variables, and the native vegetation groups were selected as the qualitative variable. The PCA considers the relationships of the ES of aboveground biomass (AGB), BGB, soil C, soil OC and soil dissolved organic carbon (DOC), and how they impact the ES of the GHGs. The analysis used only the *Spartina* portion of the dataset and excluded fine grass-dominated native vegetation and the parameter soil organic matter (SOM) due to missing values. For the same reasons, only final ES results could be used for the PCA analysis, not including the range of results or CIs.

All analyses and graphs were conducted with R software. Meta-analyses were performed using the *metafor*-package (Viechtbauer, 2010), with *rma* to calculate the ESs ± CIs and to perform moderator analyses, *funnel* to create funnel plots on publication bias and *regtest* to test the significance of the latter. Furthermore, the packages *egg* (Auguie, 2019), *ggtext* (Wilke, 2020), *tidyverse* (Wickham et al., 2019) and *VIM* (Kowarik & Templ, 2016) were used to create data figures. The package *clusterSim* (Walesiak & Dudek, 2020) was used for data normalisation prior to PCA analysis, which was performed using the package *FactoMineR* (Lê et al., 2008).

3 | RESULTS

There was a net total increase (ES: 1.76, CI: 1.50–2.03, $p < 0.001$) of GHG and carbon pools in coastal wetlands invaded by *Spartina* or *Phragmites* (Figure 2). When considering different groups of parameters, the net impact of invasive *Spartina* and *Phragmites* is lowest on GHG fluxes (ES: 1.08, CI: 0.68–1.48, $p < 0.001$), slightly higher on plant biomass (ES: 1.24, CI: 0.68–1.80, $p < 0.001$), and about twice as high on soil carbon parameters (ES: 2.49, CI: 2.20–2.79, $p < 0.001$). Both invasive species cause a large increase of CH_4 fluxes from invaded wetlands, while the effect on CO_2 and N_2O fluxes is mostly negligible (Figure 2), resulting in a net increase of GHG fluxes by *Spartina* (ES: 1.18, CI: 0.73–1.64, $p < 0.001$) but

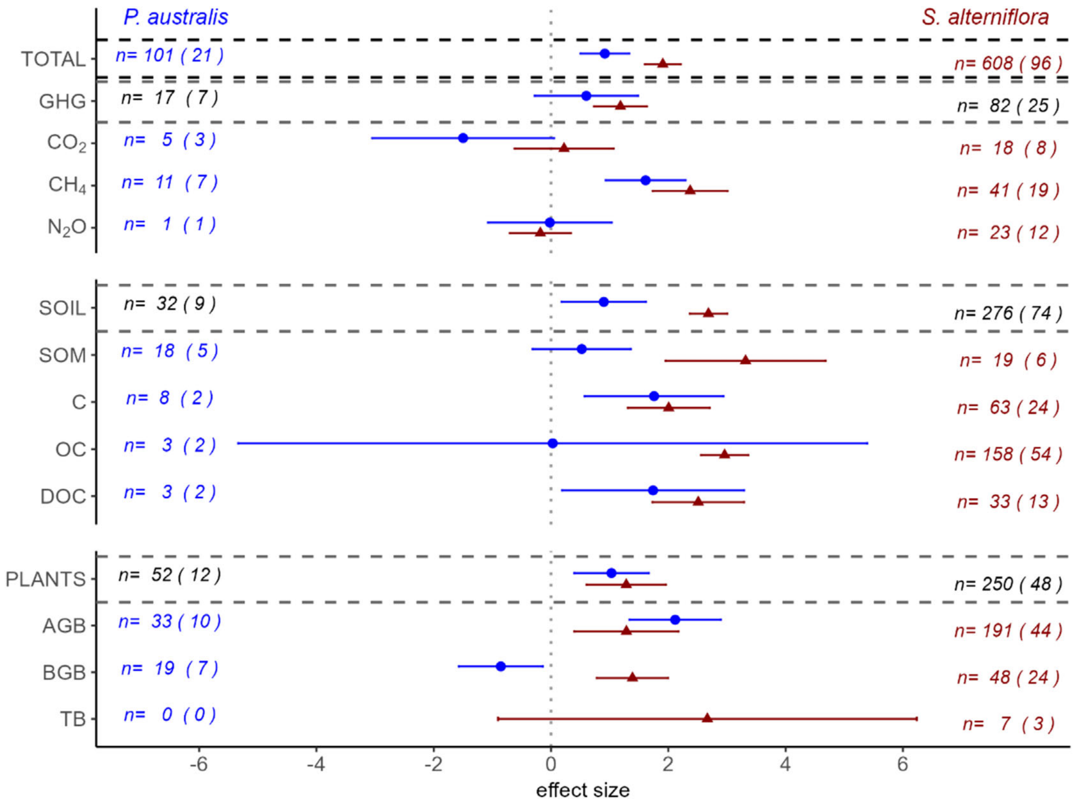

FIGURE 2 Effects (Hedges' *d* ± confidence intervals) of invasive *P. australis* (blue circles, number of observations (*n*) and studies (in brackets) on the left) and *Spartina alterniflora* (red triangles, numbers on the right) on greenhouse gas fluxes (GHG), soil carbon pools (SOIL) and plant biomass (PLANTS) from coastal wetlands.

not by *Phragmites* (ES: 0.60, CI: −0.28-1.48, $p = 0.018$). Invasive *Spartina* increased annual average fluxes of CH_4 2.2-fold (1.9-fold when considering only vegetated coastal wetlands) and of N_2O 1.2-fold (1.2-fold without mudflats), while invasive *Phragmites* increased annual fluxes from vegetated wetlands 1.3-fold for CH_4 and 0.2-fold for N_2O (Table 2). Combined, CH_4 and N_2O fluxes in CO_2-equivalents alter the GHG balance of these gases (CO_2 sequestration not considered) in *Spartina*-invaded vegetated coastal wetlands by a 1.5-fold increase (1.4-fold increase including mudflats), from 37.1 t CO_2e ha^{-1} $year^{-1}$ (native) to 57.1 t CO_2e ha^{-1} $year^{-1}$ (invaded) and by a 1.2-fold decrease in *Phragmites*-invaded vegetated coastal wetlands from 34.1 t CO_2e ha^{-1} $year^{-1}$ (native) to 29.1 t CO_2e ha^{-1} $year^{-1}$ (invaded, Table 2).

3.1 | Seasonal effects

The effect of both invasive species on coastal wetlands varies among seasons (Figure 3, Figure S3). The invasive species tended to have higher AGB than the native vegetation, an effect that increased during the growing season, reaching its maximum in summer and autumn (Figure 3). The increase in AGB ES was accompanied by a summer and autumn increase in CH_4 flux ES and a summer peak of N_2O flux ES (Figure 3). ESs of the soil parameters SOM, OC and DOC were highest in autumn as well but do not show a clear seasonal trend (Figure 4). Effects on soil OC and DOC in invaded coastal wetlands were lower during the growing season, peaked in autumn, and remained elevated during winter (Figure S3). CO_2 flux ESs were highest in winter (Figure 3), when AGB and BGB were lowest (Figure 3). A few studies investigated the long-term impact of invasive species over several years, which indicate a strongly decreasing impact of the invasive species on plant AGB and BGB after a decade, while CH_4 emissions remain elevated (Figure S4).

3.2 | Environmental drivers

Invasive *Spartina* significantly increased CH_4 fluxes (ES: 2.37, CI: 1.73–3.01, $p < 0.001$), soil parameters (ES: 2.68, CI: 2.36–3.00, $p < 0.001$), as well as above- and belowground plant biomass (AGB ES: 1.29, CI: 0.40–2.17, $p = 0.005$; BGB ES: 1.39, CI: 0.78–2.00, $p < 0.001$), compared to the native vegetation (Figure 2). There was no difference in the impact of invasive *Spartina* on plant or soil parameters by geographic region (Figure 4). The impact of invasive *Phragmites*, by contrast, was much weaker and mostly insignificant. Only CH_4 (ES: 1.61, CI: 0.93–2.29, $p < 0.001$), C (ES: 1.76, CI: 0.57–2.94,

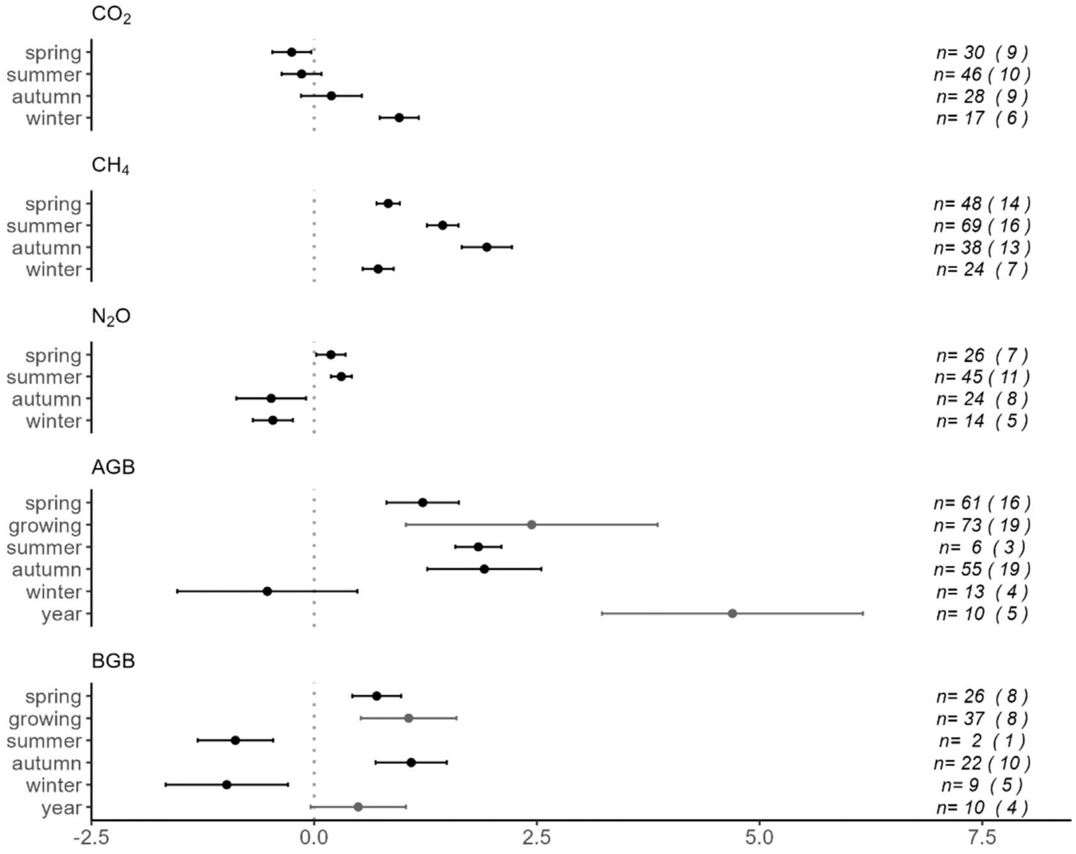

FIGURE 3 Effects (Hedges' *d* ± confidence intervals) of invasive *Spartina* and *Phragmites* on GHG fluxes and plant biomasses per season. The meta-analysis was performed only on "complete," uncollapsed data from studies that provided information on the month or sampling season. Numbers of observation (*n*) and studies (in brackets) are shown on the right.

$p = 0.004$), DOC (ES: 1.74, CI: 0.19–3.29, $p = 0.028$) and AGB (ES: 2.12, CI: 1.34–2.89, $p < 0.001$) were increased by *Phragmites* invasion (Figure 2), with AGB being the parameter most affected by invasive *Phragmites*, and the only one being affected more strongly by invasive *Phragmites* than by *Spartina*.

The effect of the invaders on soil carbon contents varies among the two species with soil depth (Figure 5). Invasive *Phragmites* has low impact on soil carbon contents within the upper soil layers but increasingly elevates DOC with increasing depth. In contrast, invasive *Spartina* has its highest impact in the upper soil layers, strongly

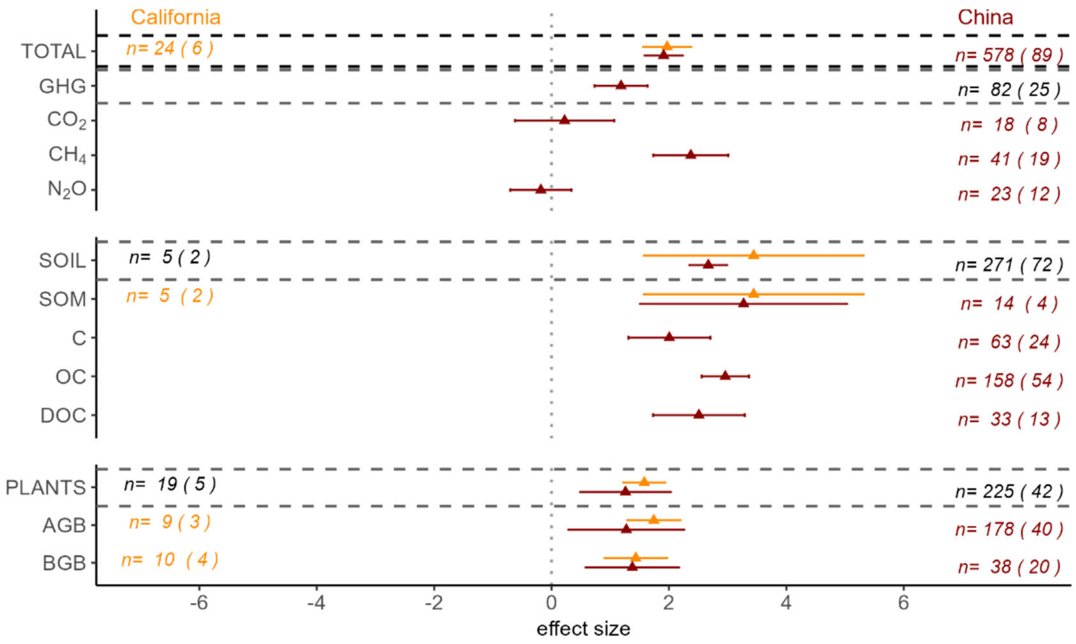

FIGURE 4 Effect (Hedges' *d* ± confidence intervals) of invasive *Spartina* on GHG emissions, soil parameter and plant biomass in coastal wetlands in California, USA (orange) and China (red).

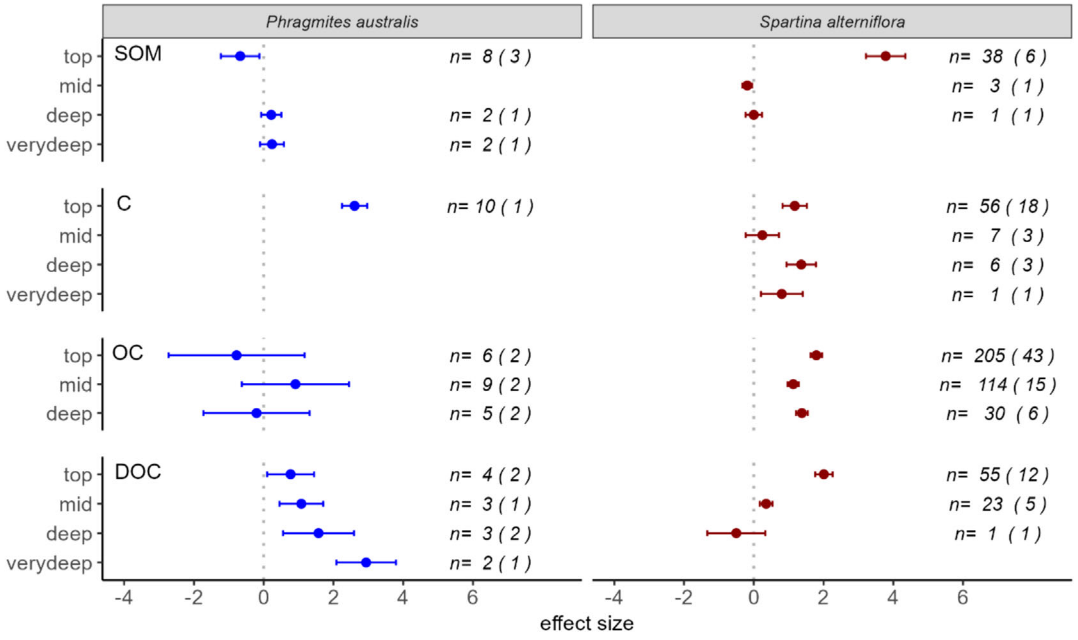

FIGURE 5 Effects (Hedges' *d* ± confidence intervals) of invasive *Phragmites* (blue) and invasive *Spartina* (red) on soil carbon contents per depth. The meta-analysis was performed on uncollapsed, "complete" data. Depths are defined as top (0–20 cm), mid (20–50 cm), deep (50–75 cm) and very deep (75–100 cm). Numbers of observations (*n*) and studies (in brackets) are shown to the right of each panel.

increasing SOM, C, OC and DOC, with much weaker effects in the lower depths of invaded wetland soils.

Effects of *Spartina* invasion on AGB and DOC appear to be very closely linked to each other and correlated positively to effects on CH_4 fluxes and negatively to effects on N_2O fluxes (Figure 6). Effects of *Spartina* invasion on BGB are strongly negatively correlated to effects on N_2O fluxes and weakly positively correlated to effects on CH_4 fluxes (Figure 6). Impacts of *Spartina* on CO_2 fluxes did not correlate to any of the measured parameters (Figure 6). Furthermore, *Spartina* invasions have opposite effects on mangrove ecosystems than on succulent forb-dominated and unvegetated wetlands, with native large graminoids-dominated habitats remaining unaffected overall (Figure 6).

3.3 | Variability among native vegetation

The identity and type of native vegetation plays an important role in the direction and magnitude of change that occurs in invaded wetlands (Figure 7). In general, measured parameters increased in invaded habitats compared to uninvaded fine grass (including relatively small, soft grasses), succulent forb and native large graminoid (including reeds, cordgrasses, sedges and *Typha*) habitats and decreased compared to native mangrove habitats (Figure 7). Large effects of invasive species on soil and plant parameters can be attributed to the massive impact of invasive plant incursions on unvegetated wetlands (net ES on soils: vegetated 1.44, CI: 1.16–1.72, $p < 0.001$, vs. unvegetated mudflats 4.80, CI: 4.12–5.50, $p < 0.001$). SOM contents did not differ between invasive *Phragmites* and native succulent forbs and fine grasses but were higher than in large graminoids habitats, despite these native plants being structurally very similar to the invaders (Figure 7). Invasive *Spartina* increased all soil parameters compared to mudflats, succulent forbs and large graminoids (except SOM compared to large graminoids; Figure 7). Mangroves are the most structurally different from the invaders and other native vegetation, as their trees or bushes are larger, less dense and support an equal or higher AGB than invasive *Spartina* (Figure 7), and they maintain a higher content of soil C and OC in their uninvaded state compared to cases when mangroves are invaded (Figure 7).

The relative impact of invasive *Spartina* on CO_2e fluxes of CH_4 and N_2O from native succulent forbs, large graminoids and unvegetated habitats was similar (Table 2), raising the potential net CO_2e fluxes by three- to fourfold, while the impact was lower and negative (0.7-fold and 0.9-fold increases) on native fine grasses and mangrove habitats. Invasive *Phragmites* had opposite effects on the potential net CO_2e fluxes of CH_4 and N_2O from native fine grasses and large graminoids habitats, strongly increasing the former (37-fold) and decreasing the latter (6-fold decrease). In accordance, the largest mean ES of invasive *Spartina* and *Phragmites* on CH_4 fluxes was observed from unvegetated mudflats (*Spartina*: ES 3.17, CI 1.37–4.98, $p < 0.001$; *Phragmites*: ES 2.75, CI 0.52–4.98, $p = 0.016$), while the effects of both invasive species on CO_2 and N_2O fluxes from mudflats were insignificant and tended to be negative (Figure 7). However, ESs vary at species level among native plants. Large increases in CH_4 fluxes and decreases of N_2O fluxes were observed from invaded habitats compared to the native succulent forb species *Suaeda salsa* (CH_4: $n = 7(5)$, N_2O: $n = 2(2)$), while there was no difference in fluxes compared to the native succulent forb species *Suaeda glauca* (CH_4: $n = 1(1)$, N_2O: $n = 1(1)$; Table S5). In native mangrove habitats, CH_4 fluxes were increased by *Spartina* invasions in *Avicennia marina* habitats but insignificantly affected in *Kandelia obovata* habitats, and vice versa for N_2O fluxes (Table S5).

3.4 | Quality tests

Moderator analyses showed that model outcomes were most affected by the group of parameters, native vegetation groups and country of study (Table S4). Most studies were performed in China (75%, Figure 1), where *Spartina* is the main invasive species in coastal wetlands (100% of studies in China), whereas *Spartina* is also an invasive species in California, USA. All studies on native mangroves were performed in China. However, a broad range of wetlands along the

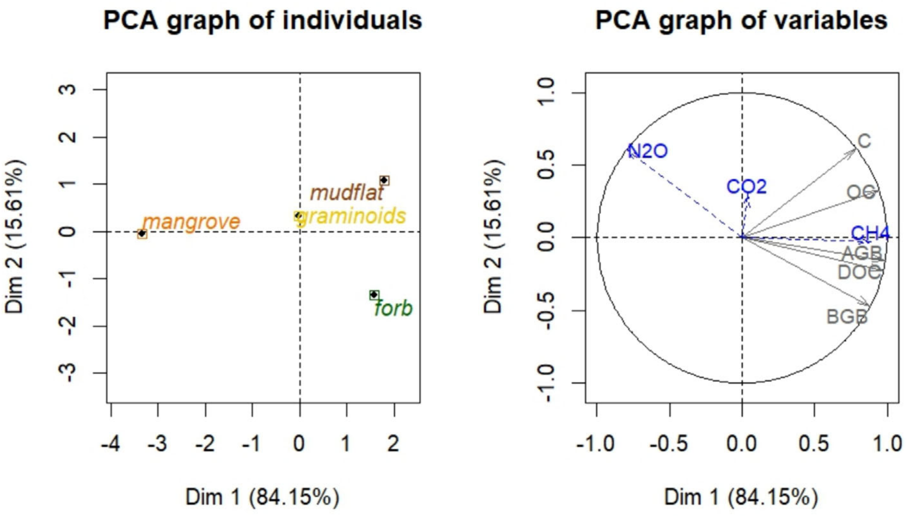

FIGURE 6 Principal component analysis (PCA) of the effect sizes resulting from invasion by *Spartina alterniflora* on plant (aboveground biomass [AGB] and belowground biomass [BGB]) and soil (C, organic carbon [OC], dissolved organic carbon [DOC]) parameters, and how they affect GHG (CO_2, CH_4, N_2O).

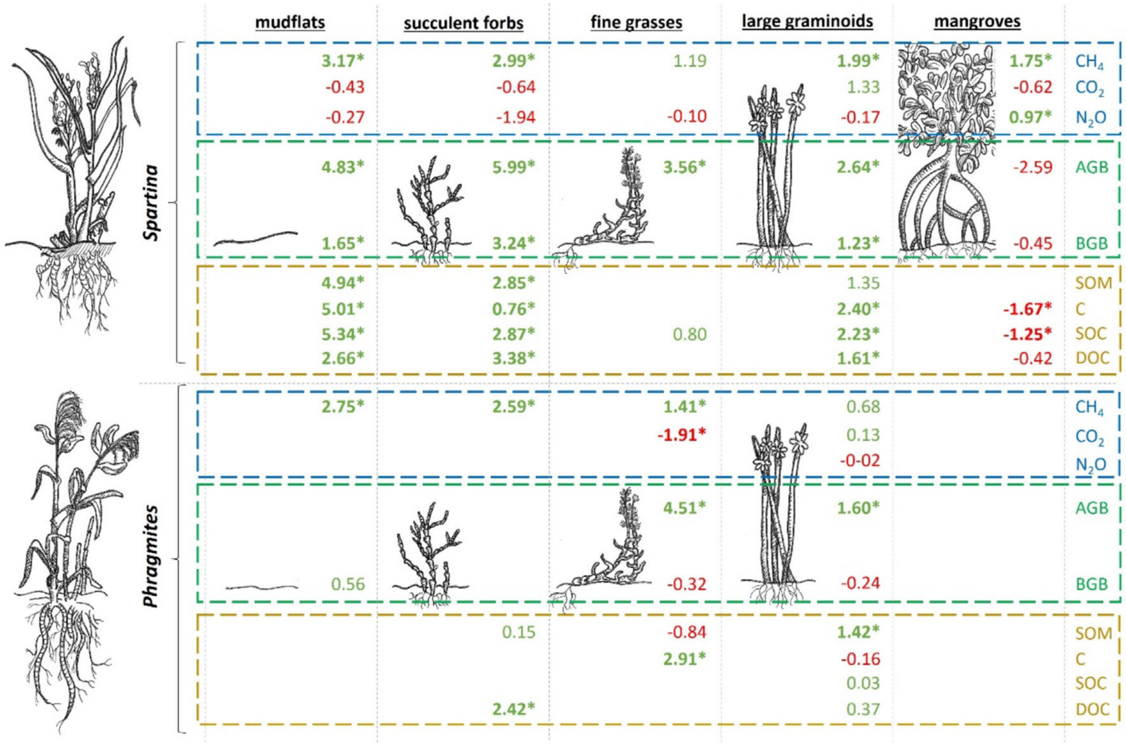

FIGURE 7 Summary schematic of the effects of invasive *Spartina* (top row, depicted on the left side) and invasive *Phragmites* (bottom row, depicted on the left side) on different groups of native vegetation (depicted in each panel). Numbers represent effect sizes (in bold and marked with an asterisk when significant) and are shown in green when the impact was positive and in red when the impact was negative. Results are shown for the greenhouse gases (blue box) methane (CH_4), carbon dioxide (CO_2), nitrous oxide (N_2O), plant biomasses (green box) aboveground (AGB) and belowground (BGB) and soil (yellow box) organic matter (soil organic matter [SOM]), carbon (C), organic carbon (SOC) and dissolved organic carbon (DOC).

Southwest coast of China was investigated and provided data on short-term and long-term invasions, sometimes following decades of invasion. As such, the dataset covers a good range of timelines in the invasion history of these species and their invaded habitats.

The outcomes of the meta-analysis are affected by multiple decisions, such as selecting the methods to estimate missing data, calculating variation, dealing with time- and depth-series and weighting the models (Table S2, S3). Although each decision affects the outcome, the trend always remains the same. Estimates of standard deviations (Table S2) and model weighting (Table S3) have a significant impact on Hedges' *d*, while collapsing time- and depth-series (Table S2) and the calculation method of variation (Table S3) is less significant for the model outcome. In addition, funnel plots show a publication bias towards positive ES (Figure S2), as most parameters are increased or unaffected by invasive species, but rarely decreased.

4 | DISCUSSION

Our meta-analysis shows that *Spartina* and *Phragmites* increase plant biomass in invaded coastal wetlands, while the increase in soil carbon contents and GHG fluxes is only significant for *Spartina*. For both invaders, increased GHG fluxes are attributed mainly to CH_4 (unweighted Hedges' *d*: 2.21, CI: 1.70–2.72, $p < 0.0001$), while the net effects on CO_2 and N_2O fluxes are neutral. The wetland meta-analysis by Beyene et al. (2022) showed a higher impact of invasive species on CH_4 fluxes from coastal wetlands (weighted Hedges' *d*: 3.50, CI: 2.47–4.53, $p < 0.05$) but was not limited to *Spartina* and *Phragmites* as invaders. The production and emission of each GHG from emergent plants is influenced by multiple factors, and our results suggest that various plant traits of invasive and native species play an equally significant role in controlling GHG fluxes as the sources of organic matter and abiotic conditions.

4.1 | AGB

Our analysis showed that invasive *Spartina* and *Phragmites* produce higher AGB than native species, with the exception of mangroves, and simultaneously emit more CH_4 than all types of uninvaded native habitats. Increases in CH_4 fluxes and AGB in *Spartina*-invaded habitats were strongest compared to native succulent forbs, which grow to small height (Figure S5), and unvegetated mudflats. However, *Spartina* also increased CH_4 fluxes compared to large graminoid plants (which include reeds, cordgrasses, sedges and *Typha*) and mangroves of similar or far greater plant biomass and soil carbon content (Figure 7). Our findings show that invasive *Spartina* and *Phragmites* release more CH_4 than any type of native vegetation, which begs the question if a superior mode of gas transport exists in these species. The mechanisms leading to increased CH_4 emissions from *Phragmites*, that is, convective pressurised flow, have been well described (Armstrong et al., 1996) and are estimated to be >5 times higher than diffusive emission (Brix et al., 2001). *Spartina* species release CH_4 only via diffusive transport (Zhang & Ding, 2011) and can release even higher CH_4 fluxes than native *Phragmites* in Chinese coastal wetlands (Tong et al., 2012; Zeleke et al., 2013; Zhou et al., 2015), while emitting equally high CH_4 fluxes as invasive *Phragmites* as a native species in US coastal wetlands (Emery & Fulweiler, 2014). During diffusive plant-mediated transport, GHG are released from culm micropores and leaf sheaths (Nouchi et al., 1990). Some studies suggested that higher biomass, density and stem diameter at the end of the growing season facilitate CH_4 emissions by means of transport and lacunal area (Cheng et al., 2007; Yuan et al., 2015; Zhang & Ding, 2011). In our meta-analysis, we found no link between plant height or density (Figure S5) and the impacts of *Spartina* and *Phragmites* on CH_4 fluxes. Thus, mechanisms of plant gas transport and phylogenetic relationships do not appear to explain why invasive species tend to increase CH_4 emissions.

While AGB facilitates gas fluxes from *Spartina* and *Phragmites*—as its removal reduces CH_4 emissions by 19%–75% (Cheng et al., 2007; Yin et al., 2015)—it may only capture the tail end of a chain of processes leading to increased CH_4 release. Several studies have shown no correlation between AGB and CH_4 fluxes (Ding et al., 2005; Emery & Fulweiler, 2014) and proposed that soil conditions (Emery & Fulweiler, 2014; Martin & Moseman-Valtierra, 2015) or spatial and temporal variations in abiotic conditions regulate methanogenesis (Mueller et al., 2016). In the case of mangroves, Chen et al. (2015) suggested that large canopies provide shade and cooler soil temperatures, possibly resulting in lower methanogenesis. Plant biomass is the primary source of electron donors for methanogens in the soil of these ecosystems (Vann & Megonigal, 2003), which is consistent with the largest increase in CH_4 emissions occurring where *Spartina* and *Phragmites* invaded unvegetated mudflats. Further, increases in methanogenesis in *Spartina*-invaded soils may be facilitated by reduced competition with sulphate-reducing bacteria, as *Spartina* can consume sulphate for growth (Gao et al., 2018), oxidises toxic hydrogen sulphide via oxygen release through aerenchyma (Kraus & Doeller, 1999) and facilitates noncompetitive methylotrophic methanogenesis (Oremland & Polcin, 1982) by exuding acetate and methylated compounds from its roots (Chen et al., 2018; Tong et al., 2018). The extent and significance of each of these mechanisms and others (Noyce & Megonigal, 2021) in driving CH_4 emissions from *Spartina* and *Phragmites* need further study.

4.2 | BGB

In our meta-analysis, BGB was strongly elevated by invasive *Spartina* compared to uninvaded native vegetation, but not significantly affected by invasive *Phragmites*. This may be due to the majority (82%) of studies selected for this meta-analysis investigating only the upper 30 cm of soil for BGB, where a large proportion (50%; Sheng et al., 2022) of *Spartina* roots is found (Liu et al., 2017). Lateral flux in these upper soils might contribute to *Spartina*'s increased CH_4 emissions. This depth also showed the highest increase in DOC concentrations in *Spartina*-invaded habitats, which were correlated to the increase in CH_4 emissions. In contrast, *Phragmites* roots expand deeper (Bernal et al., 2017; Moore et al., 2012; Mozdzer et al., 2023; Windham, 2001) and increased DOC concentrations predominantly in deeper soil layers, where they possibly stimulated CH_4 production (Kim et al., 2020). However, elevated concentrations of DOC with increasing soil depth could also be due to decreasing rates of hydraulic conductivity with depth (D'Andrea et al., 2002; Huettel et al., 1998). The relatively marginal ESs of DOC at the soil surface compared to uninvaded vegetation might be due to slow decomposition of *Phragmites*' recalcitrant leaf tissues (Windham, 2001) or due to inhibition of microbial decomposition by *Phragmites*-sourced phytotoxic compounds (Uddin et al., 2013, 2014). There is little known about the depth-dependent processes that regulate CH_4 production and emission in coastal wetland soils and even less known about the influence of plant traits that vary across native and invasive species, such as rooting depth.

4.3 | Photosynthetic pathways and soil C

The transformation of photosynthetically active radiation (PAR) into biomass is affected by a plant's photosynthetic pathway (Jones, 1988). A meta-analysis on freshwater and coastal wetlands (Wails et al., 2021) found *Spartina* significantly increasing C (CO_2 and CH_4) fluxes, but not *Phragmites*, which was attributed to their photosynthetic pathways. Our meta-analysis on coastal wetlands alone partly affirms these findings and indicates that both invasive species increase CH_4 but not CO_2 fluxes, with lower effects of invasive *Phragmites* on both. *Phragmites* is a C_3 plant, with C_3-C_4 intermediate ecotypes being found in salty meadows (Zheng et al., 2000). C_4 plants, such as *Spartina*, have a unique leaf anatomy and a more complex, energy-efficient system of CO_2 fixation (Sage & Zhu, 2011) that works even when stomata are partially or fully closed at daytime to avoid transpiration. Noyce and Megonigal (2021) classified a C_3 saltmarsh species (*Schoenoplectus americanus*) as a net oxidizer and a C_4 saltmarsh species (*Spartina patens*) as a net reducer of the rhizosphere, resulting in higher soil dissolved CH_4 concentrations and CH_4 emissions from the latter. As a group, C_4 plants investigated in this meta-analysis, that is, *Cyperus malaccensis*, *Distichlis spicata*, *S. alterniflora* in its native range and *S. patens*, do not show higher GHG emissions than the invasive C_3 plant *Phragmites* (Figure 8); thus, our meta-analysis does not indicate a decisive role of the photosynthetic pathway.

4.4 | Seasonal and temporal drivers

Chronosequence studies (Figure S4) showed that the impact of invasive species on CH_4 emissions continued over years, even decades

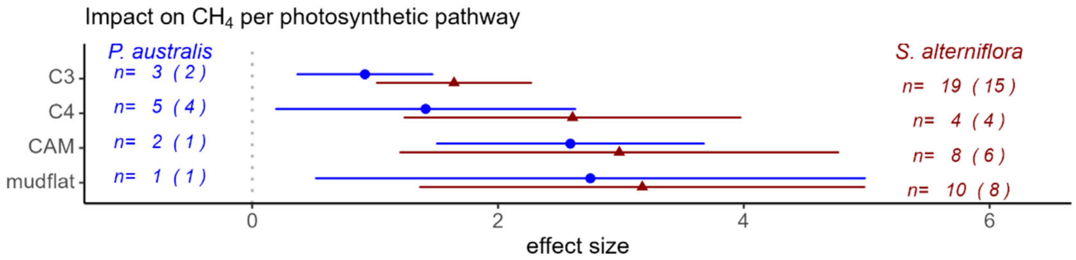

FIGURE 8 Effect (Hedges' *d* ± confidence intervals) of invasive *Spartina* (red triangles) and *Phragmites* (blue circles) on CH_4 emissions from native plants by photosynthetic pathway.

(Kim et al., 2020; Tong et al., 2012; Xiang et al., 2015). Both invasive species increased CH_4 fluxes year-round, with the largest increases measured in summer and autumn, which coincides with peak biomass, carbon inputs,and microbial activity. High temperatures are known to increase microbial activities generally, including CH_4 production (Schulz et al., 1997; Yang et al., 2019; Zeleke et al., 2013). However, Xu et al. (2014) suggested that the summer peak in CH_4 emissions in Chinese coastal wetlands, where *Spartina* is invasive, is related primarily to precipitation. The standing water during low tide may reduce CH_4 oxidation (Chen et al., 2013), increase CH_4 production (Ding et al., 2010; Shao et al., 2017) and enhance aerenchyma development (Maricle & Lee, 2022; Xu et al., 2014).

Our seasonal analysis indicated that invasive species also increase N_2O fluxes during summer, which suggests that rising temperature and plant production (Yang et al., 2020) interact to increase microbial N_2O production in the soil. However, there is no clear effect on N_2O fluxes in spring, autumn or winter, as well as no clear correlation in the PCA; thus, the function of temperature or primary productivity as drivers of N_2O fluxes is uncertain.

Interestingly, CO_2 ESs were higher from invaded than from native wetlands in winter, with no significant impact during the other seasons. Most CO_2 flux studies were undertaken during daytime, when photosynthetic CO_2 uptake exceeds the sum of plant and microbial respiration. Our results indicate that *Spartina* and *Phragmites* have higher BGB leading to higher CO_2 emissions due to root respiration and microbial respiration in winter, which are balanced by photosynthesis during the growing season.

4.5 | Soil N and N_2O fluxes

We found only one suitable study investigating the impact of *Phragmites* invasion on N_2O fluxes from coastal wetlands; therefore, our results on N_2O fluxes reflect predominantly *Spartina*-invaded habitats. *Spartina* effects on N_2O fluxes were strongly negatively correlated to BGB. Higher N_2O flux ESs reflect higher N_2O production, lower N_2O consumption or both. Invasive *Spartina* only had higher N_2O fluxes compared to mangrove habitats dominated by *Kandelia obovata*, which have prop roots (Lin et al., 2020) that are mostly below the soil surface (Chen et al., 2015). The presence of emergent plant features, such as the high culms of *Spartina* and the protruding pneumatophores of *A. marina* (Kreuzwieser et al., 2003; Purvaja et al., 2004), might contribute significantly to the transport of soil N_2O to the atmosphere.

Invasive *Spartina* strongly decreased N_2O fluxes from native *Suaeda salsa*-dominated succulent forb habitats, which are low-biomass succulents using crassulacean acid metabolism (CAM). *Spartina* has an ability to efficiently outcompete soil microbes for N sources and use excess N for growth (Jia et al., 2016; Mou et al., 2019; Zhang et al., 2013), thereby reducing microbial N_2O production. *Suaeda* has shallow root depths, and studies on *S. salsa* (Olsson et al., 2015) and *S. glauca* (Bian et al., 2019) habitats indicated the release of significant amounts of oxygen via their root system, which may stimulate N_2O production at the oxic–anoxic interfaces via coupled nitrification–denitrification (Hamersley & Howes, 2005; Qiu, 2015). The relative influence of plant trait differences on factors such as primary productivity and N uptake kinetics versus N_2O responses to invasion remain to be investigated.

4.6 | Emission rates and CO_2-equivalent fluxes

While Beyene et al. (2022) indicated that invasive plants more than doubled annual CH_4 emissions from uninvaded coastal wetlands (from 111 to 255 kg CH_4 ha^{-1} $year^{-1}$), our calculations suggest a 2.2-fold increase of mean annual CH_4 emissions (from 106 to 238 kg CH_4 ha^{-1} $year^{-1}$, Table 2) in *Spartina*-invaded but only a 1.3-fold increase (from 291 to 380 kg CH_4 ha^{-1} $year^{-1}$, Table 2) in *Phragmites*-invaded vegetated coastal wetlands. However, we wish to point out that the impact of invasive species is best expressed by ESs, while our calculated mean fluxes only serve to present the different flux ranges of each habitat. The magnitude of GHG emissions from the same invasive species varies enormously among different habitats, indicating that environmental conditions influence the level of GHG emission potential.

Annual measurements by Yuan et al. (2015) showed that the benefits of increased SOC and decreased N_2O caused by invasive *Spartina* supersede the increase of CH_4 emissions and result in net mitigation of atmospheric CO_2 by the invasive species. Our estimates suggest that fluxes of N_2O, which has a far higher global warming potential than CH_4, are not high enough to change the direction of potential net CO_2e emissions from each type of coastal wetland habitat. Native mangrove forests have the highest levels of potential net CO_2e emissions and are the only habitat with opposing effects of invasive *Spartina* on CH_4 and N_2O flux directions, which resulted in a neutral net impact. However, mangrove forests were most affected by *Spartina* invasion in terms of reduced biomass and soil carbon parameters, thus severely decreasing their value as a blue carbon habitat. In addition to expanding the geographic scope and types of invasion scenarios studied thus far, there is also a need to study coastal wetland emissions during winter, at night-time and during flooding. These considerations may change our current understanding of carbon cycling and invasion effects in blue carbon habitats and inform coastal wetland management decisions.

4.7 | Comparison with previous meta-analyses and conclusions

The impact of invasive species on blue carbon habitats has been investigated in multiple meta-analyses, most of which showed an increase in soil C stocks and CH_4 emissions. However, despite a substantial body of individual studies and various discussions of the mechanisms influencing carbon sequestration and GHG emissions, no study could identify the environmental drivers definitively, including this one. The data included in each meta-analysis differ and affect the level of impact attributed to the invasive species, leading to over- or underestimates of individual invader effects or the impact on individual ecosystems.

Meta-analyses showing increased CH_4 fluxes from invaded coastal wetlands included a variety of invasive species and showed different magnitudes of impact, with response ratios ranging from 0.73 (95% CI: 0.43 to 1.04) in mangroves and 0.83 (95% CI: 0.66 to 1.00; weighted $\overline{RRd}$, Yao et al., 2023) in saltmarshes to 3.50 (95% CI: 2.47 to 4.53; lnRR; Bezabih Beyene et al., 2022) in all types of coastal wetlands. Wails et al. (2021)'s meta-analysis resulted in increased C fluxes (mean Hedges' *g*: −1.38, 95% CI: −1.77 to −0.98; negative signs indicate invader impact in this study) due to *Spartina* invasion, whereas *Phragmites* had no significant impact on C fluxes (mean Hedges' *g*: 0.14, 95% CI: −0.46 to 0.74), but their meta-analysis grouped CO_2 and CH_4 fluxes into one C flux response variable and included freshwater marshes and swamps besides estuaries. Further meta-analyses targeted GHG emissions from coastal wetlands and focused on net radiative forcing (Taillardat et al., 2020) or land-use/land-cover (Tan et al., 2019) without differentiating between native and invasive species or analysed the impacts of invasive species on GHG emissions from coastal wetlands in reviews (Hu et al., 2020; Qi & Chmura, 2023) without the statistical power and objectivity of a meta-analysis.

Our meta-analysis addresses the issue of different magnitudes of ES by splitting the impact on CH_4 per *Spartina* (Hedges' *d*: 2.37, 95% CI: 1.73 to 3.01) and *Phragmites* (Hedges' *d*: 1.61, 95% CI: 0.93 to 2.29) as well as per native vegetation group (Figure 7), thereby providing new levels of detail and accuracy for individual invasion scenarios. Our analysis shows that known drivers of methanogenesis in soils, such as biomass and anaerobic conditions, are important impacts of invasive species but are not sufficient to predict CH_4 fluxes from different vegetation groups or the direction and magnitude of invasive species on GHG fluxes. Our results indicate that invasive *Phragmites* increases CH_4 fluxes compared to fine grasses, succulent forbs and unvegetated mudflats but has no significant impact when invading coastal wetlands with structurally similar native vegetation (large graminoids). This finding will enable coastal wetland managers to adjust measures in specific habitats. The differences we found in the impacts of two different invasive species on four distinct native vegetation groups suggests an important role for plant traits, such as leaf degradability, canopy structure, aerenchyma development and rooting depths. Such traits determine key mechanisms that regulate GHG emissions including excretion of labile organic matter and availability to methanogens as well as transport of gases through the plant. We addressed the suggestion of C4 plants increasing CH_4 emissions compared to C3 plants (Wails et al., 2021) and found no association to photosynthetic pathways. Further, we highlighted the longevity of invader impacts, as chronosequence studies indicate the increase of CH_4 emissions from invaded coastal wetlands can persist over decades. The radiative forcing impacts of higher CH_4 emissions from invaded habitats are slightly offset by a small trend towards decreased N_2O fluxes. The number of studies describing the impact of invasive species on GHG emissions from coastal wetlands is low and dominated by the comprehensive literature on invasive *Spartina* in Chinese wetlands. As such, the results of our meta-analysis have to be considered with care in this context. More studies in different regions are needed to broaden our understanding of invasion impacts on wetland GHG emissions. In addition to expanding the geographic scope and types of invasion scenarios studied thus far, there is also a need to study coastal wetland emissions during winter, at night-time and during flooding. These considerations may change our current understanding of carbon cycling and invasion effects in blue carbon habitats and inform coastal wetland management decisions.

AUTHOR CONTRIBUTIONS

Andrea Fuchs: Writing—original draft; writing—review and editing; methodology; data acquisition; formal analysis; conceptualization. **Ian C. Davidson:** Writing—review and editing; data acquisition. **J. Patrick Megonigal:** Writing—review and editing. **John L. Devaney:** Writing—review and editing; data acquisition. **Christina Simkanin:** Writing—review and editing; methodology; data acquisition. **Genevieve L. Noyce:** Writing—review and editing; data acquisition. **Meng Lu:** Writing—review and editing;data acquisition. **Grace M. Cott:** Writing—original draft; writing—review and editing; methodology; conceptualization. All authors approved the final version of the manuscript.

ACKNOWLEDGEMENTS

AF and GC were funded by Science Foundation Ireland (18/SIRG/5614), GN and JPM were funded by the Smithsonian Institution and the National Science Foundation Long-Term Research in Environmental Biology Program (DEB-0950080, DEB-1457100, DEB-1557009, DEB-2051343), and ML received funding from the National Natural Science Foundation of China (grant number: 32160288). Open access funding provided by IReL.

CONFLICT OF INTEREST STATEMENT

The authors declare that there are no competing interests.

DATA AVAILABILITY STATEMENT

All data from primary studies used for this meta-analysis are available in the data repository Figshare (10.6084/m9.figshare.26898166). References of studies used are listed in Methods S2.

ORCID

Andrea Fuchs https://orcid.org/0000-0002-7204-6142
Ian C. Davidson https://orcid.org/0000-0002-8729-6048
J. Patrick Megonigal https://orcid.org/0000-0002-2018-7883
John L. Devaney https://orcid.org/0000-0002-7676-0378
Christina Simkanin https://orcid.org/0000-0003-3091-9109
Genevieve L. Noyce https://orcid.org/0000-0003-0423-6478
Meng Lu https://orcid.org/0000-0001-6923-7493
Grace M. Cott https://orcid.org/0000-0003-1233-3788

REFERENCES

Abram, J. W., & Nedwell, D. B. (1978). Hydrogen as a substrate for methanogenesis and sulphate reduction in anaerobic saltmarsh sediment. *Archives of Microbiology*, *117*, 93–97. https://doi.org/10.1007/BF00689357

An, S. Q., Gu, B. H., Zhou, C. F., Wang, Z. S., Deng, Z. F., Zhi, Y. B., Li, H. L., Chen, L., Yu, D. H., & Liu, Y. H. (2007). *Spartina* invasion in China: Implications for invasive species management and future research. *Weed Research*, *47*, 183–191. https://doi.org/10.1111/j.1365-3180.2007.00559.x

Armstrong, J., Armstrong, W., Beckett, P. M., Halder, J. E., Lythe, S., Holt, R., & Sinclair, A. (1996). Pathways of aeration and the mechanisms and beneficial effects of humidity- and Venturi-induced convections in *Phragmites australis* (Cav.) Trin. Ex Steud. *Aquatic Botany*, *54*, 177–197. https://doi.org/10.1016/0304-3770(96)01044-3

Armstrong, W., & Wright, E. J. (1975). Radial oxygen loss from roots: The theoretical basis for the manipulation of flux data obtained by the cylindrical platinum electrode technique. *Physiologia Plantarum*, *35*, 21–26. https://doi.org/10.1111/j.1399-3054.1975.tb03861.x

Auguie B. (2019). Egg : Extensions for "ggplot2": Custom geom, custom themes, plot alignment, labelled panels, symmetric scales, and fixed panel size. *R package* version 0.4.5. https://CRAN.R-project.org/package=egg

Bart, D., Burdick, D., Chambers, R., & Hartman, J. M. (2006). Human facilitation of *Phragmites australis* invasions in tidal marshes: A review and synthesis. *Wetlands Ecology and Management*, *14*, 53–65. https://doi.org/10.1007/s11273-005-2566-z

Bernal, B., Megonigal, J. P., & Mozdzer, T. J. (2017). An invasive wetland grass primes deep soil carbon pools. *Global Change Biology*, *23*, 2104–2116. https://doi.org/10.1111/gcb.13539

Bertness, M. D. (1992). The ecology of a New England salt marsh. *American Scientist*, *80*, 260–268.

Beyene, B. B., Li, J., Yuan, J., Dong, Y., Liu, D., Chen, Z., Kim, J., Kang, H., Freeman, C., & Ding, W. (2022). Non-native plant invasion can accelerate global climate change by increasing wetland methane and terrestrial nitrous oxide emissions. *Global Change Biology*, *00*, 1–16.

Bian, R., Xin, D., & Chai, X. (2019). Methane emissions from landfill: Influence of vegetation and weather conditions. *Environmental Technology*, *40*, 2173–2181. https://doi.org/10.1080/09593330.2018.1439109

Brix, H., Sorrell, B. K., & Lorenzen, B. (2001). Are *Phragmites*-dominated wetlands a net source or net sink of greenhouse gases? *Aquatic Botany*, *69*, 313–324. https://doi.org/10.1016/S0304-3770(01)00145-0

Buck, R. J., Fieberg, J., & Larkin, D. J. (2022). The use of weighted averages of Hedges' *d* in meta-analysis: Is it worth it? *Methods in Ecology and Evolution*, *00*, 1–13. https://doi.org/10.1111/2041-210X.13818

Chen, H., Wu, N., Wang, Y., Zhu, D., Zhu, Q., Yang, G., Gao, Y., Fang, X., Wang, X., & Peng, C. (2013). Inter-annual variations of methane emission from an open fen on the Qinghai-Tibetan Plateau: A three-year study. *Plos One*, *8*, e53878. https://doi.org/10.1371/journal.pone.0053878

Chen, Y., Chen, G., & Ye, Y. (2015). Coastal vegetation invasion increases greenhouse gas emission from wetland soils but also increases soil carbon accumulation. *Science of the Total Environment*, *526*, 19–28. https://doi.org/10.1016/j.scitotenv.2015.04.077

Chen, X. P., Sun, J., Wang, Y., Zhang, H. Y., He, C. Q., Liu, X. Y., Bu, N. S., & Long, X.-E. (2018). Temporal and spatial impact of *Spartina alterniflora* invasion on methanogens community in Chongming Island, China. *Journal of Microbiology*, *56*, 507–515. https://doi.org/10.1007/s12275-018-8062-y

Cheng, X., Peng, R., Chen, J., Luo, Y., Zhang, Q., An, S., Chen, J., & Li, B. (2007). CH_4 and N_2O emissions from *Spartina alterniflora* and *Phragmites australis* in experimental mesocosms. *Chemosphere*, *68*, 420–427. https://doi.org/10.1016/j.chemosphere.2007.01.004

Conrad, R. (2009). The global methane cycle: Recent advances in understanding the microbial processes involved. *Environmental Microbiology Reports*, *1*, 285–292. https://doi.org/10.1111/j.1758-2229.2009.00038.x

D'Andrea, A. F., Aller, R. C., & Lopez, G. R. (2002). Organic matter flux and reactivity on a South Carolina sandflat: The impacts of porewater advection and microbiological structures. *Limnology and Oceanography*, *47*, 1056–1070. https://doi.org/10.4319/lo.2002.47.4.1056

Davidson, I., Cott, G. M., Devaney, J. L., & Simkanin, C. (2018). Differential effects of biological invasions on coastal blue carbon: A global review and meta-analysis. *Global Change Biology*, *24*, 5218–5230. https://doi.org/10.1111/gcb.14426

Ding, W., Cai, Z., & Tsuruta, H. (2005). Plant species effects of methane emissions from freshwater marshes. *Atmospheric Environment*, *39*, 3199–3207. https://doi.org/10.1016/j.atmosenv.2005.02.022

Ding, W., Zhang, Y., & Cai, Z. (2010). Impact of permanent inundation on methane emissions from a *Spartina alterniflora* coastal salt marsh. *Atmospheric Environment*, *44*, 3894–3900. https://doi.org/10.1016/j.atmosenv.2010.07.025

Duarte, C. M., Losada, I. J., Hendriks, I. E., Mazarrasa, I., & Marbà, N. (2013). The role of coastal plant communities for climate change mitigation and adaptation. *Nature Climate Change*, *3*, 961–968. https://doi.org/10.1038/nclimate1970

Duarte, C. M., Middelburg, J. J., & Caraco, N. (2005). Major role of marine vegetation on the oceanic carbon cycle. *Biogeosciences*, *2*, 1–8.

Ehrenfeld, J. G. (2003). Effects of exotic plant invasions on soil nutrient cycling processes. *Ecosystems*, *6*, 503–523. https://doi.org/10.1007/s10021-002-0151-3

Emery, H. E., & Fulweiler, R. W. (2014). *Spartina alterniflora* and invasive *Phragmites australis* stands have similar greenhouse gas emissions in a New England marsh. *Aquatic Botany*, *116*, 83–92.

Foster, S. Q., & Fulweiler, R. W. (2016). Sediment nitrous oxide fluxes are dominated by uptake in a temperate estuary. *Frontiers in Marine Science*, *3*, 40. https://doi.org/10.3389/fmars.2016.00040

Gao, D., Hou, L., Liu, M., Zheng, Y., Yin, G., & Niu, Y. (2022). N_2O emission dynamics along an intertidal elevation gradient in a subtropical estuary: Importance of N_2O consumption. *Environmental Research*, *205*, 112432. https://doi.org/10.1016/j.envres.2021.112432

Gao, G. F., Li, P. F., Shen, Z. J., Qin, Y. Y., Zhang, X., Ghoto, K., Zhu, X. Y., & Zheng, H. L. (2018). Exotic *Spartina alterniflora* invasion increases CH_4 while reduces CO_2 emissions from mangrove wetland soils in southeastern China. *Scientific Reports*, *8*, 9243. https://doi.org/10.1038/s41598-018-27625-5

Hamersley, M. R., & Howes, B. L. (2005). Coupled nitrification-denitrification measured *in situ* in a *Spartina alterniflora* marsh with a

$^{15}NH_4^+$ tracer. *Marine Ecology Progress Series*, *299*, 123–135. https://doi.org/10.3354/meps299123

Henneberg, A., Sorrell, B. K., & Brix, H. (2012). Internal methane transport through Juncus effusus: Experimental manipulation of morphological barriers to test above- and below-ground diffusion limitation. *The New Phytologist*, *196*, 799–806. https://doi.org/10.1111/j.1469-8137.2012.04303.x

Hu, M., Sardans, J., Yang, X., Penuelas, J., & Tong, C. (2020). Patterns and environmental drivers of greenhouse gas fluxes in the coastal wetlands of China: A systematic review and synthesis. *Environmental Research*, *186*, 109576. https://doi.org/10.1016/j.enres.2020.109576

Huettel, M., Ziebis, W., Forster, S., & Luther, W. III (1998). Advective transport affecting metal and nutrient distributions and interfacial fluxes in permeable sediments. *Geochimica et Cosmochimica Acta*, *62*, 613–631. https://doi.org/10.1016/S0016-7037(97)00371-2

Jia, D., Qi, F., Xu, X., Feng, J., Wu, H., Guo, J., Lu, W., Peng, R., Zhu, X., Luo, Y., & Lin, G. (2016). Co-regulations of *Spartina alterniflora* invasion and exogenous nitrogen loading on soil N_2O efflux in subtropical mangrove mesocosms. *PLoS ONE*, *11*, e0146199. https://doi.org/10.1371/journal.pone.0146199

Jones, M. B. (1988). Photosynthetic responses of C_3 and C_4 wetland species in a tropical swamp. *Journal of Ecology*, *76*, 253–262. https://doi.org/10.2307/2260467

Lu, W., Xiao, J., Liu, F., Zhang, Y., Liu, C., & Lin, G. (2017). Contrasting ecosystem CO2 fluxes of inland and coastal wetlands: A meta-analysis of eddy covariance data. *Global Change Biology*, *23*, 1180–1198. https://doi.org/10.1111/gcb.13424

Kim, J., Chaudhary, D. R., Lee, J., Byun, C., Ding, W., Kwon, B.-O., Khim, J. S., & Kang, H. (2020). Microbial mechanism for enhanced methane emission in deep soil layer of *Phragmites*-introduced tidal marsh. *Environmental International*, *134*, 105251. https://doi.org/10.1016/j.envint.2019.105251

Kirwan, M. L., & Megonigal, J. P. (2013). Tidal wetland stability in the face of human impacts and sea-level rise. *Nature*, *504*, 53–60. https://doi.org/10.1038/nature12856

Kolb, S., & Horn, M. A. (2012). Microbial CH_4 and N_2O consumption in acidic wetlands. *Frontiers in Microbiology*, *3*, 78. https://doi.org/10.3389/fmicb.2012.00078

Koop-Jakobsen, K., & Wenzhöfer, F. (2015). The dynamics of plant-mediated sediment oxygenation in *Spartina anglica* rhizospheres – A planar optode study. *Estuaries and Coasts*, *38*, 951–963. https://doi.org/10.1007/s12237-014-9861-y

Koricheva, J., & Gurevitch, J. (2014). Uses and misuses of meta-analysis in plant ecology. *Journal of Ecology*, *102*, 828–844. https://doi.org/10.1111/1365-2745.12224

Koricheva, J., Gurevitch, J., & Mengersen, K. (2013). *Handbook of meta-analysis in ecology and evolution*. Princeton University Press. https://doi.org/10.1515/9781400846184

Kowarik, A., & Templ, M. (2016). Imputation with the R package VIM. *Journal of Statistical Software*, *74*, 1–16. https://doi.org/10.18637/jss.v074.i07

Kraus, D. W., & Doeller, J. E. (1999). Oxidation of sulfide by *Spartina alterniflora* roots. *Limnology and Oceanography*, *44*, 1155–1159.

Kreuzwieser, J., Buchholz, J., & Rennenberg, H. (2003). Emission of methane and nitrous oxide by Australian mangrove ecosystems. *Plant Biology*, *5*, 423–431. https://doi.org/10.1055/s-2003-42712

Laanbroek, H. J. (2010). Methane emission from natural wetlands: Interplay between emergent macrophytes and soil microbial processes. A mimni-review. *Annals of Botany*, *105*, 141–153. https://doi.org/10.1093/aob/mcp201

Lajeunesse, M. J. (2013). Recovering missing or partial data from studies: A survey of conversions and imputations for meta-analysis. In J. Koricheva, J. Gurevitch, & K. Mengersen (Eds.), *Handbook of meta-analysis in ecology and evolution* (pp. 195–206). Princeton University Press. https://doi.org/10.23943/princeton/9780691137285.003.0013

Lê, S., Josse, J., & Husson, F. (2008). FactoMineR: An R package for multivariate analysis. *Journal of Statistical Software*, *25*, 1–18. https://doi.org/10.18637/jss.v025.i01

Li, B., Liao, C. H., Zhang, X. D., Chen, H. L., Wang, Q., Chen, Z. Y., Gan, X. J., Wu, J. H., Zhao, B., Ma, Z. J., Cheng, X. L., Jiang, L. F., & Chen, J. K. (2009). *Spartina alterniflora* invasions in the Yangtze River estuary in China: An overview of current status and ecosystem. *Ecological Engineering*, *35*, 511–520. https://doi.org/10.1016/j.ecoleng.2008.05.013

Liao, C., Peng, R., Luo, Y., Zhou, X., Wu, X., Fang, C., Chen, J., & Li, B. (2008). Altered ecosystem carbon and nitrogen cycles by plant invasion: A meta-analysis. *New Phytologist*, *177*, 706–714. https://doi.org/10.1111/j.1469-8137.2007.02290.x

Liikanen, A., Silvennoinen, H., Karvo, A., Rantakokko, P., & Martikainen, P. J. (2009). Methane and nitrous oxide fluxes in two coastal wetlands in the northeastern Gulf of Bothnia, Baltic Sea. *Boreal Environment Research*, *14*, 351–368.

Lin, C.-W., Kao, Y.-C., Chou, M.-C., Wu, H.-H., Ho, C.-W., & Lin, H.-J. (2020). Methane emissions from subtropical and tropical mangrove ecosystems in Taiwan. *Forests*, *11*, 470. https://doi.org/10.3390/f11040470

Liu, J., Han, R.-M., Su, H.-R., Wu, Y.-P., Zhang, L.-M., Richardson, C. J., & Wang, G.-X. (2017). Effects of exotic *Spartina alterniflora* on vertical soil organic carbon distribution and storage amount in coastal salt marshes in Jiangsu, China. *Ecological Engineering*, *106*, 132–139. https://doi.org/10.1016/j.ecoleng.2017.05.041

Lovley, D. R., & Klug, M. J. (1983). Sulfate reducers can outcompete methanogens at freshwater sulfate concentrations. *Applied and Environmental Microbiology*, *45*, 187–192. https://doi.org/10.1128/aem.45.1.187-192.1983

Maricle, B. R., & Lee, R. W. (2022). Aerenchyma development and oxygen transport in the estuarine cordgrasses *Spartina alterniflora* and *S. Anglica*. *Aquatic Botany*, *74*, 109–120. https://doi.org/10.1016/S0304-3770(02)00051-7

Martin, R., & Moseman-Valtierra, S. (2015). Greenhouse gas fluxes vary between *Phragmites australis* and native vegetation zones in coastal wetlands along a salinity gradient. *Wetlands*, *35*, 1021–1031. https://doi.org/10.1007/s13157-015-0690-y

Megonigal, J. P., & Schlesinger, W. H. (2002). Methane-limited methanotrophy in tidal freshwater swamps. *Global Biogeochemical Cycles*, *16*, 35-1-35-10. https://doi.org/10.1029/2001GB001594

Moore, G. E., Burdick, D. M., Peter, C. R., & Keirstead, D. R. (2012). Belowground biomass of *Phragmites australis* in coastal marshes. *Northeastern Naturalist*, *19*, 611–626. https://doi.org/10.1656/045.019.0406

Moseman-Valtierra, S., Abdul-Aziz, O. I., Tang, J., Ishtiaq, K. S., Morkeski, K., Mora, J., Quinn, R. K., Martin, R. M., Egan, K., Brannon, E. Q., Carey, J., & Kroeger, K. D. (2016). Carbon dioxide fluxes reflect plant zonation and belowground biomass in a coastal marsh. *Ecosphere*, *7*, e01560. https://doi.org/10.1002/ecs2.1560

Mou, X., Liu, X., Sun, Z., Tong, C., & Lu, X. (2019). Short-term effect of exogenous nitrogen on N_2O fluxes from native and invaded tidal marshes in the min river estuary, China. *Wetlands*, *39*, 139–148. https://doi.org/10.1007/s13157-018-1060-3

Mozdzer, T. J., & Megonigal, J. P. (2013). Increased methane emissions by an introduced *Phragmites australis* lineage under global change. *Wetlands*, *33*, 609–615. https://doi.org/10.1007/s13157-013-0417-x

Mozdzer, T. J., Meschter, J., Baldwin, A. H., Caplan, J. S., & Megonigal, J. P. (2023). Mining of deep nitrogen facilitates *Phragmites australis* invasion in coastal saltmarshes. *Estuaries and Coasts*, *46*, 998–1008. https://doi.org/10.1007/s12237-022-01146-x

Mueller, P., Do, H. T., Smit, C., Reisdorff, C., Jensen, K., & Nolte, S. (2020). With a little help from my friends: Physiological integration facilitates invasion of wetland grass *Elymus athericus* into flooded soils. *Oikos*, *00*, 1–9. https://doi.org/10.1111/oik.07863

Mueller, P., Hager, R. N., Meschter, J. E., Mozdzer, T. J., Langley, J. A., Jensen, K., & Megonigal, J. P. (2016). Complex invader-ecosystem interactions and seasonality mediate the impact of non-native *Phragmites* on CH_4 emissions. *Biological Invasions*, *18*, 2635–2647. https://doi.org/10.1007/s10530-016-1093-6

Murray, N. J., Worthington, T. A., Bunting, P., Duce, S., Hagger, V., Lovelock, C. E., Lucas, R., Saunders, M. I., Sheaves, M., Spalding, M., Waltham, N. J., & Lyons, M. B. (2022). High-resolution mapping of losses and gains of Earth's tidal wetlands. *Science*, *376*, 744–749. https://doi.org/10.1126/science.abm9583

Neubauer, S. C. (2021). Global warming potential is not an ecosystem property. *Ecosystems*, *24*, 2079–2089. https://doi.org/10.1007/s10021-021-00631-x

Neubauer, S. C., & Megonigal, J. P. (2015). Moving beyond global warming potentials to quantify the climatic role of ecosystems. *Ecosystems*, *18*, 1000–1013. https://doi.org/10.1007/s10021-015-9879-4

Ni, X.-L., Gui, M.-Y., Tan, L.-L., Zhu, Q., Liu, W.-Z., & Li, C.-X. (2019). Programmed cell death and aerenchyma formation in water-logged sunflower stems and its promotion by ethylene and ROS. *Frontiers in Plant Science*, *9*, 1928. https://doi.org/10.3389/fpls.2018.01928

Nouchi, I., Mariko, S., & Aoki, K. (1990). Mechanism of methane transport from the rhizosphere to the atmosphere through rice plants. *Plant Physiology*, *94*, 59–66. https://doi.org/10.1104/pp.94.1.59

Noyce, G. L., & Megonigal, J. P. (2021). Biogeochemical and plant trait mechanisms drive enhanced methane emissions in response to whole-ecosystem warming. *Biogeosciences*, *18*, 2449–2463. https://doi.org/10.5194/bg-18-2449-2021

Olsson, L., Ye, S., Yu, X., Wei, M., Krauss, K. W., & Brix, H. (2015). Factors influencing CO_2 and CH_4 emissions from coastal wetlands in the Liaohe Delta, Northeast China. *Biogeosciences*, *12*, 4965–4977. https://doi.org/10.5194/bg-12-4965-2015

Oremland, R. S., & Polcin, S. (1982). Methanogenesis and sulfate reduction: Competitive and noncompetitive substrates in estuarine sediments. *Applied and Environmental Microbiology*, *44*, 1270–1276. https://doi.org/10.1128/aem.44.6.1270-1276.1982

Purvaja, R., Ramesh, R., & Frenzel, P. (2004). Plant-mediated methane emission from an Indian mangrove. *Global Change Biology*, *10*, 1825–1834. https://doi.org/10.1111/j.1365-2486.2004.00834.x

Qi, X., & Chmura, G. L. (2023). Invasive Spartina alterniflora marshes in China: A blue carbon sink at the expense of other ecosystem services. *Frontiers in Ecology and the Environment*, *21*, 182–190. https://doi.org/10.1002/fee.2611

Qin, P., & Chung, C. H. (1992). *Applied studies on Spartina* (pp. I10–I128). Ocean Press. (in Chinese)

Qiu, J. (2015). A global synthesis of the effects of biological invasions on greenhouse gas emissions. *Global Ecology and Biogeography*, *24*, 1351–1362. https://doi.org/10.1111/geb.12360

R Core Team. (2021). *R: A language and environment for statistical computing*. The R Foundation for Statistical Computing. URL https://www.R-project.org

Riddin, T., van Wyk, E., & Adams, J. (2016). The rise and fall of an invasive estuarine grass. *South African Journal of Botany*, *107*, 74–79. https://doi.org/10.1016/j.sajb.2016.07.008

Sage, R. F., & Zhu, X.-G. (2011). Exploiting the engine of C_4 photosynthesis. *Journal of Experimental Botany*, *62*, 2989–3000. https://doi.org/10.1093/jxb/err179

Saltonstall, K. (2002). Cryptic invasion by a non-native genotype of the common reed, *Phragmites australis* into North America. *Proceedings of the National Academy of Sciences*, *99*, 2445–2449. https://doi.org/10.1073/pnas.032477999

Schulz, S., Matsuyama, H., & Conrad, R. (1997). Temperature dependence of methane production from different precursors in a profundal sediment (Lake Constance). *FEMS Microbial Ecology*, *22*, 207–213. https://doi.org/10.1111/j.1574-6941.1997.tb00372.x

Senga, Y., Mochida, K., Fukumori, R., Okamoto, N., & Seike, Y. (2006). N_2O accumulation in estuarine and coastal sediments: The influence on H_2S on dissimilatory nitrate reduction. *Estuarine, Coastal and Shelf Science*, *67*, 231–238. https://doi.org/10.1016/j.ecss.2005.11.021

Shao, X., Sheng, X., Wu, M., Wu, H., & Ning, X. (2017). Methane production potential and emission at different water levels in the restored reed wetland of Hangzhou Bay. *PLoS ONE*, *12*, e0185709. https://doi.org/10.1371/journal.pone.0185709

Shen, Y., & Zhu, B. (2021). Arbuscular mycorrhizal fungi reduce soil nitrous oxide emission. *Geoderma*, *402*, 115179. https://doi.org/10.1016/j.geoderma.2021.115179

Sheng, Y., Luan, Z., Yan, D., Li, J., Xie, S., Liu, Y., Chen, L., Li, M., & Wu, C. (2022). Effects of *Spartina alterniflora* invasion on soil carbon, nitrogen and phosphorous in Yancheng coastal wetlands. *Landscape*, *11*, 2218. https://doi.org/10.3390/land11122218

Sørensen, J., Tiedje, J. M., & Firestone, R. B. (1980). Inhibition by sulfide of nitric and nitrous oxide reduction by denitrifying *Pseudomonas fluorescens*. *Applied and Environmental Microbiology*, *39*, 105–108. https://doi.org/10.1128/aem.39.1.105-108.1980

Srivastava, J., Kalra, S. J. S., & Naraian, R. (2014). Environmental perspectives of *Phragmites australis* (Cav.) Trin. Ex. Steudel. *Applied Water Science*, *4*, 193–202. https://doi.org/10.1007/s13201-013-0142-x

Taillardat, P., Thompson, B. S., Garneau, M., Trottier, K., & Friess, D. A. (2020). Climate change mitigation potential of wetlands and the cost-effectiveness of their restoration. *Interface Focus*, *10*, 20190129. https://doi.org/10.1098/rsfs.2019.0129

Tan, L., Ge, Z., Zhou, X., Li, S., Li, X., & Tang, J. (2019). Conversion of coastal wetlands, riparian wetlands, and peatlands increases greenhouse gas emissions: A global meta-analysis. *Global Change Biology*, *26*, 1638–1653. https://doi.org/10.1111/gcb.14933

Temmerman, S., Meire, P., Bouma, T. J., Herman, P. M. J., Ysebaert, T., & De Vriend, H. J. (2013). Ecosystem-based coastal defence in the face of global change. *Nature*, *504*, 79–83. https://doi.org/10.1038/nature12859

Tong, C., Morris, J. T., Huang, J., Xu, H., & Wan, S. (2018). Changes in pore-water chemistry and methane emission following the invasion of *Spartina alterniflora* into an oligohaline marsh. *Limnology and Oceanography*, *63*, 384–396. https://doi.org/10.1002/lno.10637

Tong, C., Wang, W. Q., Huang, J. F., Gauci, V., Zhang, L.-H., & Zeng, C.-S. (2012). Invasive alien plants increase CH_4 emissions from a subtropical tidal estuarine wetland. *Biogeochemistry*, *111*, 677–693. https://doi.org/10.1007/s10533-012-9712-5

Uddin, M. N., Robinson, R. W., & Caridi, D. (2014). Phytotoxicity induced by *Phragmites australis*: An assessment of phenotypic and physiological parameters involved in germination process and growth of receptor plant. *Journal of Plant Interactions*, *9*, 338–353. https://doi.org/10.1080/17429145.2013.835879

Uddin, M. N., Robinson, R. W., Caridi, D., & Harun, M. A. Y. (2013). Is phytotoxicity of *Phragmites australis* residue influenced by decomposition condition, time and density? *Marine and Freshwater Research*, *65*, 505–516.

Vann, C. D., & Megonigal, J. P. (2003). Elevated CO_2 and water depth regulation of methane emissions: Comparison of woody and non-woody wetland plant species. *Biogeochemistry*, *63*, 117–134. https://doi.org/10.1023/A:1023397032331

Viechtbauer, W. (2010). Conducting meta-analyses in R with the *metafor* package. *Journal of Statistical Software*, *36*, 1–48. https://doi.org/10.18637/jss.v036.i03

Wails, C. N., Baker, K., Blackburn, R., Del Vallé, A., Heise, J., Herakovich, H., Holthuijzen, W. A., Nissenbaum, M. P., Rankin, L., Savage, K., Vanek, J. P., & Jones, H. P. (2021). Assessing changes to ecosystem structure and function following invasion by *Spartina alterniflora* and *Phragmites australis*: A meta-analysis. *Biological Invasions*, *23*, 2695–2709. https://doi.org/10.1007/s10530-021-02540-5

Walesiak, M., & Dudek, A. (2020). The choice of variable normalization method in cluster analysis. In K. S. Soliman (Ed.), *Education excellence and innovation management: A 2025 vision to sustain economic development during global challenges* (pp. 325–340). International Business Information Management Association (IBIMA).

Wickham, H., Averick, M., Bryan, J., Chang, W., D'Agostino McGowan, L., François, R., Grolemund, G., Hayes, A., Henry, L., Hester, J., Kuhn, M., Pedersen, T. L., Miller, E., Milton Bache, S., Müller, K., Ooms, J., Robinson, D., Paige Seide, D., Spinu, V., … Yutani, H. (2019). Welcome to the tidyverse. *Journal of Open Source Software.*, *4*, 1686. https://doi.org/10.21105/joss.01686

Wilke, C. O. (2020). Ggtext: Improved text rendering support for 'ggplot2'. *R package* version 0.1.1. https://CRAN.R-project.org/package=ggtext.

Windham, L. (2001). Comparison of biomass production and decomposition between *Phragmites australis* (common reed) and *Spartina patens* (salt hay grass) in brackish tidal marshes of New Jersey, USA. *Wetlands*, *21*, 179–188. https://doi.org/10.1672/0277-5212(2001)021[0179:COBPAD]2.0.CO;2

Xiang, J., Liu, D., Ding, W., Yuan, J., & Lin, Y. (2015). Invasion chronosequence of *Spartina alterniflora* on methane emission and organic carbon sequestration in a coastal salt marsh. *Atmospheric Environment*, *112*, 72–80. https://doi.org/10.1016/j.atmosenv.2015.04.035

Xu, X., Zu, X., Cao, L., Zhamangulova, N., Zhao, Y., Tang, D., & Liu, D. (2014). Seasonal and spatial dynamics of greenhouse gas emissions under various vegetation covers in a coastal saline wetland in southeastern China. *Ecological Engineering*, *73*, 469–477. https://doi.org/10.1016/j.ecoleng.2014.09.087

Yang, B., Li, X., Lin, S., Xie, Z., Yuan, Y., Espenberg, M., Pärn, J., & Mander, Ü. (2020). Invasive *Spartina alterniflora* can mitigate N_2O emission in coastal salt marshes. *Ecological Engineering*, *147*, 105758. https://doi.org/10.1016/j.ecoleng.2020.105758

Yang, P., Wang, M. H., Lai, D. Y. F., Chun, K. P., Huang, J. F., Wan, S. A., Bastviken, D., & Tong, C. (2019). Methane dynamics in an estuarine brackish *Cyperus malaccensis* marsh: Production and porewater concentration in soils, and net emissions to the atmosphere over five years. *Geoderma*, *337*, 132–142. https://doi.org/10.1016/j.geoderma.2018.09.019

Yao, Y., Song, Y., Su, P., Wang, J., Miao, C., Luo, Y., Sun, Q., Wang, J., Zhang, G., Bu, N., & Li, Z. (2023). Asymmetric responses of functional microbes in methane and nitrous oxide emissions to plant invasion: A meta-analysis. *Soil Biology and Biochemistry*, *178*, 108931. https://doi.org/10.1016/j.soilbio.2022.108931

Yin, S., An, S., Deng, Q., Zhang, J., Ji, H., & Cheng, X. (2015). *Spartina alterniflora* invasions impact CH_4 and N_2O fluxes from a salt marsh in eastern China. *Ecological Engineering*, *81*, 192–199. https://doi.org/10.1016/j.ecoleng.2015.04.044

Yuan, J., Ding, W., Liu, D., Kang, H., Freeman, C., Xiang, J., & Lin, Y. (2015). Exotic *Spartina alterniflora* invasion alters ecosystem-atmosphere exchange of CH_4 and N_2O and carbon sequestration in a coastal salt marsh in China. *Global Change Biology*, *21*, 1567–1580. https://doi.org/10.1111/gcb.12797

Zedler, J. B., & Kercher, S. (2004). Causes and consequences of invasive plants in wetlands: Opportunities, opportunists, and outcomes. *Critical Reviews in Plant Sciences*, *23*, 431–452. https://doi.org/10.1080/07352680490514673

Zeleke, J., Sheng, Q., Wang, J.-G., Huang, M.-Y., Xia, F., Wu, J.-H., & Quan, Z.-X. (2013). Effects of *Spartina alterniflora* invasion on the communities of methanogens and sulfate-reducing bacteria in estuarine marsh sediments. *Frontiers in Microbiology*, *4*, 243. https://doi.org/10.3389/fmicb.2013.00243

Zhang, Y., & Ding, W. (2011). Diel methane emissions in stands of *Spartina alterniflora* and *Suaeda salsa* from a coastal salt marsh. *Aquatic Botany*, *95*, 262–267. https://doi.org/10.1016/j.aquabot.2011.08.005

Zhang, X.-d., Jia, X., Chen, Y.-y., Shao, J.-j., Wu, X.-r., Shang, L., & Li, B. (2013). Crabs mediate interactions between native and invasive salt marsh plants: A mesocosm study. *PLoS ONE*, *8*, e74095. https://doi.org/10.1371/journal.pone.0074095

Zheng, W. J., Zheng, X. P., & Zhang, C. L. (2000). A survey of photosynthetic carbon metabolism in 4 ecotypes of *Phragmites australis* in Northwest China: Leaf anatomy, ultrastructure, and activities of ribulose 1.5-bisphosphate carboxylase, phosphoenolpyruvate carboxylase and glycollate oxidase. *Physiologia Plantarium*, *110*, 201–208. https://doi.org/10.1034/j.1399-3054.2000.110209.x

Zhou, C., Zhao, H., Sun, Z., Zhou, L., Fang, C., Xiao, Y., Deng, Z., Zhi, Y., Zhao, Y., & An, S. (2015). The invasion of *Spartina alterniflora* alters carbon dynamics in China's Yangcheng natural reserve. *Clean: Soil, Air, Water*, *43*, 159–165. https://doi.org/10.1002/clen.201300839

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Fuchs, A., Davidson, I. C., Megonigal, J. P., Devaney, J. L., Simkanin, C., Noyce, G. L., Lu, M., & Cott, G. M. (2025). Stronger increase of methane emissions from coastal wetlands by non-native *Spartina alterniflora* than non-native *Phragmites australis*. *Plants, People, Planet*, *7*(1), 62–79. https://doi.org/10.1002/ppp3.10578