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Contrasting ecosystem CO_2 fluxes of inland and coastal wetlands: a meta-analysis of eddy covariance data

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Abstract

Wetlands play an important role in regulating the atmospheric carbon dioxide (CO_2) concentrations and thus affecting the climate. However, there is still lack of quantitative evaluation of such a role across different wetland types, especially at the global scale. Here, we conducted a meta-analysis to compare ecosystem CO_2 fluxes among various types of wetlands using a global database compiled from the literature. This database consists of 143 site-years of eddy covariance data from 22 inland wetland and 21 coastal wetland sites across the globe. Coastal wetlands had higher annual gross primary productivity (GPP), ecosystem respiration (R_e), and net ecosystem productivity (NEP) than inland wetlands. On a per unit area basis, coastal wetlands provided large CO_2 sinks, while inland wetlands provided small CO_2 sinks or were nearly CO_2 neutral. The annual CO_2 sink strength was 93.15 and 208.37 g C m^{-2} for inland and coastal wetlands, respectively. Annual CO_2 fluxes were mainly regulated by mean annual temperature (MAT) and mean annual precipitation (MAP). For coastal and inland wetlands combined, MAT and MAP explained 71%, 54%, and 57% of the variations in GPP, R_e, and NEP, respectively. The CO_2 fluxes of wetlands were also related to leaf area index (LAI). The CO_2 fluxes also varied with water table depth (WTD), although the effects of WTD were not statistically significant. NEP was jointly determined by GPP and R_e for both inland and coastal wetlands. However, the NEP/R_e and NEP/GPP ratios exhibited little variability for inland wetlands and decreased for coastal wetlands with increasing latitude. The contrasting of CO_2 fluxes between inland and coastal wetlands globally can improve our understanding of the roles of wetlands in the global C cycle. Our results also have implications for informing wetland management and climate change policymaking, for example, the efforts being made by international organizations and enterprises to restore coastal wetlands for enhancing blue carbon sinks.

Keywords: carbon budget, cross-site synthesis, ecosystem respiration, gross primary productivity, mangroves, marshes, net ecosystem productivity

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Introduction

The global carbon (C) cycle has become one of the key topics in ecological and global change research. C sequestration is an important ecosystem service that terrestrial, marine, and freshwater ecosystems provide (Chapin *et al.*, 2009; McLeod *et al.*, 2011; Turetsky *et al.*, 2014). Wetlands are believed to be highly productive ecosystems with low rates of decomposition due to low microbial activity caused by anaerobic conditions (Odum *et al.*, 1995; Chmura *et al.*, 2003). However, not all wetlands are equally effective in sequestering C and there is still a debate on whether wetlands are significant sinks or sources for atmospheric carbon dioxide (CO_2) (Kayranli *et al.*, 2010; Bernal & Mitsch, 2012). Recent research pointed out that inland waters were important C sources, and some inland aquatic ecosystems were more than just 'neutral pipes' merely conveying terrestrial C to the oceans (Chu *et al.*, 2015). Previous studies on ecosystem C exchange of global wetlands focused mainly on inland or freshwater wetlands (Chu *et al.*, 2015) although coastal wetlands such as mangroves, salt marshes, and seagrass beds sequester significant amount of CO_2, known as 'blue carbon' (Guo *et al.*, 2009; Nellemann *et al.*, 2009; McLeod *et al.*, 2011; Pendleton *et al.*, 2012; Artigas *et al.*, 2015). Coastal wetlands actively remove CO_2 from the atmosphere through burial of organic C in the sediments (Duarte *et al.*, 2005; Kathilankal *et al.*, 2008). Assessing the C dynamics of coastal wetlands is essential for capitalizing blue C sequestration potential of these valuable

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ecosystems and informing wetland management (e.g., protecting coastal wetlands, increasing the area of mangroves and salt marshes) and climate change policy-making.

Previous studies showed that some of the freshwater wetlands are a sink of atmospheric CO_2 but can also function as a CO_2 source when methane (CH_4) emissions are considered (Mitsch *et al.*, 2012; Pester *et al.*, 2012). In contrast, coastal wetlands, including salt marshes, mangroves, and seagrass beds, can sequester a great amount of CO_2 but have negligible emissions of other greenhouse gases such as CH_4 (Chmura, 2013). The presence of high salt and sulfate in these ecosystems inhibits CH_4 production and emissions, and therefore, coastal wetlands are expected to play a larger role in reducing global warming potential than freshwater wetlands (Purvaja & Ramesh, 2001; Cheng *et al.*, 2007; Kirschke *et al.*, 2013; Turetsky *et al.*, 2014). In the meanwhile, anthropogenic perturbations on coastal ecosystems have become increasingly acute due to centuries of population growth and human activities including shoreline development, eutrophication, sea level rise, and overfishing (Halpern *et al.*, 2008; Regnier *et al.*, 2013; Coverdale *et al.*, 2014; Ma *et al.*, 2014). More and more studies indicated that because of land use conversion, a large amount of C that is stored in the biomass and deep sediments of coastal ecosystems is released into the atmosphere as greenhouse gases (Pendleton *et al.*, 2012; Petrescu *et al.*, 2015).

During the last two decades, the observations of wetland ecosystem CO_2 fluxes have been extended both in temporal coverage and spatial density. The most common method of measuring CO_2 fluxes at the ecosystem level is perhaps the eddy covariance (EC) technique. The EC flux towers continuously measure net ecosystem exchange of CO_2 (NEE) at the half-hourly time step. NEE is equal to net ecosystem productivity (NEP) but has the opposite sign (NEP = −NEE). NEE is routinely partitioned into its two components: gross primary productivity (GPP) and ecosystem respiration (R_e). The EC technique has been widely used to examine ecosystem CO_2 fluxes around the world, and there is currently over 500 EC flux sites over the globe (Baldocchi *et al.*, 2001; Baldocchi, 2008). Recently, synthesis studies have been conducted to examine the spatial patterns and climatic controls of CO_2 fluxes at regional and global scales using EC observations from multiple sites (e.g., Amiro *et al.*, 2010; Xiao *et al.*, 2013; Yu *et al.*, 2013). Although more EC sites have been established for inland wetlands than for coastal wetlands, there have been a growing number of EC sites for coastal wetlands mainly consisting of mangroves and salt marshes (Amiro *et al.*, 2010). A synthesis study of the CO_2 fluxes and climate regulation for inland and coastal wetlands is now feasible and timely. Few studies have synthesized flux observations from wetlands at regional scales, and these studies typically use observations from a few sites (e.g., Lund *et al.*, 2010; Xiao *et al.*, 2013; Yu *et al.*, 2013; Chen *et al.*, 2014; Turetsky *et al.*, 2014; Petrescu *et al.*, 2015). To our knowledge, no cross-site synthesis has been conducted to compare the differences in ecosystem CO_2 exchange between inland and coastal wetlands at the global scale using EC observations from a large number of sites.

Here we compiled a global database of EC flux data for wetlands from the literature, and conducted a meta-analysis of CO_2 fluxes for contrasting the annual CO_2 fluxes between inland and coastal wetlands. The specific objectives of our study were to (i) synthesize flux measurements for coastal and inland wetlands by building a database with flux and meteorology data, (ii) examine the magnitude and spatial patterns of annual CO_2 fluxes for both inland and coastal wetlands and identify their key climatic controls, and (iii) compare the latitudinal patterns of the NEP/R_e and NEP/GPP ratios between inland and coastal wetlands. We hypothesize that the CO_2 fluxes between inland and coastal wetlands were significantly different because of their differences in climate, vegetation, and hydrological factors. This study can provide a theoretical basis for developing an assessment model of CO_2 budgets in wetland ecosystems at the global scale and scientific data for supporting wetland management for CO_2 sequestration.

Materials and methods

Data collection and processing

The site-level CO_2 flux data used in our research were collected from 43 wetland sites in Asia, Europe, North America, and Australia, where EC observations were conducted for at least 1 year. We performed a literature search using the ISI Web of Science for articles published before August 2014 using keywords 'carbon flux' and 'eddy' and 'wetland', or 'carbon flux' and 'eddy' and 'coastal'. The annual CO_2 flux data and environmental factors were compiled from the papers. Only those sites having at least 1 year of continuous flux measurements via open-path or closed-path EC methods were selected for calculating annual CO_2 fluxes (GPP, R_e, and NEP). We also collected climatic, vegetation, and hydrological variables including mean annual temperature (MAT, based on mean daily temperature), mean annual precipitation (MAP, i.e., mean yearly sum of precipitation), leaf area index (LAI), and annual average water table depth (WTD). A total of 48 papers were selected for this meta-analysis (Tables 1 and 2). For those sites containing only 1 year of data, the observed fluxes and climatic variables were directly used in the analysis. For the remaining sites, we calculated the means of annual CO_2 fluxes and climatic variables during the measurement period. For those sites that data were published several times,

Table 1 Annual environmental conditions* and carbon dioxide fluxes† of inland wetlands from published year-long studies based on the eddy covariance technique

Site name	Wetland types	Plant growth	Latitude	Longitude	MAT (°C)	MAP (mm)	LAI (m^2 m^{-2})	WTD (cm)	GPP (g C m^{-2} yr^{-1})	R_e (g C m^{-2} yr^{-1})	NEP (g C m^{-2} yr^{-1})	Available years	Gap-filling techniques	Observation year(s)	References
Western Peatland	PL	Woody	54.95	−112.47	1.70	465		−30	869.00	674.00	195.50	2004–2007	NLR_FCRN	4	Sulman *et al.* (2012)
					2.00	440	2.1		692.00	440.00	252.00	2004–2005	MDS, ANN_S, NLR_LM	1	Lund *et al.* (2010)
					1.20	486	2.61		713.00	569.00	144.00	2004	NLR_FCRN	1	Syed *et al.* (2006)
					1.70	**465**	**2.355**	−30	**869.00**	**674.00**	**195.50**	**2004–2007**		**4**	
Mer Bleue-Bog	PL	Herbaceous	45.40	−75.50	6.20	779		−43	617.00	548.00	68.60	1999–2006	NLR_FCRN	1	Sulman *et al.* (2012)
							1.4		600.13	540.38	59.88	1999–2006	NLR_FCRN	7	Wu *et al.* (2011)
					5.80	910	1.3		390.33	336.00	54.67	1999–2001	NLR	3	Lafleur *et al.* (2003)
					5.80	910	1.3	−20	524.00	456.00	68.00	1998–1999	NLR, SPM	1	Lafleur *et al.* (2001)
					6.00	815	1.3		524.00	467.00	57.00	2003–2005	MDS, ANN_S, NLR_LM	1	Lund *et al.* (2010)
					6.07	**793**	**1.3**	**−31.5**	**591.67**	**531.00**	**60.78**	**1998–2006**		**9**	
Glencar	PL	Herbaceous	51.92	−9.92	10.46	2433	0.7	−6.5			55.00	2003–2004	NLR	2	Sottocornola & Kiely (2005)
					10.66	2579	0.6	−7.5			47.78	2003–2008	NLR	6	Koehler *et al.* (2011)
					10.66	**2579**	**0.65**	**−7**			**47.78**	**2003–2008**		**6**	
Bog Lake Fen	PL	Herbaceous	47.51	−93.49	4.43	646		5			35.27	2009–2011	NLR_FCRN	3	Olson *et al.* (2013)
Fajemyr peatland	PL	Woody	56.25	13.55	6.20	788		−10			4.92	2006–2009	MDS, ANN_S, NLR_LM	4	Lund *et al.* (2012)
					6.20	700		−10			21.50	2005–2006	MDS, ANN_S, NLR_LM	1	Lund *et al.* (2007)
					7.80	700			523.00	493.00	30.00	2005–2006	MDS, ANN_S, NLR_LM	1	Lund *et al.* (2010)
					7.80	**700**		**−10**	**523.00**	**493.00**	**30.00**	**2005–2009**		**5**	
Degero Stormyr	PL	Herbaceous	64.18	19.55	2.29	666	0.9	−14.1	336.42	278.33	58.00	2001–2012	NLR	12	Peichl *et al.* (2014)
					1.20	523		−12	201.00	139.67	56.00	2001–2003	NLR	3	Yurova *et al.* (2007)

Table 1 (continued)

Site name	Wetland types	Plant growth	Latitude	Longitude	MAT (°C)	MAP (mm)	LAI (m^2 m^{-2})	WTD (cm)	GPP (g C m^{-2} yr^{-1})	R_e (g C m^{-2} yr^{-1})	NEP (g C m^{-2} yr^{-1})	Available years	Gap-filling techniques	Observation year(s)	References
					2.10	453		−15	351.00	277.00	74.00	2001–2005	MDS, ANN_S, NLR_LM	1	Lund *et al.* (2010)
					1.20	523			448.50	404.17	48.00	2001–2006	NLR	6	Wu *et al.* (2013)
					2.29	**666**	**0.9**	−14	**336.42**	**278.33**	**58.00**	**2001–2012**		**12**	
Skjern meadows	FSM	Herbaceous	55.91	8.40	8.00	783					142.00	2009–2011	NLR	3	Herbst *et al.* (2013)
Fogg dam wetland	FSM	Herbaceous	−12.57	131.28	23.75	1446		125			310.91	2006–2008	ANN_S	3	Beringer *et al.* (2013)
Mokre louky	FSM	Herbaceous	49.03	14.77	8.50	650		0			209.50	2006–2007	NLR	2	Dusek *et al.* (2009)
									1327.8	1201.5	126.3	2009	NLR	1	Marek *et al.* (2011)
					8.50	**650**		**0**	**1327.8**	**1201.5**	**126.3**	**2009**		**1**	
Mer Bleue	FSM	Herbaceous	45.40	−75.50	7.64	896	3.63		831.00	567.00	264.00	2006	NLR	1	Bonneville *et al.* (2008)
California's Central Valley	FSM	Woody	38.27	−121.40	15.00	375	2.6				310.00	2004	LUT	1	Kochendorfer *et al.* (2011)
Siikaneva fen	FSM	Herbaceous	61.83	24.19	4.10	715	0.4				55.50	2004–2005	NLR	1	Aurela *et al.* (2007)
					4.20	713	0.4		376.00	339.00	37.00	2004–2005	NLR	1	Lund *et al.* (2010)
					4.20	**713**	**0.4**		**376.00**	**339.00**	**37.00**	**2004–2005**		**1**	
Sanjiang SJS	FSM	Herbaceous	47.58	133.52	2.00	549			497.00	453.00	61.67	2004–2006	NLR	1	Yu *et al.* (2013)
Lost Creek	FSS	Woody	46.08	−89.99	5.08	799		−30.064	812.37	734.79	83.89	2001–2006	NLR_ FCRN	6	Sulman *et al.* (2009)
					3.80	666		−33	849.00	771.00	77.90	2001–2006	NLR_ FCRN	1	Sulman *et al.* (2012)
					5.08	**799**		**−32**	**812.37**	**734.79**	**83.89**	**2001–2006**		**6**	
Rzecin	FSS	Woody	52.77	16.30					829.00	573.00	255.00	2004	NLR	1	Owen *et al.* (2007)
					8.50	509	2.3		856.00	600.00	256.00	1998–2005	MDS, ANN_S, NLR_LM	1	Lund *et al.* (2010)
					8.50	**509**	**2.3**		**856.00**	**600.00**	**256.00**	**1998–2005**		**7**	
Kaamanen	FSS	Woody	69.14	27.30					264.50	219.00	45.50	2001–2002	NLR	2	Owen *et al.* (2007)

Table 1 (continued)

Site name	Wetland types	Plant growth	Latitude	Longitude	MAT (°C)	MAP (mm)	LAI (m^2 m^{-2})	WTD (cm)	GPP (g C m^{-2} yr^{-1})	R_e (g C m^{-2} yr^{-1})	NEP (g C m^{-2} yr^{-1})	Available years	Gap-filling techniques	Observation year(s)	References
					−2.23	598	0.7	5	248.20	232.60	18.60	1998–1999	NLR	1	Aurela *et al.* (2002)
					0.20	471	0.7		263.00	241.00	22.00	2000–2006	MDS, ANN_S, NLR_LM	6	Lund *et al.* (2010)
					−0.15	**489**	**0.7**	**5**	**260.89**	**239.8**	**21.51**	**1998–1999, 2000–2006**		**7**	
Zoige plateau	ATW	Herbaceous	37.58	101.33	−1.10	510	3.9	30	629.87	737.13	−106.10	2004–2006	NLR	3	Zhao *et al.* (2010)
					−1.35	439			489.12	568.25	−79.13	2004–2008	NLR	1	Yu *et al.* (2013)
					−1.05	475	3.88	20	615.75	701.94	−86.19	2005	NLR	1	Zhang *et al.* (2008)
					−1.35	**439**	**3.88**	**20**	**489.12**	**568.25**	**−79.13**	**2004–2008**		**5**	
Kytalyk reserve	ATW	Herbaceous	70.83	147.50	−13.00	212	1		232.00	141.00	92.00	1999–2006	NLR	1	Van Der Molen *et al.* (2007)
Zoige Alpine	ATW	Herbaceous	33.93	102.87	1.10	650			630.95	567.55	63.40	2008–2009	NLR	2	Hao *et al.* (2011)
Heath tundra	ATW	Woody	68.62	−149.30	−1.35	187			188.00	219.67	−44.33	2008–2011	MDV	3	Euskirchen *et al.* (2012)
Wet sedge tundra	ATW	Herbaceous	68.62	−149.30	−1.35	187		70	189.33	219.33	−42.67	2008–2011	MDV	3	Euskirchen *et al.* (2012)
Samoylov Island	ATW	Herbaceous	72.37	126.50	−12.10	233	1.25	6	117.82	99.00	19.36	2003–2004	NLR	1	Kutzbach *et al.* (2007)

Inland wetlands included freshwater swamp marsh (FSM), freshwater shrub swamp (FSS), peatland (PL), and alpine tundra wetlands (ATW). The gap-filling techniques include ANN_S (standard artificial neural network), LUT (lookup table), MDS (marginal distribution sampling), MDV (mean diurnal variation), NLR (nonlinear regression), NLR_FCRN (nonlinear regression of Fluxnet Canada Research Network, logistic equation, Michaelis-Menten), NLR_LM (nonlinear regression, Lloyd-Taylor, Michaelis-Menten), and SPM (semiparametric model). For those sites which data were published several times, the mean annual CO_2 fluxes and climatic variables were calculated for the longest measurement period and are shown in bold.

*Mean annual temperature (MAT), mean annual precipitation (MAP), leaf area index (LAI), water table depth (WTD).

†Gross primary productivity (GPP), ecosystem respiration (R_e), and net ecosystem productivity (NEP).

Table 2 Annual environmental* conditions and carbon dioxide fluxes† of coastal wetlands from published year-long studies based on the eddy covariance technique

Site name	Wetland types	Plant growth	Latitude	Longitude	MAT (°C)	MAP (mm)	LAI (m^2 m^{-2})	WTD (cm)	GPP (g C m^{-2} yr^{-1})	R_e (g C m^{-2} yr^{-1})	NEP (g C m^{-2} yr^{-1})	Available years	Gap-filling techniques	Observation year(s)	References
Gaoqiao	IFW	Woody	21.57	109.76	22.90	1770	4.4		1763.68	1095.65	721.65	2010–2012	NLR_LM	3	Lu (2013)
Yunxiao	IFW	Woody	23.92	117.42	22.20	999	2.6		1871.33	1286.98	683.98	2009–2012	NLR_LM	4	Chen (2013)
Everglades National Park	IFW	Woody	25.36	−81.08	22.50	1410	2.29		2093.67	1144.00	949.83	2004–2010	LUT, MDV	6	Barr *et al.* (2010, 2012)
Vancouver Island DF49	IFW	Woody	49.87	−125.34	8.50	1113	8.4		1991.00	1737.00	254.00	2002	NLR	1	Humphreys *et al.* (2006)
Loblolly pine	IFW	Woody	35.80	−76.67	17.50	1320	4.07		2719.00	2082.00	640.00	2005–2007	NLR	3	Noormets *et al.* (2010)
Chongming Dongtan1	IM	Herbaceous	31.52	121.96	16.15	867	4.7		1294.20	656.20	635.20	2005–2006	NLR_LM	2	Guo (2010)
Chongming Dongtan2	IM	Herbaceous	31.52	121.97	16.15	867	3.8		1283.95	792.95	493.90	2005–2006	NLR_LM	2	Guo (2010)
Chongming Dongtan3	IM	Herbaceous	31.58	121.90	16.15	867	2.6		1022.50	501.90	514.15	2005–2006	NLR_LM	2	Guo (2010)
					15.60	817			1512.63	1067.21	445.41	2004–2008	NLR_LM	5	Yu *et al.* (2013)
					15.60	**817**	**2.6**		**1512.63**	**1067.21**	**445.41**	**2004–2008**		**5**	
Horstermeer	CFM	Herbaceous	52.14	5.04	9.80	797		−0.2	1215.67	886.33	329.67	2004–2006	NLR	3	Hendriks *et al.* (2007)
San Joaquin Freshwater Marsh	CFM	Herbaceous	33.66	−117.85	16.56	266	4.92		1464.56	1316.91	134.05	1999–2003	NLR, LUT	5	Rocha & Goulden (2008)
Winous Point Marsh Conservancy	CFM	Herbaceous	27.46	−83.00	12.00	1083		−0.5	800.20	779.20	20.95	2011–2012	MDS	2	Chu *et al.* (2014)
Panjin	CFM	Herbaceous	41.13	121.90	8.97	590	4		1298.16	1233.16	65.00	2005	MDV, NLR	1	Zhou *et al.* (2009)
Kennedy Space Center	CFF	Woody	28.60	−80.70	19.88	1144	1.7				318.67	2000–2006	NLR_LM	6	Powell *et al.* (2006)
Cypress wetland	CFF	Woody	29.73	−82.16	20.50	1280	3.25	70			60.50	1996–1997	NLR	2	Clark *et al.* (1999)
Vancouver Island	APCW	Woody	49.87	−125.29	8.63	1163	1.385		463.33	1043.33	−580.00	2000–2003	NLR	3	Humphreys *et al.* (2005)
Sacramento-San Joaquin Delta	APCW	Herbaceous	38.04	−121.75	14.90	438	1	−65	1369.50	1629.00	−236.50	2009–2011	ANN_S	2	Hatala *et al.* (2012)
Sacramento-San Joaquin Delta	APCW	Herbaceous	38.11	−121.65	14.05	404	5	7.5	1417.50	1263.00	183.50	2009–2011	ANN_S	2	Hatala *et al.* (2012)
Shark river slough	APCW	Herbaceous	25.55	−80.78	24.60	1090	0.63		239.75	289.95	−49.95	2008–2009	NLR	2	Jimenez *et al.* (2012)
Taylor slough	APCW	Herbaceous	25.44	−80.59	23.70	1245			462.15	417.25	44.90	2008–2009	NLR	2	Jimenez *et al.* (2012)

Table 2 (continued)

Site name	Wetland types	Plant growth	Latitude	Longitude	MAT (°C)	MAP (mm)	LAI (m^2 m^{-2})	WTD (cm)	GPP (g C m^{-2} yr^{-1})	R_e (g C m^{-2} yr^{-1})	NEP (g C m^{-2} yr^{-1})	Available years	Gap-filling techniques	Observation year(s)	References
					23.90	1206			496.00	446.10	49.90	2008	NLR	1	Schedlbauer *et al.* (2010)
					23.70	**1245**	**1.03**		**462.15**	**417.25**	**44.90**	**2008–2009**		**2**	
Vancouver Island HDF88	IFW	Woody	49.52	−124.90	9.50	1246	4.85		1347.00	1214.00	133.00	2002	NLR	1	Humphreys *et al.* (2006)
Vancouver Island HDF00	IFW	Woody	49.87	−125.29	8.80	1123	1.35		1041.00	435.00	606.00	2002	NLR	1	Humphreys *et al.* (2006)

Coastal wetlands included intertidal marshes (IM), intertidal forested wetlands (IFW), coastal freshwater marshes (CFM), coastal freshwater forests (CFF), and anthropogenic perturbations coastal wetlands (APCW). The full names of the gap-filling techniques can be found in the caption of Table 1. For those sites thatdata were published several times, the mean annual CO_2 fluxes and climatic variables were calculated for the longest measurement period and are shown in bold.

*Mean annual temperature (MAT), mean annual precipitation (MAP), leaf area index (LAI), water table depth (WTD).

†Gross primary productivity (GPP), ecosystem respiration (R_e), and net ecosystem productivity (NEP).

we calculated the mean annual CO_2 fluxes and climatic variables for the longest measurement period.

For each site, the NEE was measured using the EC technique, and the details of each individual EC measurement and data processing protocol can be found in the references listed in Tables 1 and 2. NEE data were processed, gap filled, and partitioned to R_e and GPP. NEP was calculated as the sum of gap-filled NEE with the opposite sign. Positive NEP values indicate C gain, while negative values indicate C release. R_e was calculated based on empirical equations between night-time NEE measurements and temperature (Reichstein *et al.*, 2005). GPP was then calculated as the sum of NEP and R_e. The data processing was mainly based on the standardized processing procedures of each regional network, and the gap-filling techniques mainly included ANN_S (standard artificial neural network), LUT (lookup table), MDS (marginal distribution sampling), MDV (mean diurnal variation), NLR (nonlinear regression), NLR_FCRN (nonlinear regression of Fluxnet Canada Research Network, logistic equation, Michaelis-Menten), NLR_LM (nonlinear regression, Lloyd-Taylor, Michaelis-Menten), and SPM (semiparametric model). The gap-filling technique for each site was specified in Tables 1 and 2. All these gap-filling techniques showed good overall performance (Moffat *et al.*, 2007). The effect of gap-filling on the annual sums of NEE is modest and the associated uncertainty is within 25 g C m^{-2} yr^{-1} (Moffat *et al.*, 2007).

All sites were broadly classified into inland wetlands and coastal wetlands based on the geographical location and the dominant plant species. The database that we complied consists of 22 inland wetland sites and 21 coastal wetland sites (Tables 1 and 2). Most of the inland wetland sites are distributed in the middle and high latitudes, while the coastal wetland sites are mainly located in the low and middle latitudes. Meanwhile, some climate zones only had one or two wetland study sites. Although most sites had data available for all the CO_2 fluxes (GPP, R_e, and NEP), some sites only had data for some of the fluxes. Therefore, the number of sites varied with the type of CO_2 flux.

Following the Ramsar Convention on wetlands and the rule of 'The directory of important wetlands in Australia' (ANCA, 1996; Larmour, 2001), the inland wetlands of our study include the following types: freshwater swamp marsh (FSM), freshwater shrub swamp (FSS), peatland (PL), and alpine tundra wetlands (ATW). The coastal wetlands mainly include intertidal forested wetlands (IFW), intertidal marshes (IM), coastal freshwater marshes (CFM), and coastal freshwater forests (CFF). Seven anthropogenic perturbations coastal wetland (APCW) sites were also identified to assess the effects of human activities on the CO_2 fluxes of coastal wetlands, and all of these sites experienced large anthropogenic disturbances causing hydrological alternation or vegetation changes.

The site descriptions including site name, wetland types, plant growth, location, MAT, MAP, LAI, WTD, annual CO_2 fluxes, duration of observations, and the gap-filling techniques were summarized in Table 1 for inland wetlands and in Table 2 for coastal wetlands. The other available environmental and vegetation factors such as annual aboveground biomass, canopy height, temperature sensitivity of ecosystem respiration (Q_{10}), litterfall productivity, tree age, volumetric

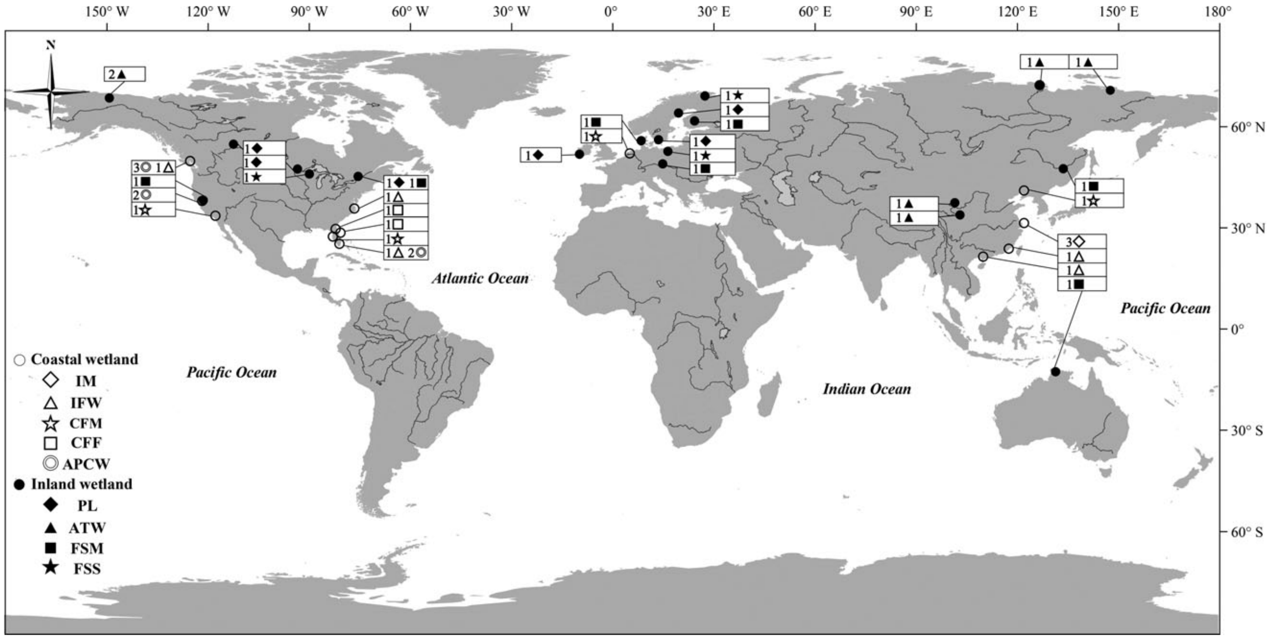

Fig. 1 Location and distribution of the wetland sites selected in this meta-analysis. The wetland sites are grouped into inland wetlands and coastal wetlands. The inland wetlands include peatland (PL), freshwater swamp marsh (FSM), freshwater shrub swamp (FSS), and alpine tundra wetlands (ATW). Coastal wetlands include intertidal forested wetlands (IFW), intertidal marshes (IM), coastal freshwater marshes (CFM), coastal freshwater forests (CFF), and anthropogenic perturbations coastal wetlands (APCW).

water content of soil, flooded period, and soil property were also included in Table S1. The locations and geographical distribution of all the sites were illustrated in Fig. 1. The inland wetland data set consists of six peatland sites, seven freshwater swamp marsh sites, three freshwater shrub swamp sites and six alpine tundra wetlands sites (Table 1 and Fig. 1). Coastal wetland sites include five intertidal forested wetlands sites, three intertidal marshes sites, four coastal freshwater marshes sites, two coastal freshwater forests sites, and seven anthropogenic perturbations coastal wetland sites (Table 2 and Fig. 1). The majority of the sites are located in Asia, North America, and Europe; one site is located in Australia; there are no sites in Africa or South America (Fig. 1).

We also compared the annual CO_2 fluxes of wetlands to those of other terrestrial ecosystems. To analyze the differences in CO_2 fluxes between wetlands (inland and coastal wetlands) and other ecosystems, data of different terrestrial ecosystems (Yi *et al.*, 2010; Xiao *et al.*, 2013), including 97 forests, 33 grasslands, and 19 croplands, were used for comparison.

Statistical analysis

The one-way analysis of variance (ANOVA) was used to test the significance of the differences in CO_2 fluxes between inland wetlands and coastal wetlands and the significance of the differences in CO_2 fluxes, MAT, MAP, and LAI among different subwetland types within both inland and coastal wetlands. With one-way ANOVA, the significance test was based on the significance level $\alpha = 0.05$. Given the large differences in sample size among different wetland types, the assumptions of the one-way ANOVA test, including normal distribution and homogenous variance of the data, were first tested. If the difference was statistically significant ($P < 0.05$), a Tukey *post hoc* test was employed to determine exactly where the difference was. The generalized linear model (GLM) was used to conduct regression analysis of CO_2 fluxes with climatic, vegetation, and hydrological variables: MAT, MAP, LAI, and WTD and to test the significance of the regressions. The stepwise regression was used to analyze binary linear regressions of CO_2 fluxes with MAT and MAP and the interactions between the two climatic variables. The ratio of GPP to R_e (GPP/R_e) that provides a measure of the strength of C sequestration (Barr *et al.*, 2010) was calculated for each site. The correlations of GPP, R_e, NEP, the ratio NEP/R_e, and the ratio NEP/GPP with latitude were evaluated for the inland wetlands and coastal wetlands, respectively. The GLM was used to conduct regression analysis between CO_2 fluxes (or the ratio NEP/R_e, the ratio NEP/GPP) and latitude and to test the significance of the regressions. All statistical analyses were performed with SPSS version 16.0 (SPSS Inc., Chicago, IL, USA).

Results

Annual carbon dioxide fluxes of wetlands

We compared the annual CO_2 fluxes between inland wetlands and coastal wetlands (Fig. 2). The average annual GPP of inland and coastal wetlands were 536.96 ± 78.34 and 1311.01 ± 146.00 g C m^{-2} yr^{-1},

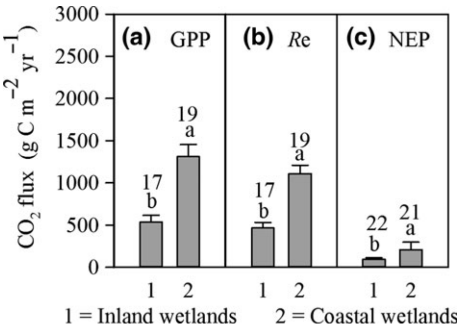

Fig. 2 Comparisons in mean annual carbon dioxide (CO_2) fluxes between inland and coastal wetlands: (a) gross primary productivity (GPP), (b) ecosystem respiration (R_e), and (c) net ecosystem productivity (NEP). The error bars stand for the standard error among sites. Same letters denote no significant differences based on the Tukey *post hoc* comparison of the means. The number above each bar is the actual number of sites for each wetland type.

respectively (Fig. 2a). The average annual R_e of inland and coastal wetlands were 466.25 ± 65.72 and 1110.95 ± 99.81 g C m^{-2} yr^{-1}, respectively (Fig. 2b). The average annual NEP of inland and coastal wetlands were 93.15 ± 23.65 and 208.37 ± 89.32 g C m^{-2} yr^{-1}, respectively (Fig. 2c). The average annual GPP, R_e, and NEP between inland wetlands and coastal wetlands all exhibited significant differences ($P < 0.001$). We calculated coefficients of variation (CV) for these CO_2 fluxes and found that annual GPP and NEP exhibited lower variability among subtypes for inland wetlands (CV = 0.33 and 0.81 for GPP and NEP, respectively) than for coastal wetlands (CV = 0.40 and 1.29 for GPP and NEP, respectively). By contrast, R_e had higher variability among subtypes for inland wetlands (CV = 0.29) than for coastal wetlands (CV = 0.25).

We also compared the CO_2 fluxes within both inland wetlands and coastal wetlands (Fig. 3). Among the inland wetlands, annual GPP, R_e, and NEP all exhibited insignificant differences ($P > 0.05$) (Fig. 3a–c). For the coastal wetlands, there was no significant difference for GPP between intertidal forested wetlands and intertidal marshes ($P > 0.05$), while intertidal forested wetlands had significantly higher GPP than coastal freshwater marshes and anthropogenic perturbations coastal wetland ($P < 0.001$) (Fig. 3d). For R_e in coastal wetlands, there was no significant difference among all the four coastal wetland types ($P > 0.05$) (Fig. 3e). The NEP of intertidal marshes, coastal freshwater marshes, and coastal freshwater forests showed no significant difference ($P > 0.05$), while the NEP of coastal freshwater marshes and coastal freshwater forests were significantly lower than that of intertidal forested wetlands ($P < 0.01$) (Fig. 3f). Similarly, the NEP of anthropogenic perturbations coastal wetland was significantly lower than that of intertidal forested wetlands ($P < 0.01$) or intertidal marshes ($P < 0.01$) (Fig. 3f).

Compared with inland wetlands, intertidal forested wetlands had significantly higher GPP than any of the four inland wetland types ($P < 0.05$) (Fig. 3a, d). Intertidal marshes had significantly higher GPP than alpine tundra wetlands ($P < 0.05$), although it showed no significant difference in GPP from peatland, freshwater swamp marsh, and freshwater shrub swamp ($P > 0.05$). Similarly, coastal freshwater marshes showed no significant difference in GPP from peatland, freshwater swamp marsh, and freshwater shrub swamp ($P > 0.05$) and had significantly higher GPP than alpine tundra wetlands ($P < 0.05$). Anthropogenic perturbations coastal wetlands had the lowest GPP in coastal wetlands and showed no significant difference in GPP from the four types of inland wetlands ($P > 0.05$). Intertidal forested wetlands had the highest mean R_e and had significantly higher R_e than the four types of inland wetlands ($P < 0.05$) (Fig. 3b, e). The other three coastal wetlands showed no significant difference in R_e from the four inland wetlands ($P > 0.05$). Compared with inland wetlands, intertidal forested wetlands had significantly higher NEP than all the inland wetland types ($P < 0.01$). Meanwhile, intertidal marshes showed no significant difference in NEP from freshwater swamp marsh and freshwater shrub swamp ($P > 0.05$), but had significantly higher NEP than peatland and alpine tundra wetlands ($P < 0.05$) (Fig. 3c, f). The NEP of coastal freshwater marshes, coastal freshwater forests, and anthropogenic perturbations coastal wetland was not significantly different from that of peatland, freshwater swamp marsh, freshwater shrub swamp, and alpine tundra wetlands ($P > 0.05$), although the anthropogenic perturbations coastal wetland had the lowest mean value (Fig. 3f).

We also compared annual GPP, R_e, and NEP between woody and herbaceous ecosystems for both inland and coastal wetlands (Fig. 4). The inland wetlands, either woody ecosystems or herbaceous ecosystems, had lower GPP than coastal woody wetlands ($P < 0.001$). There were no significant differences in GPP between herbaceous and woody ecosystems for inland and coastal wetlands ($P = 0.15$ and 0.05, respectively). The pattern of R_e was similar to that of GPP (Fig. 4b). However, there were no significant differences in NEP among all types of wetland ecosystems ($P > 0.05$) (Fig. 4c).

We also compared annual CO_2 fluxes of wetlands with those of other terrestrial ecosystems (Fig. S1). Inland wetlands had much lower annual GPP and R_e than other terrestrial ecosystems (forests, grasslands, and croplands) ($P < 0.001$) (Fig. S1a, b). By contrast, the

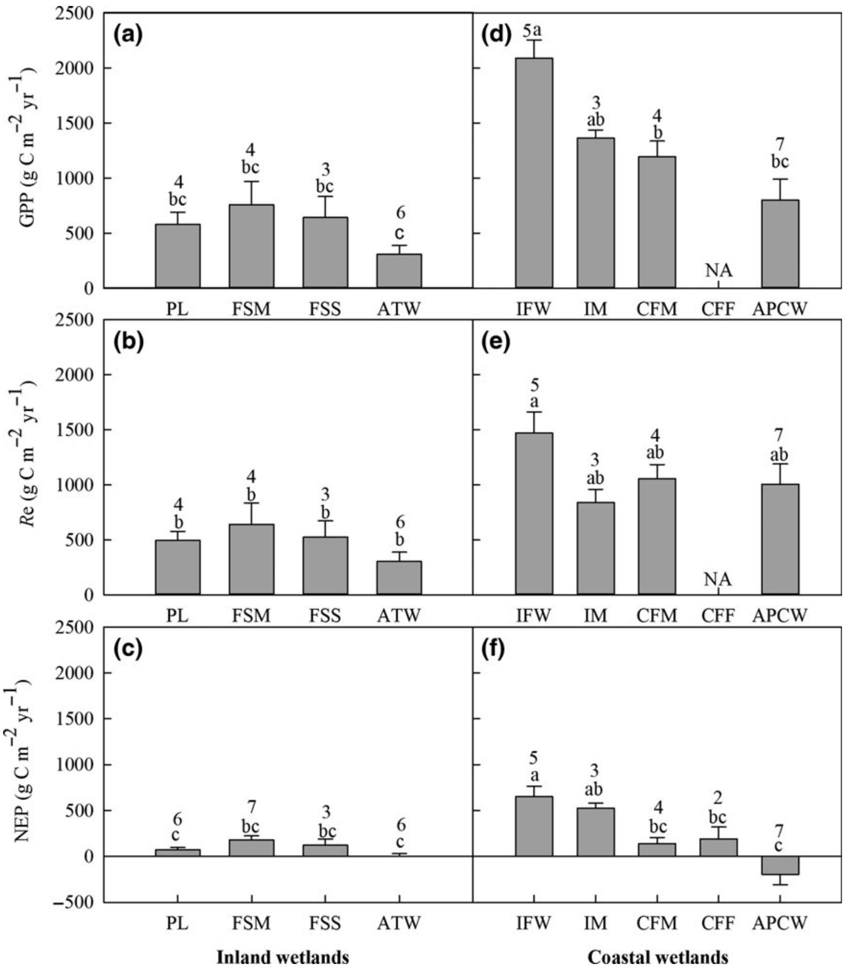

Fig. 3 Comparisons in annual carbon dioxide fluxes among different inland wetlands (left panels) and coastal wetlands (right panels): (a) gross primary productivity (GPP), (b) ecosystem respiration (R_e), and (c) net ecosystem productivity (NEP). The full names for the wetland types were provided in the caption of Fig. 1. The error bars stand for the standard error among sites. Same letters denote no significant differences based on the Tukey *post hoc* comparison of the means. The number above each bar is the actual number of site-years for each wetland type.

annual GPP and R_e of coastal wetlands were comparable to those of forests and croplands ($P > 0.05$), but were significantly higher than those of grasslands ($P < 0.001$). Inland wetlands had the lowest NEP although it was insignificantly different from that of grassland; grasslands and croplands had intermediate NEP; coastal wetlands and forests had the highest annual NEP. Coastal wetlands generally had CO_2 sequestration capacity comparable to forests, while the inland wetlands had lower CO_2 sequestration capacity than other terrestrial ecosystems.

Climate regulation of wetland carbon dioxide fluxes

We examined the effects of MAT and MAP on annual CO_2 fluxes of wetlands (Figs 5 and 6; Table 3). We first analyzed the effects of a single factor (MAT or MAP) on the spatial patterns of GPP, R_e, and NEP for all natural wetlands (i.e., all wetlands except anthropogenic perturbations coastal wetland sites). All CO_2 fluxes exhibited moderate to strong correlations with MAT (Fig. 5).

Annual GPP, R_e, and NEP all increased linearly with the increase of MAT (Fig. 5). For every degree increase in MAT, GPP increased by 60.53 g C m^{-2} yr^{-1}, while R_e and NEP increased by 38.06 and 19.14 g C m^{-2} yr^{-1}, respectively, which indicates that the wetlands with higher MAT had stronger C uptake capacity.

There were also significant relationships between CO_2 fluxes and MAP (Fig. 6). MAP explained 53%, 37%, and 19% of the variations in GPP, R_e, and NEP, respectively. GPP, R_e, and NEP increased significantly in a linear way with increasing MAP (Fig. 6). For every

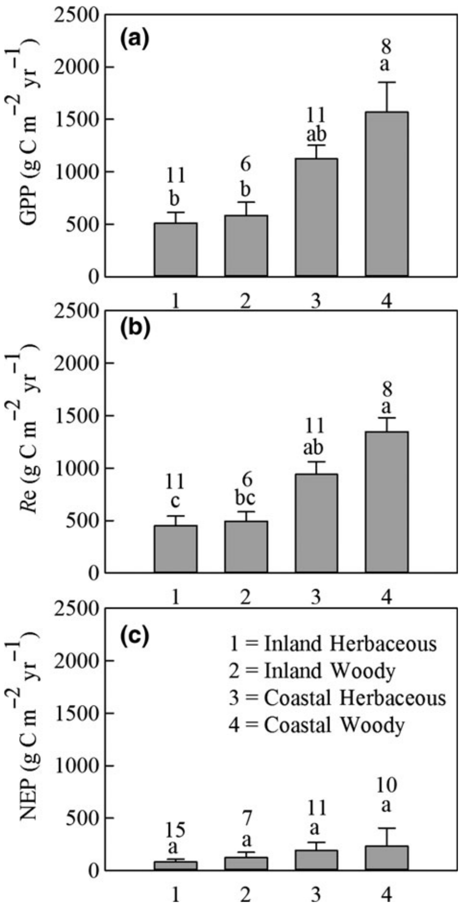

Fig. 4 Comparisons in the annual carbon dioxide fluxes among plant growth of each wetland type: (a) gross primary productivity (GPP), (b) ecosystem respiration (R_e), and (c) net ecosystem productivity (NEP). The error bars stand for the standard error among sites. Same letters denote no significant differences based on the Tukey *post hoc* comparison of the means. The number above each bar is the actual number of sites for each plant growth of specific wetland type.

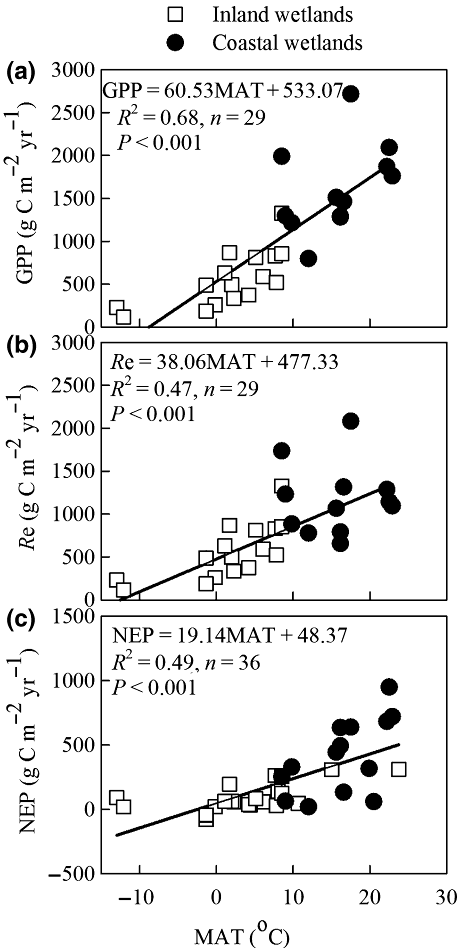

Fig. 5 Relationship between annual carbon dioxide flux [gross primary productivity (GPP), ecosystem respiration (R_e), and net ecosystem productivity (NEP)] and mean annual temperature (MAT) for all inland and coastal wetland sites except for the coastal wetland sites with heavy anthropogenic perturbations.

1 mm growth in MAP, GPP increased by 1.30 g C m^{-2} yr^{-1}, while R_e and NEP increased by 0.78 and 0.22 g C m^{-2} yr^{-1}, respectively, which indicates that the wetlands with higher MAP also had higher net CO_2 uptake.

Compared to MAP, MAT explained slightly higher variance of annual CO_2 fluxes (GPP, R_e, and NEP) (Table 3). Temperature and precipitation were both important controlling factors of annual CO_2 fluxes. We then conducted a binary linear regression analysis to assess the combined effects of MAT and MAP. MAT and MAP together explained higher variances in CO_2 fluxes than MAT or MAP alone (Table 3). MAT and MAP jointly explained 71% of the variation of GPP for coastal and inland wetlands taken together. The combined contribution of MAT and MAP to the variations of R_e increased to 53%, while their combined contribution to the variations of NEP did not increase.

An interaction term was included in the regression analysis to account for the effects of the interactions between MAT and MAP on CO_2 fluxes. With the interaction term, MAT and MAP explained 71% of the variance in GPP (Table 3). After taking the interactions between MAT and MAP into account, R^2 increased from 0.49 to 0.57 for NEP. Therefore, based on these analyses, the following three regression equations can best describe the spatial patterns of GPP, R_e, and NEP in wetland ecosystems:

$$\mathrm{GPP} = 416.61 + (41.91 * \mathrm{MAT}) + (0.21 * \mathrm{MAP}) + (0.01 * \mathrm{MAT} * \mathrm{MAP}) \quad (1)$$

$$R_e = 295.61 + (37.58 * \mathrm{MAT}) + (0.39 * \mathrm{MAP}) - (0.01 * \mathrm{MAT} * \mathrm{MAP}) \quad (2)$$

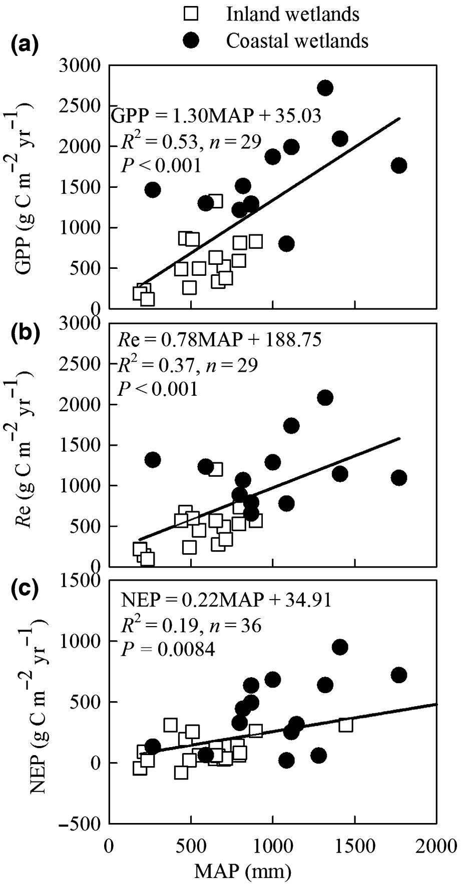

Fig. 6 Relationship between annual carbon dioxide flux [gross primary productivity (GPP), ecosystem respiration (R_e), and net ecosystem productivity (NEP)] and mean annual precipitation (MAP) for all inland and coastal wetland sites except for the coastal wetland sites with heavy anthropogenic perturbations.

$$\mathrm{NEP} = 159.29 + (7.75 * \mathrm{MAT}) - (0.24 * \mathrm{MAP}) + (0.02 * \mathrm{MAT} * \mathrm{MAP}) \quad (3)$$

We also conducted regression analysis for each individual wetland type. There was a strong relationship between NEP and MAT for freshwater swamp marsh (R^2 = 0.68, P = 0.02) and intertidal forested wetlands (R^2 = 0.83, P = 0.03). For other wetland types, however, the relationships of CO_2 fluxes with MAP or MAT were weak mainly because of the limited number of data points.

Vegetation and hydrological regulations of wetland carbon dioxide fluxes

We examined possible effects of vegetation and hydrological factors on the spatial patterns of GPP, R_e, and NEP for all natural wetlands (i.e., all wetlands except anthropogenic perturbations coastal wetland sites) and the results were shown in Figs 7 and 8. Annual GPP and R_e exhibited strong relationships with LAI for inland and coastal wetlands taken together, and both GPP and R_e increased linearly with the increase of LAI (Fig. 7). The relationship between NEP and LAI was not statistically significant (Fig. 7).

We also analyzed the relationships between annual CO_2 fluxes and WTD (Fig. 8). There was no significant correlation between any CO_2 flux and WTD (all P > 0.05, Fig. 8). However, the trends for GPP and R_e indicated that both GPP and R_e decreased with increasing WTD (R^2 was 0.19 and 0.23, respectively), while NEP increased with increasing WTD (R^2 = 0.13).

GPP : R_e ratio of inland and coastal wetlands

A strong linear relationship was observed between GPP and R_e for both coastal and inland wetlands (Fig. 9). The intercept of the GPP and R_e relationships differed significantly between inland wetlands and coastal wetlands. Coastal wetlands had a much larger Y intercept (270.27 g C m^{-2} yr^{-1}) than inland wetlands (0.93 g C m^{-2} yr^{-1}) (Fig. 9). The slope of the GPP and R_e relationships was 1.14 and 1.10 for inland and coastal wetlands, respectively. Moreover, all inland and coastal wetlands sites except some anthropogenic perturbations coastal wetland sites were scattered on or above the 1 : 1 line, while some of the anthropogenic perturbations coastal wetland sites were located below the 1 : 1 line (Fig. 9).

Latitudinal patterns of ecosystem carbon dioxide fluxes, NEP/R_e, and NEP/GPP

Despite the wide range of species composition, stand structure, and site history, the annual C fluxes (GPP,

Table 3 The coefficient of determination (R^2), F value, and P value of the regression analysis between annual carbon fluxes (GPP, gross primary productivity; R_e, ecosystem respiration; and NEP, net ecosystem productivity) and climatic variables (MAP, mean annual precipitation; MAT, mean annual temperature)

	MAT			MAP			MAT, MAP			MAT, MAP, MAT*MAP		
Model	R^2	F	P value	R^2	F	P value	R^2	F	P value	R^2	F	P value
GPP	0.69	58.61	<0.001	0.53	31.17	<0.001	0.71	31.50	<0.001	0.71	20.65	<0.001
R_e	0.52	29.46	<0.001	0.37	16.22	<0.001	0.53	14.67	<0.001	0.54	9.74	<0.001
NEP	0.49	32.82	<0.001	0.19	7.83	0.008	0.49	15.93	<0.001	0.57	14.37	<0.001

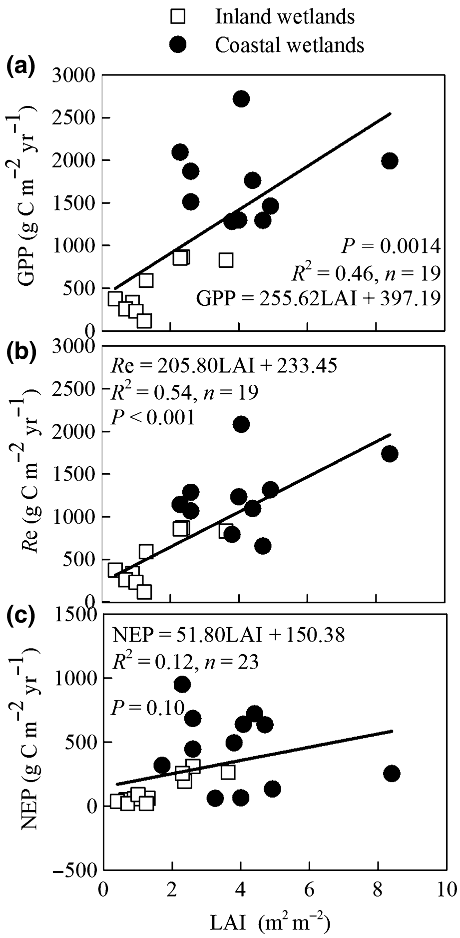

Fig. 7 Relationship between annual carbon dioxide flux [gross primary productivity (GPP), ecosystem respiration (R_e), and net ecosystem productivity (NEP)] and leaf area index (LAI) for all inland and coastal wetland sites except for the coastal wetland sites with heavy anthropogenic perturbations.

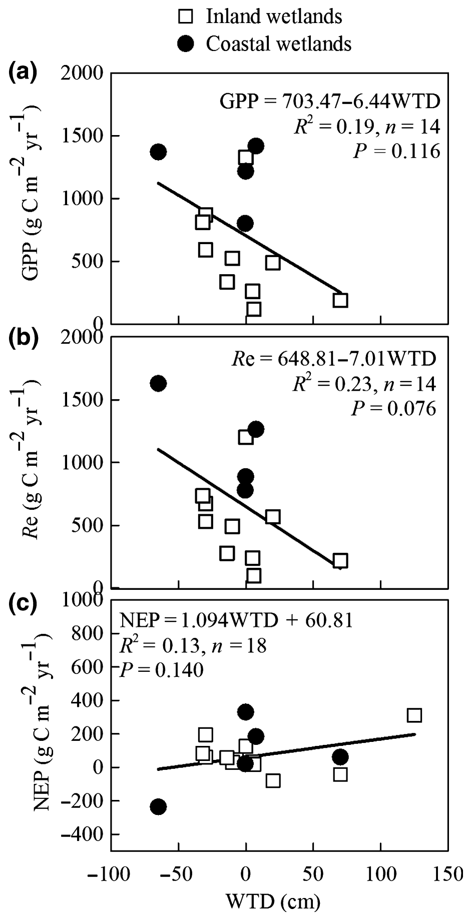

Fig. 8 Relationship between annual carbon dioxide flux [gross primary productivity (GPP), ecosystem respiration (R_e), and net ecosystem productivity (NEP)] and water table depth (WTD) for all inland and coastal wetland sites except for the coastal wetland sites with heavy anthropogenic perturbations.

R_e, and NEP) decreased with increasing latitude for inland wetlands (all $P < 0.05$) (Fig. 10a–c). By contrast, there was no significant latitudinal pattern for GPP, R_e, or NEP of coastal wetlands (all $P > 0.05$) (Fig. 10a–c). Both NEP/R_e and NEP/GPP ratios exhibited little variability with increasing latitude for inland wetlands, while both ratios showed significant latitudinal patterns for coastal wetlands ($P = 0.03$ and 0.02, respectively) (Fig. 10d, e).

Discussion

Differences in carbon dioxide fluxes between inland and coastal wetlands

Our global-scale meta-analysis provides useful results for settling the debate whether wetlands are significant CO_2 sinks or sources (Kayranli *et al.*, 2010; Bernal & Mitsch, 2012) by demonstrating that inland wetlands provided small CO_2 sinks or were nearly CO_2 neutral, while coastal wetlands generally had high CO_2 sequestration capacity. Wetlands were believed to be highly productive ecosystems with low decomposition rates due to low microbial activity caused by anaerobic conditions (Odum *et al.*, 1995; Chmura *et al.*, 2003). Our results showed that annual CO_2 fluxes differed substantially between inland and coastal wetlands.

Coastal wetlands were highly productive with annual GPP and NEP comparable to forests, which is consistent with results from recent regional-scale synthesis efforts (Xiao *et al.*, 2013; Yu *et al.*, 2013). However, it should be noted that inland wetlands cover a much larger land area (3.32×10^7 km^2; Zhu & Gong, 2014) than coastal wetlands (4.89×10^5 km^2; Pendleton *et al.*, 2012), while coastal wetlands only accounted for 1.47% of global wetlands. If the mean annual NEP rates of inland and coastal wetlands were applied to

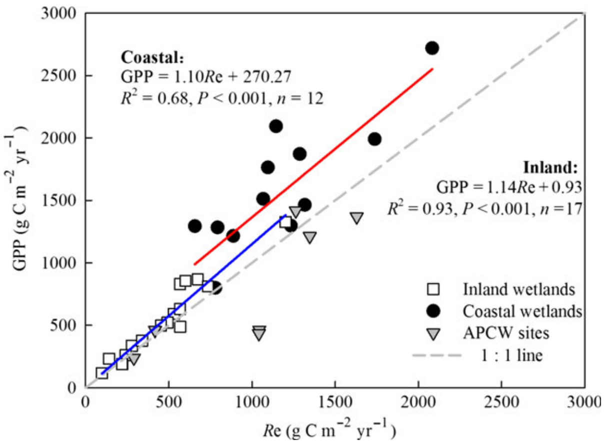

Fig. 9 Relationship between annual gross primary productivity (GPP) and annual ecosystem respiration (R_e) for the inland wetlands (blue line), the coastal wetlands (red line), and the coastal wetland sites with heavy anthropogenic perturbations.

wetlands over the globe, the annual net CO_2 uptake of inland and coastal wetlands would be 3092.49 and 101.89 Tg C yr^{-1}, respectively. Therefore, global inland wetlands together likely provide a larger CO_2 sink than global coastal wetlands.

The annual CO_2 fluxes exhibited relatively large variability among different types of wetlands for both inland and coastal wetlands because of the differences in environmental factors and dominant plant species. Annual GPP and NEP exhibited lower variability among subtypes for inland wetlands than for coastal wetlands. By contrast, R_e had higher variability among subtypes for inland wetlands than for coastal wetlands. A part of these differences between inland and coastal wetlands can be attributed to anthropogenic perturbations coastal wetlands. The anthropogenic activities led to significantly lower GPP for these sites, while R_e was comparable to that of other coastal wetlands. As a result, the anthropogenic perturbations coastal wetlands were CO_2 sources.

Anthropogenic perturbance has been shown to exert significant negative effects on the CO_2 fluxes of coastal wetlands (Regnier *et al.*, 2013; Petrescu *et al.*, 2015). Our restuls showed that the anthropogenic perturbations coastal wetlands exhibited significant differences in

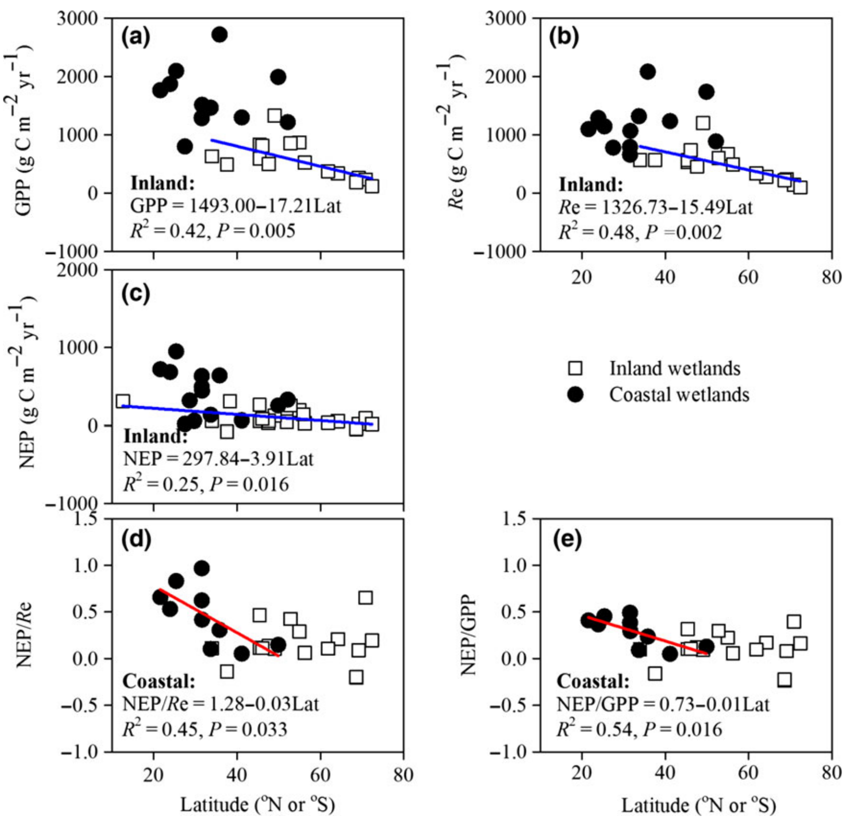

Fig. 10 Latitudinal patterns of annual (a) gross primary productivity (GPP), (b) ecosystem respiration (R_e), (c) net ecosystem productivity (NEP), (d) NEP/R_e, and (e) NEP/GPP for the inland and coastal wetlands. Blue line represents the relationship between carbon fluxes and latitude for the inland wetlands, and the red line represents the relationship between NEP/R_e or NEP/GPP and latitude for the coastal wetlands.

CO_2 fluxes from natural coastal wetlands, and some anthropogenic perturbations coastal wetlands sites were even CO_2 sources. Two types of human perturbations existed for wetlands: the conversion of natural wetlands to agricultural land and the conversion of national forested wetlands to managed forested wetlands (Humphreys *et al*., 2005; Hatala *et al*., 2012; Jimenez *et al*., 2012). During the past two centuries, human activities have led to land use change and habitat conversions and have greatly altered the exchange of CO_2 and nutrients among the land, atmosphere, freshwater bodies, coastal zones, and the open ocean (Regnier *et al*., 2013; Coverdale *et al*., 2014; Petrescu *et al*., 2015). Our present results demonstrate that the anthropogenic perturbance on coastal wetlands strongly influences the CO_2 sink strengh and suggest that future releases of greenhouse gas inventories based on IPCC guidelines for wetlands should indeed address the impacts of human activity.

Our results showed that the spatial patterns of GPP, R_e, and NEP of wetlands were largely determined by MAT and MAP not only independently but also interactively. For inland and coastal wetlands taken together, the annual CO_2 fluxes were significantly correlated with MAT and MAP. The climate regulation of CO_2 fluxes for other terrestrial ecosystems has been reported in previous studies (Law *et al*., 2002; Luyssaert *et al*., 2007; Yu *et al*., 2008; Fu *et al*., 2009). Besides the climate factors, vegetation characteristics could also regulate the CO_2 fluxes of inland and coastal wetlands. A previous study indicated that LAI was significantly correlated with NEP for a coastal wetland over the growing season (Zhong *et al*., 2016). Our study showed that for inland and coastal wetlands, the LAI was significantly correlated with GPP and R_e, but not with NEP. The inland wetlands had relatively lower LAI than the coastal wetlands, which might be another reason why the coastal wetlands had larger GPP and R_e than the inland wetlands.

Wetlands also differed from other terrestrial ecosystems in that the lateral C flux should be considered for C budget studies. Some inland aquatic ecosystems (e.g., river, wetlands, lakes) are just ‘neutral pipes’ that merely convey terrestrial C to the oceans (Cole *et al*., 2007; Aufdenkampe *et al*., 2011), while some closed-basin inland wetlands do not transport C to streams or oceans (Pennock *et al*., 2010; Euliss *et al*., 2014; Tangen *et al*., 2015). Previous research also indicated that besides acting as a CO_2 sink, the coastal wetlands can also serve as a source of C in that they may supply a significant amount of C to adjacent oceans (Cai, 2011). On one hand, the inclusion of lateral flow could reduce C sequestration within these wetlands but on the other hand a part of the transported C will be deposited in coastal and shelf sediments (Valiela *et al*., 2000). With the inclusion of the lateral flows, coastal wetlands could sequester significantly more C than inland wetlands and other terrestrial ecosystems (Chen *et al*., 2008). Many studies provided rough estimates of the lateral transport of C to adjacent oceans by multiplying C concentrations suspended in wetland creeks and waterways within the tidal range by the creek/waterway cross-sectional area. For mangroves, the net C exchange was measured in twelve ecosystems with no clear patterns among the locations, although most mangroves exported particle organic C as litter with rates ranging widely from 0.1 to 27.7 mol C m^{-2} yr^{-1} (Alongi, 2009). This export equates globally to about 10% of total C fixed by vegetation, at least for tidal marshes (Chmura *et al*., 2003) and subtidal seagrass beds (Fourqurean *et al*., 2012). Recent studies indicated that it is promising to develop process-based models for quantifying C export (Adame & Lovelock, 2011; Maher *et al*., 2013).

Although we focused only on CO_2 exchange, other major greenhouse gas especially CH_4 should not be ignored because of their significant contributions to global warming (Forster *et al*., 2007). More and more studies showed that inland waters are important sources of CH_4 to the atmosphere (Panneer Selvam *et al*., 2014). Freshwater sediments, including wetlands, rice paddies, and lakes, are thought to contribute 40–50% of the annual atmospheric CH_4 flux (Kirschke *et al*., 2013; Petrescu *et al*., 2015). CH_4 emissions could almost turn productive freshwater marshes into net C sources (Chu *et al*., 2014). Some freshwater wetlands have low CH_4 emissions because of high sulfate and/or short hydroperiods (Pennock *et al*., 2010; Badiou *et al*., 2011; Euliss *et al*., 2014; Tangen *et al*., 2015). For coastal wetlands, however, the CH_4 production and emissions are almost negligible because of the presence of sulfate (Ueda *et al*., 2000; Segarra *et al*., 2013). However, coastal wetlands are potentially significant sources of atmospheric CH_4 under anthropogenic perturbations (Purvaja & Ramesh, 2001; Allen *et al*., 2011).

Coupling of GPP, R_e, and NEP in wetlands

Annual GPP and R_e exhibited a highly positive coupling correlation for both inland and coastal wetlands, indicating that GPP was the main substrate supplier of R_e. However, this coupling correlation between the two types of wetlands exhibited different trends, with 67% of GPP contributed to R_e and 33% to NEP for the coastal wetlands, and with 93% of GPP contributed to R_e and 7% to NEP for the inland wetlands. Previous studies showed that the R_e of forests in Europe increased exponentially with the increase of GPP (Van Dijk & Dolman, 2004), and 77% of global GPP was consumed through R_e (Baldocchi, 2008). Law *et al.* (2002) also found that NEP grew linearly with the increase of GPP in forests in Europe and the United States, with 44–67% of GPP contributed to R_e and 29% to NEP. The underlying mechanisms of the tight correlation among GPP, R_e, and NEP over space are likely similar to those over time. In general, the C fixed via photosynthesis is returned to atmosphere through ecosystem respiration, and the allocation processes are highly relevant to understanding C cycling and C storage (Zhang *et al.*, 2014). The obvious difference between inland and coastal wetlands implied that the coastal wetlands had significantly higher CO_2 sequestration capability.

Latitudinal patterns of C fluxes and C allocation in wetlands

Previous studies showed that GPP and R_e linearly decreased with increasing latitude for terrestrial ecosystems in the northern hemisphere, and NEP had a similar but weaker trend (Van Dijk & Dolman, 2004; Yu *et al.*, 2013; Chen *et al.*, 2014). Both GPP and R_e have been shown to decrease linearly with increasing latitude mainly because of the controlling of temperature and growth period duration (Chen *et al.*, 2014). In our present study, the inland wetlands exhibited similar latitudinal patterns, while such patterns were not observed for the coastal wetlands. This is likely because the inland wetland sites encompass a much wider range of latitude (59.8°) than the coastal wetlands sites (28.3°). Another reason is that MAP, a determinant of CO_2 fluxes, exhibited a significant latitudinal pattern for inland wetlands ($R^2 = 0.58$) but not for coastal wetlands ($R^2 = 0.06$), although another determinant-MAT-showed significant latitudinal patterns for both inland and coastal wetlands (R^2 was 0.54 and 0.79, respectively).

The C balance is ultimately a delicate equilibrium between photosynthesis and respiration (Valentini *et al.*, 2000). The decreasing patterns of the NEP/R_e and NEP/GPP ratios with increasing latitude observed for coastal wetlands indicated that the allocation of GPP to NEP decreased with increasing latitude. The decreasing patterns of the NEP/R_e and NEP/GPP ratios with increasing latitude observed for coastal wetlands indicated that the allocation of GPP to NEP decreased with increasing latitude. We found that plant forms played a major role in regulating C partition. The average NEP/R_e of woody plant ecosystem (0.45 ± 0.09) was significantly larger than that of herbaceous ecosystem (0.20 ± 0.07). The NEP/GPP of woody plant ecosystem (0.30 ± 0.04) was also larger than that of herbaceous ecosystem (0.13 ± 0.05). Previous studies showed that the coastal wetlands in subtropical and tropical latitudes mainly grow woody plants such as mangroves (Duke *et al.*, 2007), while coastal wetlands in the middle and high latitudes are dominated by herbaceous plants such as reed (Mitsch & Gosselink, 2000; Scott *et al.*, 2014). This explains why the low–middle latitude coastal wetlands had higher NEP/R_e and NEP/GPP than the middle–high coastal wetlands. The inland wetlands did not exhibit similar patterns in NEP/R_e and NEP/GPP likely because of the complex distribution of the vegetation and the controlling factors (e.g., temperature, precipitation, topography, and soil properties).

Summary

In summary, we found that coastal wetlands had high net CO_2 uptake rates, while inland wetlands had low CO_2 uptake rates or were nearly CO_2 neutral. Moreover, ecosystem CO_2 fluxes of both inland and coastal wetlands were mainly regulated by MAT and MAP, and the combined effects of MAT and MAP explained 71%, 54%, and 57% of the variations in GPP, R_e, and NEP, respectively. The CO_2 fluxes were also related to LAI for the inland and coastal wetlands. The CO_2 fluxes also varied with WTD, although the effects of WTD were not statistically significant. Anthropogenic perturbations could exert large negative effects on net CO_2 uptake of coastal wetlands. The allocation of GPP to NEP decreased with increasing latitude for coastal wetlands but not for inland wetlands. The contrasting of annual CO_2 fluxes between inland and coastal wetlands at the global scale can improve our understanding of the roles of wetlands in the global C cycle. Our results also have implications for informing wetland management (e.g., protecting coastal wetlands, increasing the area of mangroves and salt marshes) and climate change policymaking. For example, our results can inform the efforts being made by international organizations and enterprises to restore coastal wetlands for enhancing blue carbon sinks.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Annual (a) gross primary productivity (GPP), (b) ecosystem respiration (R_e), and (c) net ecosystem productivity (NEP) averaged for inland wetlands, coastal wetlands, forests, grasslands, and croplands sites.

Figure S2. Environmental and vegetation conditions within inland and coastal wetlands: (a) mean annual temperature (MAT), (b) mean annual precipitation (MAP), and (c) leaf area index (LAI) for inland wetlands (Left panels) and annual fluxes for coastal wetlands (Right panels) respectively.

Table S1. Environmental conditions and other vegetation information for the selected sites both inland and coastal wetlands.