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# Climatic temperature controls the geographical patterns of coastal marshes greenhouse gases emissions over China

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**Abstract:** Coastal marshes contribute greatly to atmospheric greenhouse gases (GHGs) and have thus attracted considerable attention at regional and global scales. However, the relative importance of climates and soil variables to the geographical variation of GHG emissions at a large geographical scale remains poorly understood. We thus investigated the spatial patterns of GHG ($CO_2$, $CH_4$ and $N_2O$) emissions from coastal marshes along a latitudinal gradient in China and identified the climatic and soil variables controlling the emissions. Emissions of $CO_2$, $CH_4$ and $N_2O$ were estimated at rates of 12.8–310 mg $CO_2$ $m^{-2}$ $h^{-1}$, 23.6–986 µg $CH_4$ $m^{-2}$ $h^{-1}$ and 1.58–110 µg $N_2O$ $m^{-2}$ $h^{-1}$, respectively. The emissions of $CH_4$, $N_2O$ and $CO_2$ increased from high to low latitudes and were strongly correlated with climatic temperature. These emissions also varied significantly between temperate and subtropical climates and between winter and summer. Soil Eh, total organic carbon (TOC), dissolved organic carbon (DOC), total nitrogen, microbial biomass carbon (MBC) and nitrogen (MBN), bacterial abundance were the key regulators of $CH_4$ emissions. Soil Eh, TOC, DOC, MBC and MBN were the crucial variables controlling $N_2O$ emissions. $CO_2$ emissions across the coastal marshes were controlled mainly by soil pH, TOC, DOC, MBC, MBN and bacterial abundance. Although GHG emissions were strongly correlated with climatic temperature, 28–67% of the variations in GHG emissions were attributed to soil variables. The relative amplitudes (%) of the increases in GHG emissions, estimated on the basis of projected annual increases of 2 or 4 °C by 2100, were larger in temperate than subtropical coastal marshes, indicating that the coastal marshes with lower temperature were more sensitive to global warming. The annual emissions of $CO_2$, $CH_4$ and $N_2O$ estimated from the Chinese coastal marshes accounted for 6.6, 0.62 and 0.70‰ of the annual emissions from global terrestrial ecosystems, respectively. These results suggest that coastal marshes will be important to future global warming and will play a critical role in global GHG emissions.

**Keywords:** Greenhouse gases; climatic gradient; global warming; Chinese coastal marshes

## 1. Introduction

Greenhouse gases (GHGs) have attracted much attention due to their environmental consequences including global-warming potential (GWP) and ozone depletion (Lashof and Ahuja, 1990; Meinshausen et al., 2009; IPCC, 2013). Methane ($CH_4$) and nitrous oxide ($N_2O$) are important GHGs because they have approximately 30- and 300-fold higher GWP over a 100 year time frame, respectively, than carbon dioxide ($CO_2$) (IPCC, 2013). $CO_2$ is the largest contributor to GHGs and is expected to greatly affect GWP. Many recent studies have been devoted to identifying the natural sources of GHGs, estimating their emissions and predicting the global climatic consequences of their increasing concentrations at regional and global scales (Meinshausen et al., 2009; Yvon-Durocher et al., 2014; Yuan et al., 2015; Murray et al., 2015; Abdul-Aziz et al., 2018). Coastal wetlands store an estimated 10% of global soil carbon (C), so they are important sources of $CH_4$ and $CO_2$ emissions (Murray et al., 2015; Yuan et al., 2015; Lu et al., 2017; Abdul-Aziz et al., 2018). Coastal wetlands can intercept 93% of the terrestrial inputs of nitrogen (N) (Brin et al., 2010; Yang and Silver, 2016) and are also predicted to increase $N_2O$ emissions under the increasing nitrate level (Turner et al., 2016). Although the coastal wetlands account for a minor part of terrestrial area, they contribute largely to atmospheric $CH_4$, $N_2O$ and $CO_2$ (Morrissey et al., 2014a; Murray et al., 2015; Yuan et al., 2015; Yang and Silver, 2016; Jeffrey et al., 2018). Quantifying the emissions of $CH_4$, $N_2O$ and $CO_2$ from coastal marshes and understanding the variables controlling these emissions are therefore crucial for predicting future emissions and their effects on climate change.

Coastal marshes have been reported to be responsible for the large global emissions of GHGs because the microbial processes for GHGs production can be enhanced by some changing environmental factors (Chen et al., 2015; Yuan et al., 2015; Abdul-Aziz et al., 2018; Jeffrey et al., 2018; Emery et al., 2019). C and N availability, vegetation invasion, tides, water level, pH and redox dynamics are the important factors affecting local GHG emissions (Chen et al., 2015; Yuan et al., 2015; Yang and Silver, 2016; Jeffrey et al., 2018; Emery et al., 2019). Soil organic matter characteristics (dissolved organic carbon and total organic carbon) are suggested to be the important factors controlling emissions of $CO_2$ and $CH_4$ because the enhanced microbial respiration and anoxic organic matter decomposition can increase the yields of $CO_2$ and $CH_4$ (Morrissey et al., 2014a; Yuan et al., 2015; Abdul-Aziz et al., 2018). The microbial communities and enzymatic activities for the $CO_2$ and $CH_4$ production are also greatly affected by soil organic matter characteristics (Morrissey et al., 2013). Most studies reported that $N_2O$ emissions are mainly controlled by $NH_4^+$ and $NO_3^-$ (Borges et al., 2015; Murray et al., 2015; Wells et al., 2018) because $N_2O$ production is primarily attributed to nitrification and denitrification (Hu et al., 2012; Beaulieu et al., 2015). Soil microbial biomass carbon (MBC) and nitrogen (MBN) indicting the microbial activities and assimilating C and N capabilities can also predict the GHG emissions (Morrissey et al., 2014a; Li et al., 2019). Although functional gene abundances and microbial activities are crucial for GHG production (Hu et al., 2012; Emery et al., 2019), they are also significantly affected by soil substrates and conditions (Morrissey et al., 2014a; von Sperber et al., 2017; Abdul-Aziz et al., 2018). Temperature, however, was identified as an important factor accounting for the variations in GHG emissions in coastal marshes (Abdul-Aziz et al., 2018). Soil substrates availabilities and microbial processes for GHG production can be favored by higher temperature (Walter and Heimann, 2000; Yvon-Duroche et al., 2014). Climatic temperatures can affect soil properties and alter microbial communities (Kirwan et al., 2009; von Sperber et al., 2017), thereby affecting GHG emissions (Nahlik and Mitsch, 2011). Therefore, the effects of climatic temperature variability on GHG emissions may become stronger at a continental scale.

The geographical patterns of GHG emissions along a latitudinal gradient, however, remain unclear at the continental scale, which may limit the predictions of climate change models. This kind of information can highlight an understanding of how global warming may influence GHG emissions. More studies of GHG emissions across climatic gradient are therefore required to determine the importance of climatic temperature (the 30-year average) and soil characteristics on the geographical variation of GHG emissions.

Coastal marshes are important ecosystems in China, with an area of 5.8×$10^4$ $km^2$ (Guan, 2012), representing various climatic types and a long latitudinal gradient from temperate to tropical monsoon climates. Mean month air temperature (2011-2015) along the gradient is highly variable in winter (–20 to +20 °C) but less variable in summer (28–35 °C). Mean annual temperature (MAT) (1985-2015) from north to south along the gradient increases from 9.0 to 22.9 °C, which can drive the variation in GHG emissions. In addition, the climatic temperature can shape microbial communities and affect soil substrates availabilities, further affecting GHG emissions along the coastal marshes. The scale of this climatic gradient is ideal for predicting changes in GHG emissions under scenarios of global warming and for identifying associated environmental consequences on the global scale. We thus characterized these coastal marshes with divergent climatic types to answer three questions. (1) Do $CH_4$, $N_2O$ and $CO_2$ emissions have a latitudinal gradient because the temperature increases from the temperate to the subtropical coastal marshes? (2) What is the role of the main soil variables individually and together with temperature in controlling the emissions of $CH_4$, $N_2O$ and $CO_2$ from the coastal marshes across the climatic gradient? (3) Do coastal marshes located in temperate climate have stronger feedbacks to global warming than marshes in subtropical climate? We addressed these questions by investigating 11 coastal marshes along a latitudinal gradient. We measured the emissions of $CH_4$, $N_2O$ and $CO_2$ and soil and climatic variables to identify the crucial factors controlling the emissions. Our study can enable the understanding of GHG emissions mediated by climate and the effect of global warming on emissions at a large geographical scale.

## 2. Materia and methods

### 2.1. Study area and sample collection

The coastal marshes in China span from temperate to tropical climates (approximately 20–40°N, 108–124°E) (Figure 1). These marshes across a broad geographical region are characterized by the irregularal and regular semi-diurnal tides and divergent environmental conditions (Guan, 2012). The climate, especially the temperature, varies greatly along the latitudinal gradient. The sample sites were located in the cities of Dandong (DD), Tangshan (TS), Weifang (WF), Qingdao (QD), Dafeng (DF), Shanghai (SH), Wenzhou (WZ), Fuzhou (FZ), Shantou (ST), Zhuhai (ZH) and Beihai (BH). These sites spanned two climatic zones: DD, TS, WF, QD and DF have a temperate monsoon climate, and SH, WZ, FZ, ST, ZH and BH have a subtropical monsoon climate. More detail information on the sites and climatic temperatures is provided in Table 1.

We collected gas and soil samples from the low-tide bare flat of each site on 4–20 July and 5–21 December 2016. Coastal marshes vegetation had a great influence on GHGs emissions. There were more than five vegetation types at some sites, so it was very difficult to collect gas and soil samples. The precipitation and monsoons between the study sites were different due to the large climatic gradient. However, the bare flat in the coastal marsh was permanently water saturated and strongly affected by the tides. Therefore, we only investigate the bare flat after the ebb tide to compare the GHGs emissions under the consistent settings and methodologies. Three independent plots of the low-tide bare flat were investigated at each sampling site. Gas samples for GHG analyses were collected using static chambers (Li et al., 2019). The chambers were made of polypropylene with a diameter of 30 cm and a height of 50 cm. When the lid was closed, it compressed a rubber gasket cemented to its underside against a horizontal flange at the top of the base walls, thus providing a gas seal (Li et al., 2019). The chambers were inserted in the coastal marshes, maintaining an airtight system. Gas samples (50 mL) were collected at 0, 2 and 4 h at the bare flat after the ebb tide using a syringe. The samples were then immediately transferred to pre-evacuated airtight gas bags (Dalian Delin Gas Packing Co., Ltd., China). After collection of gas samples, soil (10 cm deep) samples for determination of geochemical characteristics were also taken with PVC tubes from the sampling plots of each site. Totally, 99 gas samples and 33 soil samples were collected for each seasonal survey, and they were stored in coolers with ice and transported to the laboratory within two days. The materials for collecting the pore water were not prepared, thus the soil pore water was not collected during the sampling. Air temperature (AT) near the marshes was determined using a temperature sensor (U333S, UTI-T Instrument Corp., Guangdong, China), soil redox potential (Eh) at a depth of 10 cm was measured using an ORP meter (AZ8551, AZ Instrument Corp., Taiwan, China), and surface water salinity was determined using a conductivity meter (Model 30, YSI Inc., Yellow Springs Instrument, Yellow Springs, OH, USA).

## 2.2. Measurement of soil parameters

The soil of 0-10 cm was homogenized to measure the soil properties. Soil bulk density was measured from core samples (Yuan et al., 2015). Water content was determined from the weight lost from fresh soil after drying at 60 °C for 72 h. Soil pH was measured using a pH meter (Mettler-Toledo, Zurich, Switzerland) after soil was mixed with $CO_2$-

free water at a ratio (w/v) of 1:2.5 and. Soil $NH_4^+$ and $NO_x^-$ (including $NO_3^-$ and $NO_2^-$) were extracted from 5 g of soil with 25 mL of 2 mol $L^{-1}$ KCl, and the extraction solution was filtered through a 0.45-μm membrane filter (Whatman, Clifton, USA). Their concentrations were determined using a continuous-flow analyzer (SAN++, Skalar Analytical B.V., Breda, Netherlands). Dissolved organic C (DOC) and sulfate ($SO_4^{2-}$) were extracted from 25 g of soil with 50 mL of deionized water, and the supernatant was filtered through a 0.45-μm membrane filter (Whatman, Clifton, USA). DOC and $SO_4^{2-}$ concentrations were measured using a Shimadzu C analyzer (TOC Vcph, Shimadzu, Kyoto, Japan) and an ion chromatograph (ICS-2000, Dionex, Camberley, UK), respectively. After 300 g of freeze-dried soil was acidized with 1 mol $L^{-1}$ HCl, total organic C (TOC) and total N (TN) contents were determined using a CN Elemental Analyzer (Vario, Elementar, Hanau, Germany) and $\delta^{13}C$ and $\delta^{15}N$ enrichments were measured using a Flash Elemental Analyzer connected to an Isotope Ratio Mass Spectrometer (Thermo Fisher Scientific Inc., Bremen, Germany). MBC and MBN contents were determined using chloroform fumigation (Vance et al., 1987; Brookes et al., 1985).

## 2.3. Determination of GHG emissions and GWP

$CH_4$, $N_2O$ and $CO_2$ concentrations in gas samples were analyzed using a gas chromatograph (GC-2014, Shimadzu, Kyoto, Japan) equipped with a flame ionization detector (FID) and electron capture detector (ECD). The column, FID and ECD temperatures were 50, 200 and 250 °C, respectively (Li et al., 2019). The concentrations of gas standards were analyzed after every 10 samples to ensure the accuracy of detection. The GHG emissions rates were estimated from 0 to 2 h and from 2 to 4 h, respectively, on the basis of equation (1): :

$$E = \frac{C_{end}-C_{init}}{(t_{end}-t_{init})\times S} \times A \times \frac{V \ \times P}{R\times T_k} \qquad (1)$$

where $E$ is the emission of $CH_4$, $N_2O$ or $CO_2$ (mg m$^{-2}$ h$^{-1}$); $C_{\mathrm{init}}$ and $C_{\mathrm{end}}$ are the initial and final concentrations of $CH_4$, $N_2O$ or $CO_2$ (μmol L$^{-1}$), respectively; $A$ is the molar weight of $CH_4$, $N_2O$ or $CO_2$ (g mol$^{-1}$); $V$ is the chamber volume (L), $P$ is the normal atmospheric pressure (1 atm = 1013.15 hPa); $R$ is the common gas constant (0.082056 L atm K$^{-1}$ mol$^{-1}$); $T_k$ is the absolute temperature at the time of gas sampling (K); $S$ is the chamber area (m$^2$), and $t_{\mathrm{init}}$ and $t_{\mathrm{end}}$ are the start and end times of the samplings (h), respectively; The molar weights of $CH_4$, $N_2O$ and $CO_2$ are the common gas constants at normal atmospheric pressure (16, 44 and 44 g mol$^{-1}$ for $CH_4$, $N_2O$ and $CO_2$, respectively). The average of the two time-interval measurements were used as the GHG emissions rates.

Annual emissions of $CH_4$, $N_2O$ and $CO_2$ were calculated as:

$$T = \frac{1}{2\times 11} \times (\sum_{i=1}^{11} Esummer + \sum_{i=1}^{11} Ewinter)\times t\times S \qquad (2)$$

where $T$ is the total annual emission of $CH_4$, $N_2O$ or $CO_2$ (Tg y$^{-1}$); $E_{summer}$ and $E_{winter}$ are the emissions of $CH_4$, $N_2O$ or $CO_2$ (mg m$^{-2}$ h$^{-1}$) in summer and winter, respectively; $t$ is the time (365 d) and $S$ is the total area of the marshes ($5.8\times10^4$ km$^2$).

Annual C and N exports from the $CH_4$, $N_2O$ and $CO_2$ emissions were calculated as:

$$C == \frac{12}{16} \times T_{CH4} + \frac{12}{44} \times T_{CO2} \qquad (3)$$

$$N = \frac{28}{44} \times T_{N2O} \qquad (4)$$

where $C$ is the annual C export by $CH_4$ and $CO_2$ emissions (Gg y$^{-1}$); $N$ is the annual N export by $N_2O$ emissions (Gg y$^{-1}$); $T_{\mathrm{CH4}}$ is the total annual emission of $CH_4$ of Chinese coastal marshes (Tg y$^{-1}$); $T_{\mathrm{CO2}}$ is the total annual emission of $CO_2$ of Chinese coastal marshes (Tg y$^{-1}$); $T_{\mathrm{N2O}}$ is the total annual emission of $N_2O$ of Chinese coastal marshes (Tg y$^{-1}$).

GWP (Mg $CO_2$eq $ha^{-1}$ $y^{-1}$) of the marshes over a 100-year horizon for evaluating the environmental implications of GHGs was calculated as (Neubauer and Megonigal, 2015):

$$GWP = (E_{CH4} \times 25 + E_{N2O} \times 298 + E_{CO2}) \times t \times 10^4 \quad (5)$$

where $E_{CH4}$, $E_{N2O}$ and $E_{CO2}$ are the mean emissions of $CH_4$, $N_2O$ and $CO_2$ (mg $m^{-2}$ $h^{-1}$), respectively; $t$ is the time (365 d) and $\times 10^4$ is a factor for converting ha to $m^2$.

## 2.4. Bacterial abundance

Genomic DNA was extracted from 0.25 g of soil using the Power Soil DNA Isolation Kit (Mo Bio, USA). The extracted DNA and the products from polymerase chain reactions (PCR) were then verified using 1.0% agarose gel electrophoresis. Bacterial abundance was estimated using qPCR targeting the 16s rRNA gene amplified with primers 341F (5'–CCT ACG GGA GGC AGC AG–3') and 534R (5'–ATT ACC GCG GCT GCT GGC A–3') (Philippot et al., 2011). The reaction mixtures included 12.5 µL of Maxima SYBR Green/RoxqPCR Master Mix (Fermentas, Lithuania), 1 µL of each primer (10 µmol $L^{-1}$, Sangon, China), 1 µL of template DNA and 9.5 µL of sterile dd$H_2O$. Thermal-cycling conditions for the qPCR were: 50 °C for 2 min, 95 °C for 15 min, followed by 35 cycles of 95 °C for 15 s, 60 °C for 30 s and 72 °C for 30 s. The qPCR was run in triplicate using an ABI 7500 Sequence Detection System (Applied Biosystems, Canada) with the SYBR Green qPCR method. Average amplification efficiency was 99.3%, and gene copies (log10) were significantly correlated with the threshold cycle number ($C_T$) ($r^2 = 0.991$). The bacterial abundances in the soils were calculated using standard curves.

## 2.5. Statistical analyses

GHG emissions, bacterial abundance and environmental properties were compared among the sampling sites using a one-way analysis of variance (ANOVA) followed by Tukey's honestly significant difference test. Significant differences in GHG emissions between the temperate and subtropical climates and between December and July were identified by independent-samples *t*-tests at $P < 0.05$. The interactive effects of site and seasonal variabilities in GHG emissions were identified using a two-way ANOVA. A partial-correlation analysis controlling for climatic temperature was used to describe the relationships between GHG emissions and soil characteristics. Stepwise multiple regression analysis was used to identify the most important factors affecting the variabilities in GHG emissions across the coastal marshes. The criteria for inclusion in the stepwise multiple regression analysis was $F$ to enter of >0.1 and $F$ to remove of <0.05 (Harrison and Matson, 2003). We performed a principal component analysis (PCA) with all soil variables and gas emissions as the variables for detecting patterns of the variable relationships ordering samples as functions of site and/or season. A structural equation model (SEM) in the path analysis was constructed to identify the direct and indirect effects of the soil and climatic variables on the GHG emissions.

## 3. Results

### 3.1. Site descriptions

Abiotic and biotic characteristics of the coastal marshes are provided in Table 2. Soil density varied slightly across the study sites, ranging from 1.13 to 1.41 g $cm^{-3}$. Water contents ranged from 50.3 to 69.2 %. The soil had a neutral pH, varying between 7.72 and 8.07. Eh varied greatly among the study sites, ranging from -32 to -158 mV. The salinity of the seawater ranged from 11.8 to 27.9 ‰. TOC and TN contents ranged largely from 1.09 to 10.2 mg $g^{-1}$ and from 0.14 to 1.15 mg $g^{-1}$, respectively, with C/N ratios of 6.4–25.8. DOC increased from high to low latitudes, with contents of 0.11–0.93 mg $g^{-1}$. MBC and MBN contents were generally higher at the subtropical than temperate sites, varying between 11.7 and 113 μg $g^{-1}$ and between 2.27 and 17.5 μg $g^{-1}$, respectively. $NH_4^+$ and $NO_x^-$ contents were higher at the subtropical than the temperate sites. $NH_4^+$ contents ranged from 1.53 to 12.1 μg $g^{-1}$, contributing 68–91% of total dissolved inorganic N (DIN). $NO_x^-$ contents ranged from 0.61 to 2.13 μg $g^{-1}$, accounting for 9–32% of total DIN. $SO_4^{2-}$ contents varied greatly, ranging from 0.21 to 0.96 mg $g^{-1}$. $\delta^{13}C$ and $\delta^{15}N$ varied between -26.3 and -20.3‰ and between 4.35 and 7.15‰, respectively. Bacterial abundances varied greatly across the sites, ranging from $1.1\times 10^9$ to $11.3 \times 10^9$ copies $g^{-1}$.

### 3.2. GHG emissions

Emissions of $CH_4$ ranged from 23.6 to 211 μg $m^{-2}$ $h^{-1}$ and from 29 to 986 μg $m^{-2}$ $h^{-1}$ in December and July, respectively (Table 3). Emissions of $N_2O$ ranged from 2.0 to 103 μg $m^{-2}$ $h^{-1}$ and from 3.9 to 110 μg $m^{-2}$ $h^{-1}$ in December and July, respectively. Emissions of $CO_2$ were 1000-fold higher than the emissions of $CH_4$ and $N_2O$, ranging from 9.9 to 310 mg $m^{-2}$ $h^{-1}$ and from 50.9 to 153 mg $m^{-2}$ $h^{-1}$ in December and July, respectively. Emissions of $CH_4$, $N_2O$ and $CO_2$ varied significantly spatially among the study sites (one-way ANOVA, $P < 0.001$, Table 4). Emissions of $CH_4$ and $N_2O$ varied significantly across seasons (one-way ANOVA, $P < 0.001$), but emissions of $CO_2$ did not significantly differ (one-way ANOVA, $P = 0.942$). The interaction between site and season, however, influenced the emissions of the three gases (two-way ANOVA, $P < 0.001$).

Emissions of $CH_4$, $N_2O$ and $CO_2$ increased from high to low latitudes in both December and July (Figure 2), indicating an important geographical pattern of GHG emissions from the marshes. Emissions were significantly higher at the subtropical than temperate sites in both December and July (*t*-test, $P < 0.05$) (Figure 3). Emissions of $CH_4$ at the subtropical sites varied significantly between December and July (*t*-test, $P < 0.05$). Emissions of $CO_2$ at the temperate sites were significantly higher in July than in December (*t*-test, $P < 0.05$). $N_2O$ emissions, however, did not significantly differ seasonally at the temperate or subtropical sites (*t*-test, $P > 0.05$).

### 3.3. Influences of climatic temperature and biogeochemical variables

AT was significantly correlated with the emissions of $CH_4$ ($r = 0.66$, $P < 0.01$), $N_2O$ ($r = 0.59$, $P < 0.01$) and $CO_2$ ($r = 0.57$, $P < 0.01$) at all sites (Figure 4a-c). MAT was also correlated with $CH_4$ ($r = 0.80$, $P < 0.01$), $N_2O$ ($r = 0.85$, $P < 0.01$) and $CO_2$ ($r = 0.66$, $P < 0.01$) emissions (Figure 4d-f). $CH_4$ emissions were negatively correlated with Eh ($r = -0.87$, $P < 0.001$) and $\delta^{13}C$ ($r = -0.45$, $P = 0.036$). $CH_4$ emissions were strongly positively correlated with C/N and TOC, DOC, TN, $NH_4^+$, $NO_x^-$, MBC and MBN contents ($r > 0.42$, $P < 0.05$). Eh and TOC, TN, $NO_x^-$ and MBC contents, however, remained significantly correlated with $CH_4$ emissions after controlling for climatic temperature in a partial-correlation analysis ($|r| > 0.51$, $P < 0.01$) (Table 5). $N_2O$ emissions were correlated negatively with Eh ($r = -0.54$, $P = 0.009$) and strongly positively with TOC, DOC, MBC and MBN contents ($r > 0.41$, $P < 0.05$). Eh and DOC contents affected $N_2O$ emissions the most along the latitudinal gradient after controlling for climatic temperature. $CO_2$ emissions were negatively correlated with Eh ($r = -0.46$, $P = 0.03$) and pH ($r = -0.58$, $P = 0.004$) in the partial-correlation analysis. The C/N ratio, TOC, DOC, MBC and MBN contents and bacterial abundance were strongly correlated with $CO_2$ emissions ($r > 0.44$, $P < 0.05$). Only pH and bacterial abundance, however, remained significantly correlated with $CO_2$ emissions ($r = -0.60$, $P = 0.005$; $r = 0.49$, $P$

= 0.029, respectively) after a partial-correlation analysis to account for climatic temperature.

The stepwise analysis identified the important predictors of the variations in the GHG emissions along the latitudinal gradient (Figure 5). MBC contents, Eh and MAT were the most important predictors of the variations in $CH_4$ emission at all sites, explaining 75.4%, 11% and 4.1% of the total variance, respectively. MAT, AT, Eh and $NO_x^-$ contents were the most important factors affecting $N_2O$ emissions, with MAT as the best predictor, explaining 70.9% of the total variance along the gradient. MAT was the most crucial factor controlling $CO_2$ emissions, explaining 40.5% of the total variance, and both pH and AT also affected $CO_2$, explaining 14% and 11.3% of the total variance across the sites, respectively. The PCA clearly indicated that the first axis was mainly loaded by the C and N contents, temperature, Eh and GHG emissions (Figure 6). The samples from the subtropical sites were loaded toward higher temperatures, C and N contents and GHG emissions and toward lower Eh, salinity and $SO_4^{2-}$ content. The samples collected in winter and summer were differently loaded, with no clear patterns among the sites in the separation of the winter and summer samples. Climatic temperature also had a strong indirect positive effect on the emissions of $CH_4$ and $CO_2$ by affecting Eh, bacterial abundance and TOC, DOC, MBC and MBN contents (Table S1), and TOC contents had an indirect negative influence on $N_2O$ emissions (Figure 7).

### 3.4. Annual C and N exports and GHG emissions

The estimated GWP for the marshes ranged from 2.96 to 21.9 Mg $CO_2$eq $ha^{-1}$ $y^{-1}$ across the sites (Table S2), with a mean GWP of approximately 10.0 Mg $CO_2$eq $ha^{-1}$ $y^{-1}$. Annual emissions of $N_2O$, $CH_4$ and $CO_2$ from the marshes (total area of $5.8\times10^4$ $km^2$) were estimated at 1.80–44.41 Gg $y^{-1}$, 14.89–304 Gg $y^{-1}$ and $1.56\times10^4$–$1.17\times10^5$ Gg $y^-$

$^{1}$, respectively. Annual C and N exports from the emissions were 1.64±0.32×10$^{4}$ Gg y$^{-1}$ and 9.14±2.89 Gg y$^{-1}$, respectively. Based on the soil densities at a depth of 10 cm, total area of the marshes and mean contents of TOC and DIN from the homogenized soils (0–10 cm), the estimated C and N storages in Chinese coastal marshes were approximately 3.89±0.43×10$^{4}$ Gg and 56.05±4.49 Gg, respectively. The annual losses of C and N from the GHG emissions were therefore about 42% and 16% of the C and N storages, respectively, regardless of the sequestration of C and N, inorganic carbon and organic nitrogen.

Increases in the emissions of $CH_4$, $N_2O$ and $CO_2$ under global-warming scenarios of 2 and 4 °C by 2100 (IPCC, 2007) were estimated using the fitting models at 2.20–5.43 μg m$^{-2}$ y$^{-1}$, 1.86–4.78 μg m$^{-2}$ y$^{-1}$ and 4.32–6.10 mg m$^{-2}$ y$^{-1}$ (Table 6), respectively (Figure 4d-f). These enhanced emissions thus represented approximately 4.62–11.4%, 27.5–70.6% and 9.13–12.9% of the current mean emissions of $CH_4$ (47.6 μg m$^{-2}$ y$^{-1}$), $N_2O$ (6.77 μg m$^{-2}$ y$^{-1}$) and $CO_2$ (47.3 mg m$^{-2}$ y$^{-1}$), respectively, for the temperate coastal marshes and approximately 0.67–1.66%, 4.03–10.3% and 2.98–4.21% of the current mean emissions of $CH_4$ (328 μg m$^{-2}$ y$^{-1}$), $N_2O$ (46.2 μg m$^{-2}$ y$^{-1}$) and $CO_2$ (145 mg m$^{-2}$ y$^{-1}$), respectively, for the subtropical coastal marshes.

## 4. Discussion

### 4.1. Geographical variation along the latitudinal gradient

Many studies have reported GHG emissions from coastal marshes (Yuan et al., 2015; Abdual-Aziz et al., 2018; Emery et al., 2019), but the geographical variations of the emissions at a continental scale remain unclear. We examined the geographical distributions and seasonal variations in emissions of $CH_4$, $N_2O$ and $CO_2$ along a latitudinal gradient of Chinese coastal marshes. Although some sites were close to the cities (Table 1), soil C and N pools and substrates availabilities may vary greatly and may be affected by temperature along the coastal marshes. The soil respiration rates and microbial communities for GHGs production are also the long-term results of sampling site temperature (Wang et al., 2016; von Sperber et al., 2017). Therefore, the variations in GHG emissions were not controlled by the urban sizes but by the climatic temperature and soil variables of the coastal marshes. The geographical patterns of the emissions increased from high to low latitudes in both summer and winter. AT and MAT were significantly correlated with the emissions of $CH_4$, $N_2O$ and $CO_2$ in all coastal marshes (Figure 4). A higher capacity of biological activity under higher temperatures in wetland areas, where water is not limited, is expected to be associated with higher C and N contents (both depending on biological fixation) in marshes (Emery et al., 2019). The higher microbial biomass and higher levels of C and N transformation processes could thus increase the $CO_2$, $CH_4$ and $N_2O$ emissions (Morrissey et al., 2014a; Abdual-Aziz et al., 2018). Therefore, our statistical analyses suggest that the high temperature and associated high MBC and MBN contents were the underlying mechanisms contributing to high GHG emissions. Some of previous studies have consistently reported that temperature was the most important factor affecting microbial respiration and GHG emissions in coastal marshes (Xie et al., 2014; Abdual-Aziz et al., 2018). The emissions of $CH_4$, $N_2O$ and $CO_2$ in our study were consistently higher in the subtropical than temperate marshes (Figure 3), even though AT did not differ significantly between them in July ($P > 0.05$), indicating that potential GHG emissions are the long-term effects of temperature. The dependency of GHG emissions on temperature is also likely attributed to that the soil microbial respiration and microbial communities for GHGs production are the results of the long-term effects of site temperature (von Sperber et al., 2017; Nottingham et al., 2019). The difference in temperature in latitude 24 and 21 was less variable between December and July. The MAT was also comparable with air temperature at sites ZH and BH where TOC, DOC, MBN and C/N were higher in December than in July, which could contribute to the higher emissions of $CO_2$ and $N_2O$ at these sites. Interestingly, the summer samples from all temperate sites were more towards the right along the PC1 axis (thus toward conditions of the subtropical sites), as expected, whereas a comparison between the summer and winter samples from the subtropical sites did not indicate this general trend (Figure 6). These results therefore suggest that the mean annual temperature in our study was the best predictor of the geographical variation in GHG emissions across the coastal marshes. Soil C and N availabilities, MBC and MBN could also explain the variation in GHG emissions across the coastal marshes.

## 4.2. Influences of temperature and soil properties on GHG emissions

### 4.2.1. Factors affecting $CH_4$ emissions

$CH_4$ emissions were significantly higher in July than in December, because high contents of labile organic C from the increased decomposition of organic matter can further favor $CH_4$ production at high temperatures (Gelesh et al., 2016). Methanogenesis, responsible for $CH_4$ production, is also substantially driven by temperature (Martin and Moseman-Valtierra, 2017) and is highly sensitive to increasing temperatures (Abdual-Aziz et al., 2018), leading to higher emissions of $CH_4$ in subtropical coastal marshes and warming seasons. Temperature had an indirect effect on the $CH_4$ emissions, because temperature strongly influences redox reactions and C availability (Figure 7a). The anaerobic decomposition of organic matter is the main pathway of $CH_4$ production, but the content and quality of organic C strongly affects $CH_4$ emission by altering the abundance and community structure of methanogenic archaea (Wagner et al., 2005). Yuan et al. (2015) found a strong link between $CH_4$ emissions and DOC contents in coastal marshes, further suggesting that degradable C was the main contributor to $CH_4$ production. Our study indicated that both TOC and DOC contents significantly influenced the $CH_4$ emissions. A partial-correlation analysis controlling for temperature suggested that DOC contents were not correlated with $CH_4$ emissions, likely because DOC contents covaried with temperature changes.

Methanogenic archaea are favored in strongly reducing and anaerobic conditions, $CH_4$ emissions are thus generally higher in the environments with lower Eh. The strong correlation between Eh and $CH_4$ emission thus likely indicated that soil Eh was an important factor for $CH_4$ emissions in the coastal marshes. Previous studies also reported that salinity had a negative effect on $CH_4$ emissions in marshes with moderate to high salinities (Vivanco et al., 2015; Abdul-Aziz, et al., 2018), the $CH_4$ emissions from the coastal marshes were strongly inhibited by the high salinity, indicating a negative relationship of salinity with $CH_4$ emission. Sulfate-reducing bacteria can outcompete methanogens, and sulfate reduction can oxidize $CH_4$ in anaerobic environments, limiting $CH_4$ emissions (Weston et al., 2014). Coastal marshes are enriched in sulfates, so $SO_4^{2-}$ content is likely a strong factor leading to low $CH_4$ emissions. It has been reported that organic matter inputs promote the microbial growth rate and further increase the amount of microbial C anabolism (Chen et al., 2020). In addition, higher microbial carbon anabolism implies more C converted to biomass, leading to higher MBC (Spohn et al., 2016; Chen et al., 2020). The more microbes can enhance the anaerobic decomposition of organic matter and further increase $CH_4$ production (Morrissey et al., 2014a). Therefore, MBC content was an important factor accounting for the variability of $CH_4$ emissions across the coastal marshes because MBC is affected by microbial C anabolism and soil C pools (Chen et al., 2020).

### 4.2.2. Factors affecting $N_2O$ emissions

Warming is predicted to intensify the metabolic biokinetics of enzymatic activity for nitrification and denitrification (Greaver et al., 2016). Both nitrification and denitrification are sensitive to the increase in temperature, with an optimal temperature of about 20–25 °C (Martens-Habbena et al., 2009; Canion et al., 2014). AT in December and MAT in subtropical zones are about 20 °C, but are <10 °C in temperate zones. The modified nitrification and denitrification driven by the changes in temperature, however, may create environmental conditions for shifting microbial activity between $NH_4^+$ and $NO_3^-$ (Martens-Habbena et al., 2009), further increasing $N_2O$ emissions. Increases in temperature are also expected to enhance the amount of dissolved organic C (Laudon et al., 2012), promoting a C-cycle feedback to N transformation, including denitrification as a heterotrophic process. $N_2O$ emissions are therefore higher in subtropical coastal marshes and warm seasons, because denitrification can increase with the amount of dissolved organic C. Xiong et al. (2017) reported that organic C was the primary factor affecting denitrification because of its yields of respiration energy. In our study, however, TOC content had an indirect negative effect on $N_2O$ emissions (Figure 7b), likely because C transformations enhanced by temperature and C availability could limit N cycling processes (Craine et al., 2007; Nottingham et al., 2019).

Denitrification is active in reducing environments with low Eh (Stelzer and Scott, 2018), thereby leading to higher $N_2O$ emissions. Eh in our study significantly influenced $N_2O$ emissions across the coastal marshes, suggesting that low Eh was favorable for $N_2O$ emission. $NO_x^-$ also had an important effect on the $N_2O$ emissions, because $NO_x^-$ is the electron acceptor for denitrification. Denitrifiers, however, can use the shift in substrates from $NO_x^-$ to $N_2O$ when environmental $NO_x^-$ content is below the threshold of ~1 μg $g^{-1}$ (Ryden, 1983; Yuan et al., 2015). The $NO_x^-$ contents in most of our sampling sites were similar to or below the threshold for denitrifiers, likely due to leaching by the tidal water, so $N_2O$ may be preferentially used in denitrification, which can lower $N_2O$ emissions. Nitrification has been suggested to both directly and indirectly affect $N_2O$ emission (Yuan et al., 2015). Nitrification can produce $N_2O$ by reducing $NH_2OH$ to NO and then to $N_2O$ (Hu et al., 2012). The community of ammonia-oxidizing archaea can use $NH_4^+$ to produce $NO_x^-$ even at extremely low $NH_4^+$ contents (Martens-Habbena et al., 2009). $NH_4^+$ content could be a potential factor affecting $N_2O$ emissions, although the relationship between $N_2O$ emissions and $NH_4^+$ contents was not significant (Table 5).

### 4.2.3. Factors affecting $CO_2$ emissions

Temperature is an important factor affecting $CO_2$ release, because the increase in temperature can enhance the yield of $CO_2$ from microbial respiration and organic-C decomposition (Bond-Lamberty and Thomson, 2010; Lu et al., 2013). More importantly, microbial respiration can be enhanced exponentially from 10 to 20 °C and further yield more $CO_2$ (Wang et al., 2016; Nottingham et al., 2019). The dependence of bacterial and fungal growth on temperature has been described in the tropical forests soils that is a very different system from the marshes, but the microbial communities were consistent with long-term adaptation to temperature (Nottingham et al., 2019). The range of MAT between the temperate and subtropical climates in our study was appropriately 10 °C, which strongly determined the distinct geographical patterns of $CO_2$ emissions between the temperate and subtropical coastal marshes. The air temperature along the gradient is highly variable in winter but less variable in summer.

The MAT increases significantly from north to south sites along the climatic gradient. The emissions of GHGs also showed increasing gradients from north to south sites. Therefore, the MAT could better explain the variations of GHGs emissions than air temperature along the climatic gradient (Figures 4 and 5). The availability of organic C also covaried with increasing temperature, and the TOC and DOC were not significantly correlated to $CO_2$ emissions after controlling for temperature (Table 5), so temperature indirectly influenced $CO_2$ emissions by affecting soil organic carbon (Figure 7c). The $CO_2$ emissions thus had a strong latitudinal gradient, increasing from high to low latitudes, mainly because microbial respiration can be enhanced by temperature.

The quality and quantity of organic C can strongly affect $CO_2$ emissions (Voigt et al., 2017; Emery et al., 2019). The TOC and DOC contents in our study, however, did not strongly affect the $CO_2$ emissions when a partial-correlation analysis controlled for climatic temperature. This relationship suggests a crucial dependence of organic-C availability on temperature across the marshes, thereby obscuring the important influences of TOC and DOC on $CO_2$ emission. The leaching and decomposition of organic C are more intensified by higher temperatures in subtropical than temperate climates, delivering more DOC for microbial respiration (Wang et al., 2016). Soil pH was negatively correlated with $CO_2$ emission (Table 5, Figure S1), but soil Eh may not be the important factor affecting $CO_2$ emission. Soil Eh is strongly affected by soil water and tidal flooding (Li et al., 2015). The low soil Eh means low oxygen content, which may inhibit the aerobic microbial respiration and further decrease the $CO_2$ emissions. The C/N ratio was also an important variable affecting the $CO_2$ emissions, further suggesting that microbial respiration can increase in the environments enriched in organic C. Bacterial abundance and MBC and MBN contents were positively correlated with $CO_2$ emissions (Table 5, Figure S1), suggesting that microbial abundance and respiration play important roles in $CO_2$ emission.

## 4.3. Implications for global warming and emissions

Increasing GHG emissions are expected to have many environmental consequences, of which global warming is the most important for global climate change (Lashof and Ahuja, 1990; Meinshausen et al., 2009). Global warming would in turn increase GHG emissions by stimulating biogeochemical cycling due to higher temperatures (Greaver et al., 2016), thus positively feeding back on GHG emission. Coastal marshes are highly sensitive to global climate change and are predicted to play an important role in GHG emissions (Martin and Moseman-Valtierra, 2017; Abdul-Aziz, et al., 2018). Global warming shows a great challenge to predict GHG emissions from coastal marshes. Some studies, however, have reported that increasing temperatures can tend to enhance GHG emissions in coastal marshes (Xie et al., 2014; Yang and Silver, 2016; Abdul-Aziz, et al., 2018).

Assuming that the latitudinal gradient was a main consequence of temperature changes and that local environmental variables remained constant across the marshes, we can conservatively estimate the response of GHG emissions to future increases in global temperature. The increased emissions of $CH_4$, $N_2O$ and $CO_2$ in response to proposed increases in annual temperature of 2–4 °C by 2100 (IPCC, 2007) represent 4.62–11.4%, 27.5–70.6% and 9.13–12.9% of the current mean emissions for temperate coastal marshes, respectively. The increases in the emissions of $CH_4$, $N_2O$ and $CO_2$ would account for 0.67–1.66%, 4.03–10.3% and 2.98–4.21% of the current mean emissions for subtropical coastal marshes, respectively. These results are consistent with the report that climatic warming has already altered the extent of biogeochemical processes (Lu et al., 2013; Greaver et al., 2016; Voigt et al., 2017), possibly contributing to increased GHG emissions. The increasing amplitudes of emissions induced by global warming in the marshes were larger for $N_2O$ than $CH_4$ and $CO_2$. The increases in the amplitudes of GHG emissions were larger in the temperate than subtropical marshes (Table 6), indicating that the temperate marshes had stronger feedbacks to the increasing temperatures. It has been reported that the soil microbial respiration rates incubated under the increasing temperature increased logarithmically with increasing latitude and the sensitivity of soil microbial respiration to the increasing temperatures is higher in the soils from locations with lower temperature relative to high temperature (Wang et al., 2016). The GHG emissions from low temperature soils showed high temperature sensitivity relative to high temperature soils (Zou et al., 2018). We therefore propose that coastal marshes at high latitudes with lower climatic temperatures are anticipated to emit more GHGs under future climatic warming.

GHG emissions in coastal marshes are currently increasing globally and contribute greatly to global emissions (Yang et al., 2016; Abdul-Aziz et al., 2018; Emery et al., 2019). The total area of Chinese coastal marshes is $5.8\times10^4$ km$^2$, equivalent to 0.39‰ of the global terrestrial area ($1.49\times10^8$ km$^2$). The $CH_4$ emissions from these marshes were estimated at approximately 0.119 Tg $CH_4$ y$^{-1}$, which represent approximately 0.62‰ of annual global $CH_4$ emissions from terrestrial environments (192 Tg $CH_4$ y$^{-1}$, Tian et al., 2015). $N_2O$ emissions from the coastal marshes were lower than $CH_4$ emissions, estimated at a rate of 0.014 Tg $N_2O$ y$^{-1}$, equivalent to approximately 0.70‰ of annual global $N_2O$ emissions from terrestrial environments (20 Tg $N_2O$ y$^{-1}$, Zaehle et al., 2011). $CO_2$ emissions were the largest of the three gases, about 500- and 3600-fold larger than for $CH_4$ and $N_2O$, respectively. The total emissions of $CO_2$ (0.051 Pg $CO_2$ y$^{-1}$) from the marshes accounted for approximately 6.60‰ of annual global $CO_2$ emissions from inland waters (7.7 Pg $CO_2$ $y^{-1}$, Raymond et al., 2013). These GHG emissions from the marshes are large, considering their small surface area, reinforcing the understanding that coastal marshes are foci of GHGs. These results suggest that Chinese coastal marshes play a critically important role in global GHG emissions and are anticipated to be important to future global climate change.

### 4.4. Study uncertainty and future outlook

This study highlights the importance of climatic temperature on GHG emissions and the relationship between global climate change and GHG emissions in coastal marshes along the latitudinal gradient. Uncertainty remains, however, about the relative importance of climatic temperature and local conditions on GHG emissions. Salinity is a crucial factor affecting biogeochemical processes at moderate ranges (Morrissey et al., 2014b), which can decrease the role of temperature in GHG emissions (Abdul-Aziz, et al., 2018). Differences in temperature and nutrient availability are highly variable both spatially and temporally, likely contributing to the local variability of annual GHG emissions across the coastal marshes. The GHG emissions and soil C and N contents missed the vertical variation within the changing soil depth, making it uncertain for projecting the contribution of GHG emissions from Chinese coastal marshes to global terrestrial environments. In addition, GHG emissions in our study were determined from the bare flat after the ebb tide, actually the vegetation exhibits a great influence on GHG emissions (Yuan et al., 2015), leading to great uncertainty of the estimates of GHG emissions from coastal wetlands. Multiple factors should thus be considered for predicting GHG emissions in coastal wetlands under a future changing climate and environment. More importantly, the variation in GHG emissions within a study site may be equivalent to the total variability in the emissions along a latitudinal gradient

(Bridgham et al., 2013). This variability emphasizes the importance of local environmental parameters other than climatic temperature in determining the geographical variation in GHG emissions from coastal marshes (Abdul-Aziz et al., 2018). Our relative large number of samples sites, however, enabled us to clarify a large and consistent latitudinal gradient in GHG emissions that was correlated strongly with climatic temperature.

The responses of biogeochemical processes to environmental conditions are inherently complex and nonlinear, so predicting the ecological consequences of global warming is difficult. C and N transformations may compete under changing environments and temperature, facilitating or inhibiting other processes (Nottingham et al., 2019). We used a linear model that was an abstraction of reality and simplified many complex processes for predicting GHG emissions in response to increases in annual temperature. Statistical analyses of experimental data for determining ecological and biogeochemical dynamics in *in situ* field environments are also difficult. The fitting model in our study suggested that mean annual temperature was crucial for predicting GHG emissions, but 28–67% of the variations in the GHG emissions were attributed to soil variables and not to climatic temperature. Our results for the tropical and subtropical marshes, however, should not be extrapolated, because the optimum temperatures for C and N transformations (e.g. enzymatic dynamics) are about 20–25°C (Canion et al., 2014), equivalent to our MAT. This equivalence suggests that the GHG emissions in the subtropical marshes were less sensitive to the increase in annual temperature relative to temperate marshes. Global warming is also expected to have a more important influence on productivity and biogeochemical processes of northern coastal marshes (Kirwan et al., 2009). These results further indicate divergent responses to global warming of coastal marshes with different climates, potentially affecting the predictions of GHG emissions at the large geographical scales.

## 5. Conclusions

Emissions of $CH_4$, $N_2O$ and $CO_2$ in the Chinese coastal marshes increased along the latitudinal gradient from high to low latitudes. These emissions were highly dependent on the increase in climatic temperature. Soil substrate availabilities and bacterial abundance affected by the temperature were also the key drivers of the geographical variations of GHG emissions. The increase in GHG emission was larger in the temperate than subtropical marshes under the proposed increase in temperatures of 2–4 °C by 2100, suggesting that the feedbacks to global warming were stronger in the temperate than subtropical marshes. Chinese coastal marshes play a crucial role in GHG emissions, representing 0.62–6.60‰ of the global annual emissions from terrestrial environments and inland waters. Our results refine our understanding of the environmental consequences of global climate change to coastal marshes and suggest that these marshes are important for predicting future GHG emissions.

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## Figure captions

**Figure 1.** Sites of Chinese coastal marshes along the latitudinal gradient. Sites DD, TS, WF, QD and DF have a temperate climate, and SH, WZ, FZ, ST, ZH and BH have a subtropical climate. DD, TS, WF, QD, DF, SH, WZ, FZ, ST, ZH and BH are abbreviations for the cities of Dandong, Tangshan, Weifang, Qingdao, Dafeng, Shanghai, Wenzhou, Fuzhou, Shantou, Zhuhai and Beihai, respectively.

**Figure 2.** Emissions of $CH_4$ (a), $N_2O$ (b) and $CO_2$ (c) from the coastal marshes along the latitudinal gradient. The bars denote standard errors ($n = 3$).

**Figure 3.** Emissions of $CH_4$ (a), $N_2O$ (b) and $CO_2$ (c) in the temperate and subtropical coastal marshes. DD, TS, WF, QD and DF are grouped into temperate sites, and SH, WZ, FZ, ST, ZH and BH are grouped into subtropical sites. The horizontal lines indicate medians, the small squares indicate means, the asterisks indicate outliers, the boxes indicate the 25th and 75th percentiles and the bars indicate the range from the 5th to the 95th percentiles. Different letters above the plots with the same color denote significant differences between the temperate and subtropical marshes ($P < 0.05$). The asterisks above and below the plots denote significant differences between December and July

($P < 0.05$).

**Figure 4.** Variations in $CH_4$, $N_2O$ and $CO_2$ emissions with air temperature (a-c) and mean annual temperature (d-f). Emissions of $CH_4$, $N_2O$ and $CO_2$ were log(10) transformed prior to testing. Correlations ($r^2$) and significance level ($P$) are shown.

**Figure 5.** Stepwise multiple regression analyses of the greenhouse-gas fluxes and environmental traits. The data were log(10) transformed normally before entry into the models. For this model, the final set of predictors are shown in sequence. (+) and (–) denote positive and negative correlations between the greenhouse-gas fluxes and the predictors, respectively. MBC, microbial biomass carbon; Eh, redox potential; MAT, mean annual temperature; AT, air temperature; $NO_x^-$, $NO_3^-$ plus $NO_2^-$.

**Figure 6.** 2D plots of the variables (A) and cases (B) of the principal component analysis(PCA) TN, total soil nitrogen; $NH_4^+$, soil extractable ammonium; $NO_x^-$, soil nitrate/nitrite extractable; $^{15}N$, $\delta^{15}N$; Eh, redox potential; pH, soil pH; $SO_4^{2-}$, soil extractable sulfate; CN, soil total C/N ratio; $^{13}C$, $\delta^{13}C$; MAT, mean annual temperature; SD, soil density; AT, air temperature; Microbes, bacterial abundance; MBC, microbial biomass carbon; MBN, microbial biomass nitrogen; TOC, total organic carbon; DOC, dissolved organic carbon; SWC, soil-water content; $CO_2$, $CO_2$ emission; $CH_4$, $CH_4$ emission; $N_2O$, $N_2O$ emission. The scores in panel B are the ±95% confidence intervals of the samples for each site and season.

**Figure 7.** Standardized direct and indirect effects derived from structural equation model (SEM) for $CH_4$ (a), $N_2O$ (b) and $CO_2$ (c). MAT, mean annual temperature; Eh, redox potential; MBC, microbial biomass carbon; $NO_x^-$, $NO_3^-$ plus $NO_2^-$; TOC, total organic carbon; MBN, microbial biomass nitrogen; DOC, dissolved organic carbon; Microbes, bacterial abundance.