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## The warming winter accelerated methane emissions during subsequent rice growing season from paddy fields

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E-mail: [rghu@mail.hzau.edu.cn](mailto:rghu@mail.hzau.edu.cn)**Keywords:** warming winter, temperature, methane, rice paddy, growing seasonSupplementary material for this article is available [online](#)**Abstract**

Global temperature is projected to increase, which impacts the ecological process in northern mid- and high-latitude ecosystems, but the winter temperature change in ecosystems is among the least understood. Rice paddy represents a significant contributor to global anthropogenic CH<sub>4</sub> emissions and has a strong climate forcing feedback; however, the legacy effects of warming winter on CH<sub>4</sub> emissions in the subsequent growing season remain uncertain. Here, we conducted field and incubation experiments to determine the effects of winter soil temperature changes on CH<sub>4</sub> emissions in the subsequent growing season. First, in the 3 year field experiment, we continuously measured CH<sub>4</sub> emissions from the rice cropping system. The winter soil temperature and its variation showed significant differences over the 3 years. In the warming-winter year, the rice paddy accumulated less NH<sub>4</sub><sup>+</sup>-N and more dissolved organic carbon (DOC) in the soil during winter, resulting in high CH<sub>4</sub> emissions. Second, we incubated the paddy soils without flooding at three temperatures (5 °C, 15 °C, and 25 °C) for 4 weeks to simulate warming winter, and subsequently incubated at same temperature (25 °C) under submerged conditions for 4 weeks to simulate growing season. The result was consistent with field experiment, increased soil temperature significantly increased soil DOC content and decreased NH<sub>4</sub><sup>+</sup>-N content in 'winter season'. The CH<sub>4</sub> emissions in the subsequent 'growing season' increased by 190% and 468% when previous incubation temperature increased 10 °C and 20 °C. We showed strong and clear links between warming winter and CH<sub>4</sub> emissions in the subsequent growing season for the first time, suggesting that CH<sub>4</sub> related processes respond not only to warming during the growing season but also in the previous winter. Our findings indicate that nonuniform global warming causes a disproportionate increase in climate forcing feedback to emit more CH<sub>4</sub>.

**1. Introduction**

Soil C content is intimately tied to global warming. This can be seen in the effects of temperature on processes like carbon storage and respiration (Beier

*et al* 2008, Xue *et al* 2011). Changing temperature has significant effects on almost all ecosystems' functions and processes. Additionally, changing temperature can cause a positive feedback that increases temperatures further (Cox *et al* 2000, Friedlingstei 2015).

Because of these close ties between temperature and soil C content, it is important to understand how these factors will interact in the future.

Warming regulates the decomposition of organic matter by changing the functional community of microorganisms (Bowden *et al* 1998, Jones and Mulholland 1998, Cheng *et al* 2017), making the retention of soil organic matter face more challenges of climate change. Warming will accelerate the decomposition of soil organic matter (SOM), the explanation of its mechanism focuses on the availability and accessibility of organic matter, and the metabolic characteristics of microorganisms (Davidson and Janssens 2006, Bradford 2013, Yan *et al* 2017, Alvarez *et al* 2018, Qin *et al* 2019). For example, in wetland system, the warming induce a much stronger C emission trend, and break the ‘latch’ of organic matter decomposition (Fellman *et al* 2017, Mau *et al* 2017). In addition, temperature regulates the end product of organic matter decomposition as well as anaerobic conditions, substrate availability, and quality. In wetlands, CH<sub>4</sub> is the main end-product and is highly related to temperature. Warming affects CH<sub>4</sub> emissions from most ecosystems by altering the soil microbial community, substrate availability, plant growth, and consequently, CH<sub>4</sub> production and oxidation (Elberling *et al* 2008, Chowdhury and Dick 2013, Treat *et al* 2015). Rice paddy is a special wetland system that accounts for 9%–19% of the global anthropogenic CH<sub>4</sub> emissions (Li *et al* 2009). In paddy soils, the methane formation often starts from 15 °C to 20 °C (Nozhevnikova *et al* 2010), and reaches a maximum at 37 °C (Yang and Chang 1998). Furthermore, many previous studies shown greater CH<sub>4</sub> emissions from rice paddies under elevated temperatures, with increase value ranged 10.9%–60.0% (Cheng 2008, Tokida *et al* 2010). Generally, elevated temperatures increase CH<sub>4</sub> emissions from rice paddies, indicating positive feedback (Allen *et al* 2003, Tokida *et al* 2010).

Most research on climate warming has concentrated on the response of ecosystem processes to temperature fluctuations during the growing season. However, for the past 100 years, the winter season has been more sensitive to the increase in annual average temperature than in other seasons (Easterling *et al* 1997, Balling *et al* 1998). The winter and spring warming occurred at a rate of exceed 0.30 °C per decade, which was faster than in summer or autumn at mid and high latitudes (Xia and Wan 2008). Warming winters change the frequency of soil freezing and modify microbial activity and plant growth, all of which alter the soil conditions both in winter (Brooks and Schmidt 1996, Blankinship and Hart 2012). There has been little recognition of the importance of legacy effects of winter climate change. However, in fact, the varied changes in ecosystem processes during the growing season not only respond to changes in temperature and precipitation in the quarter, but

also to the legacy effects from winter (Campbell *et al* 2005, Groffman *et al* 2011). Strong and consistent links exist between winter climate conditions and microbial activity (Xia and Wan 2008), nitrogen mineralization (Durán *et al* 2015), and nutrient availability (Hobbie and Chapin 1996) in the following growing season. The legacy effect of winter warming can have many unexpected consequences; however, these have not been thoroughly tested.

Here, we evaluated the legacy effect of winter warming on CH<sub>4</sub> emissions from the subsequent rice-growing season and the mechanisms involved. We hypothesized that (a) higher soil temperature in winter would increase soil organic matter mineralization and change the stock of soil C and N; and (b) warming winter would accelerate the cycling of C and N in the following growing season, which in turn would enhance CH<sub>4</sub> emissions from rice paddies in the growing season. The key to accurately estimating the legacy effect from winter warming is to assess the changes in GHG emissions during the growing season. In order to achieve our goals, we used two different approaches: a field experiment to explore the relationship between winter soil temperature and CH<sub>4</sub> emissions during the growing season by continuous interannual monitoring, and an incubation experiment to set different temperature regimes for paddy soil without flooded to simulate warming winter and submerged under same temperature to simulate growing season, comparing CH<sub>4</sub> emissions and C and N dynamics under very different ‘winter temperature’.

## 2. Materials and methods

### 2.1. Field experiment

The field experiment was conducted in Jinjing Town, Changsha City, Hunan Province, China (28°32′46″N, 113°19′50″E, elevation 81 m) in December 2012 and lasted for 3 years. The study region is characterized by a subtropical humid monsoon climate with an annual average precipitation of 1150 mm yr<sup>-1</sup>. The experimental site had three adjacent paddy plots (15 × 20 m) that had been cultivated for more than 100 years. After the harvest of rice, the stubbles were incorporated into the soil, while straw was transported to the outside of the field.

Soil-atmosphere trace gas (CO<sub>2</sub>, CH<sub>4</sub>, and N<sub>2</sub>O) fluxes were monitored using the static opaque chamber technique. The flux chambers covered six hills of rice plants each in the paddy field. During the fallow season (from November to April) and the following growing season (from April to November), gas samples were collected once every 1–3 d. When the gas flux was monitored simultaneously, the air temperature ( $T_a$ ) inside the chambers and soil temperature ( $T_s$ ) were recorded with hand-carried digital thermometers. In addition, topsoil (0–20 cm) samples were randomly collected from five points and

composited into one soil sample twice a week. The soil mixture was kept at  $-4\text{ }^{\circ}\text{C}$  for further determination of soil dissolved organic carbon (DOC) and mineral N ( $\text{NH}_4^+\text{-N}$  and  $\text{NO}_3^-\text{-N}$ ) concentrations. Daily precipitation and air temperature were recorded using an automatic meteorological monitoring system (Intelimet Advantage; Dynamax Inc., USA).

## 2.2. Incubation experiment

The paddy soils were taken from the top layer (0–20 cm) at the field experiment site, after the rice harvest. Air-dried soil samples were activated at 20% soil moisture content at  $25\text{ }^{\circ}\text{C}$  for 3 d, and then 15 g samples were loaded into 145 ml bottles. Based on the change in soil temperatures during the winter, three temperatures ( $5\text{ }^{\circ}\text{C}$ ,  $15\text{ }^{\circ}\text{C}$ , and  $25\text{ }^{\circ}\text{C}$ ) were applied in the 4 weeks aerobic incubation experiment to simulate the field conditions at different temperatures in winter. Each treatment was replicated six times.

After 4 weeks of aerobic incubation, all soil samples in the bottles were submerged in 50 ml of deionized water. Then all bottles were finally incubated at  $25\text{ }^{\circ}\text{C}$  for 2 weeks to simulate the growing season. The headspace gases in the bottles were sampled twice a week for the analysis of the  $\text{CO}_2$ ,  $\text{CH}_4$ , and  $\text{N}_2\text{O}$  concentrations. The fluxes were determined as the change in the gas concentration in the headspace gases within 1 h. After gas sampling, soils were obtained to determine the DOC, mineral N, and acetate contents.

## 2.3. Analytical techniques

Gas samples for the determination of  $\text{CH}_4$ ,  $\text{CO}_2$ , and  $\text{N}_2\text{O}$  concentrations were analyzed using a gas chromatograph (Agilent 7890A, Agilent Technologies, Palo Alto, California, USA). (Wang *et al* 2006). Mineral N was extracted by 1 M KCl from the paddy soils and determined using a continuous-flow automatic analyzer (Skalar, Holland). The DOC extracted using deionized water was measured using a TOC analyzer (TOC-VWP, Shimadzu Corporation, Japan). The concentration of acetate extracted by deionized water was determined by HPLC (Aminex HPX-87-H, BioRad, München, Germany) (Krumböck and Conrad 2006).

## 2.4. Statistical analysis

To better understand the change in winter soil temperature, the standard deviation of the log-transformed observation coefficient of winter soil temperature variation (WSTV) was used (McArdle and Gaston 1995). Data were transformed for normality before the analysis of variance. One-way ANOVA analysis was used to test the differences in soil temperature, C and N contents, and atmospheric trace gas emissions among treatments in the incubation experiment and different years in the field experiment. Linear regression analyses were used to determine whether significant relationships existed

between the annual  $\text{CO}_2$  emissions and soil temperature. Path analysis was used to evaluate the effect of WSTV on  $\text{CH}_4$  emissions to determine the relationship between winter soil temperature and  $\text{CH}_4$  emissions during the growing season. Path analysis was carried out using the lavaan package (Rosseel 2012), an add-on package in R. Statistical analyses were performed using SPSS 19.0 software for Windows (SPSS Inc., Chicago).

## 3. Result

### 3.1. Soil temperature variables in 3 years field experiments

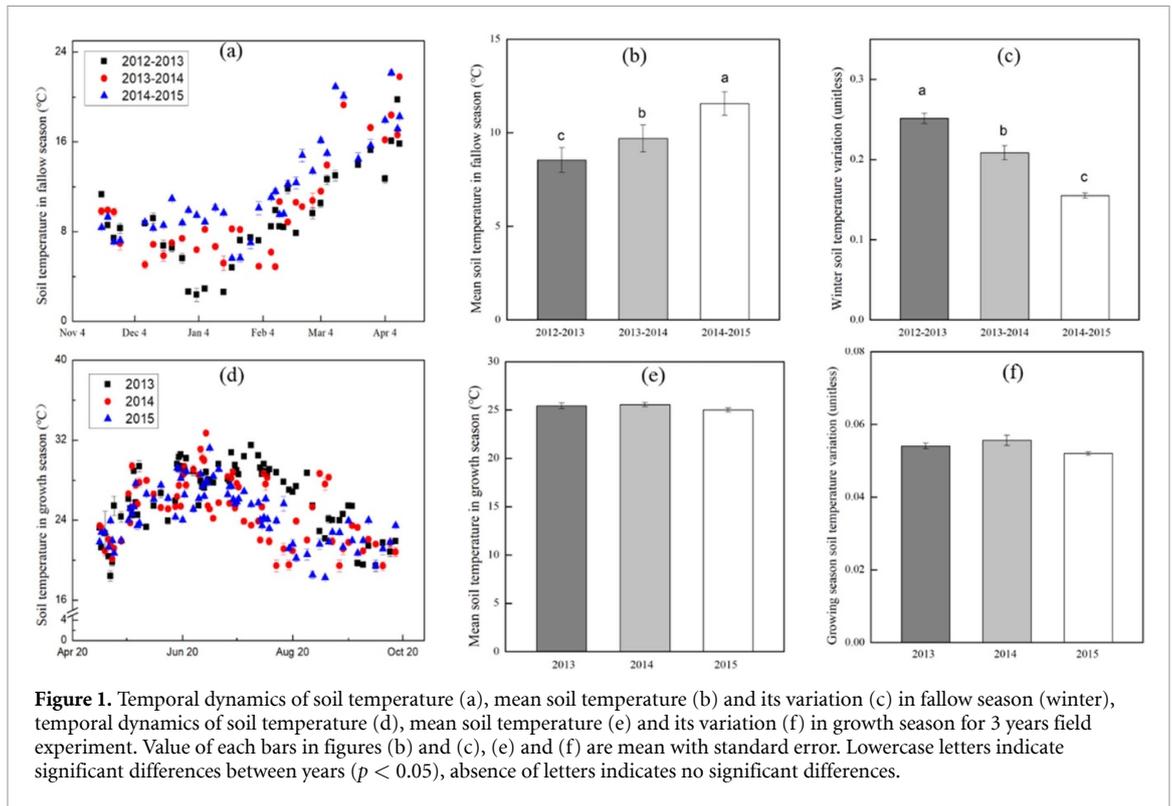
There was a significant difference in the winter soil temperature during the 3 years of the field experiments (figure 1(b)). Soil temperature increased over the years, whereas variability in soil temperature (WSTV) decreased (figures 1(a)–(c)). The change of mean temperature and WSTV in winter was due to the fewer cold days and higher minimum temperatures (figure 1(a)). However, the mean soil temperatures during the subsequent growing season were  $25.44\text{ }^{\circ}\text{C}$ ,  $25.54\text{ }^{\circ}\text{C}$  and  $25.15\text{ }^{\circ}\text{C}$  in 2013, 2014, and 2015, respectively (figure 1(e)). No obvious difference was detected in mean soil temperature and temperature variation during the growing season for the 3 years (figures 1(e) and (f)). Seasonal variations in air temperature maintained the same seasonal pattern as soil temperature.

During the rice-growing season, the surface water depth ranged from 0 to 9.0 cm and remained zero during the winter fallow season. In winter, soil water content is mainly driven by precipitation. There was no significant difference in the precipitation and soil water content in winter season over the 3 years (figure S1).

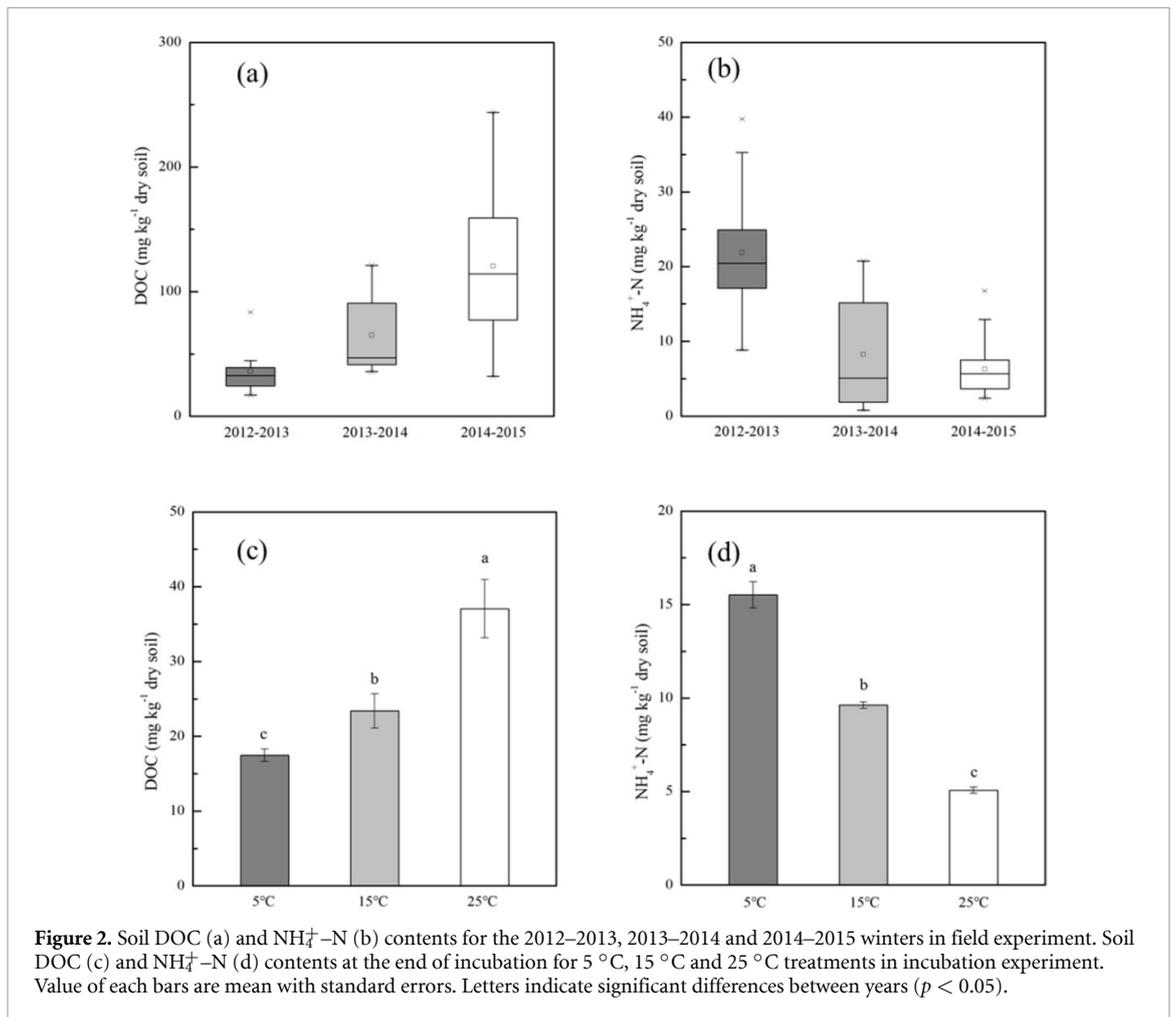
### 3.2. Variation of soil $\text{NH}_4^+\text{-N}$ , $\text{NO}_3^-\text{-N}$ , and DOC in winter season

The concentrations of soil DOC and  $\text{NH}_4^+\text{-N}$  in the topsoil were significantly different during winter (figures 2(a) and (b)). The mean value of DOC in 2015 ( $120.55\text{ mg C kg}^{-1}$ ) was significantly higher ( $p < 0.05$ ) compared with previous 2 years ( $45.40\text{ mg}$  and  $69.78\text{ mg C kg}^{-1}$ ). Soil  $\text{NH}_4^+\text{-N}$  concentrations decreased over the years (figure 2(b)). Average  $\text{NH}_4^+\text{-N}$  was 21.69, 8.63 and  $6.24\text{ mg N kg}^{-1}$  for 3 years, respectively. Variations were observed between DOC and  $\text{NH}_4^+\text{-N}$ . Soil  $\text{NO}_3^-\text{-N}$  concentrations were low during the study period.

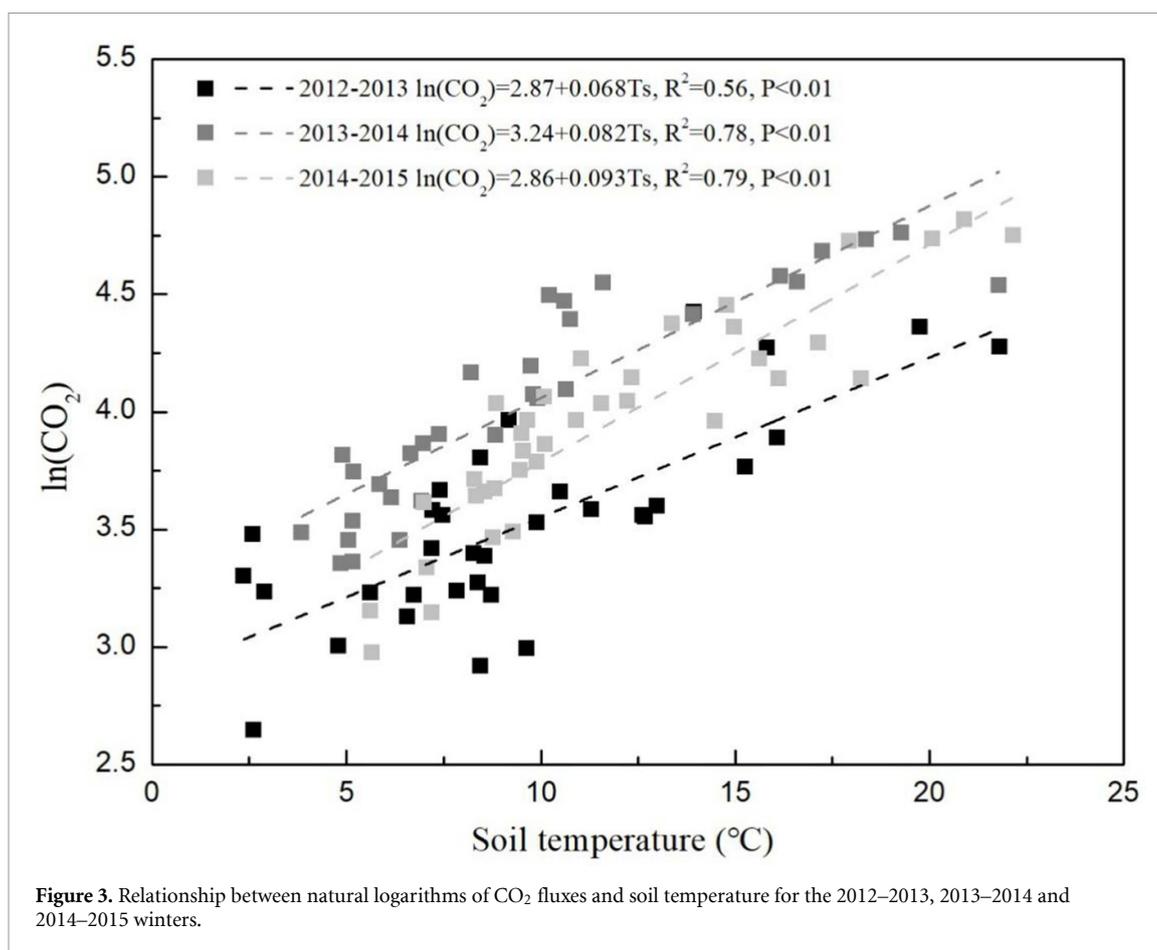
Similarly, in the incubation experiment, the different temperatures during the aerobic incubations significantly changed the soil DOC and inorganic N content. At the beginning of aerobic incubation, the soil C and N contents were at the same level, but the DOC content was high (figure 2(c)) and the  $\text{NH}_4^+\text{-N}$  content was low in the high-temperature treatment at the end of incubation (figure 2(d)). However,



**Figure 1.** Temporal dynamics of soil temperature (a), mean soil temperature (b) and its variation (c) in fallow season (winter), temporal dynamics of soil temperature (d), mean soil temperature (e) and its variation (f) in growth season for 3 years field experiment. Value of each bars in figures (b) and (c), (e) and (f) are mean with standard error. Lowercase letters indicate significant differences between years ( $p < 0.05$ ), absence of letters indicates no significant differences.



**Figure 2.** Soil DOC (a) and  $\text{NH}_4^+\text{-N}$  (b) contents for the 2012–2013, 2013–2014 and 2014–2015 winters in field experiment. Soil DOC (c) and  $\text{NH}_4^+\text{-N}$  (d) contents at the end of incubation for 5 °C, 15 °C and 25 °C treatments in incubation experiment. Value of each bars are mean with standard errors. Letters indicate significant differences between years ( $p < 0.05$ ).



NO<sub>3</sub><sup>-</sup>-N had the opposite trend to soil NH<sub>4</sub><sup>+</sup>-N at the end of the aerobic incubation (figure S2). The difference in soil NO<sub>3</sub><sup>-</sup>-N variation between the two experiments was due to strict control of the incubation experiment.

### 3.3. Variation of soil trace gas exchange in winter season

Warming during winter also affected soil trace gas emissions. In the field experiment, the CO<sub>2</sub> emissions during winter significantly increased with higher soil temperatures (figure 3), whereas the CH<sub>4</sub> and N<sub>2</sub>O emissions were negligible. In the incubation experiment, the CO<sub>2</sub> and N<sub>2</sub>O emissions were significantly different among the three treatments during aerobic incubation (figure S3). In general, the CO<sub>2</sub> and N<sub>2</sub>O emissions were higher in the high-temperature treatment. The CH<sub>4</sub> flux was negligible during aerobic incubation.

### 3.4. Variation of soil NH<sub>4</sub><sup>+</sup>-N, NO<sub>3</sub><sup>-</sup>-N and DOC in rice growing season

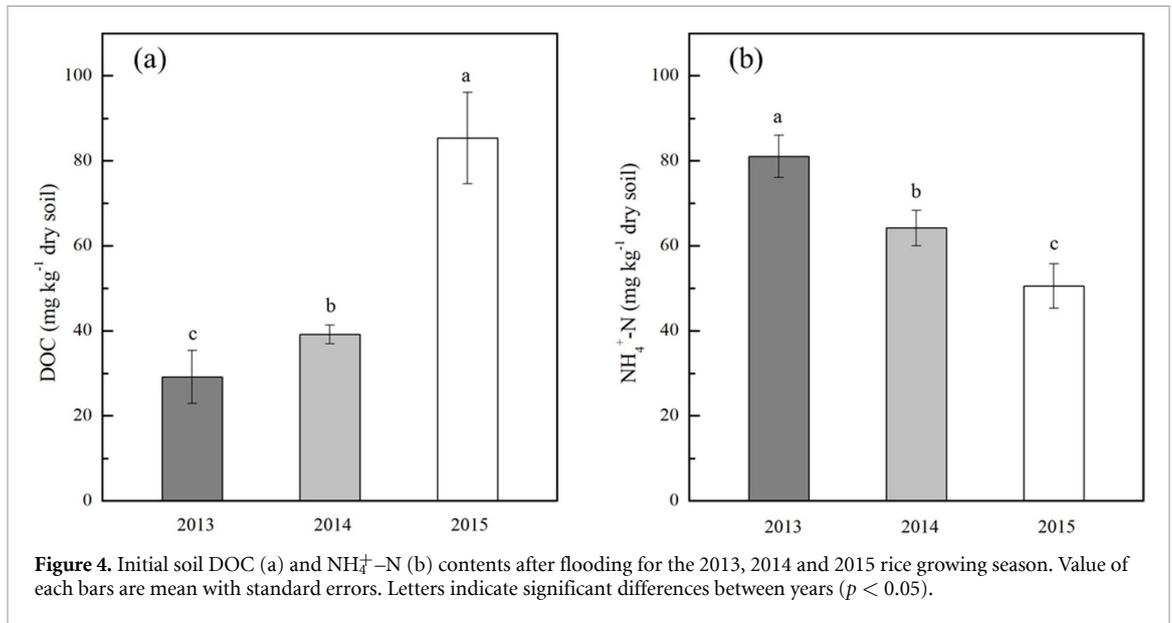
In the field experiment, the initial soil NH<sub>4</sub><sup>+</sup>-N and DOC (before rice planting) after flooding maintained the same trend as in the winter. Soil NH<sub>4</sub><sup>+</sup>-N after flooded was 81.04, 64.19 and 50.56 mg N kg<sup>-1</sup> for 3 years, respectively (figure 4(b)). In contrast, soil

DOC was significantly higher in 2015 after flooding (figure 4(a)).

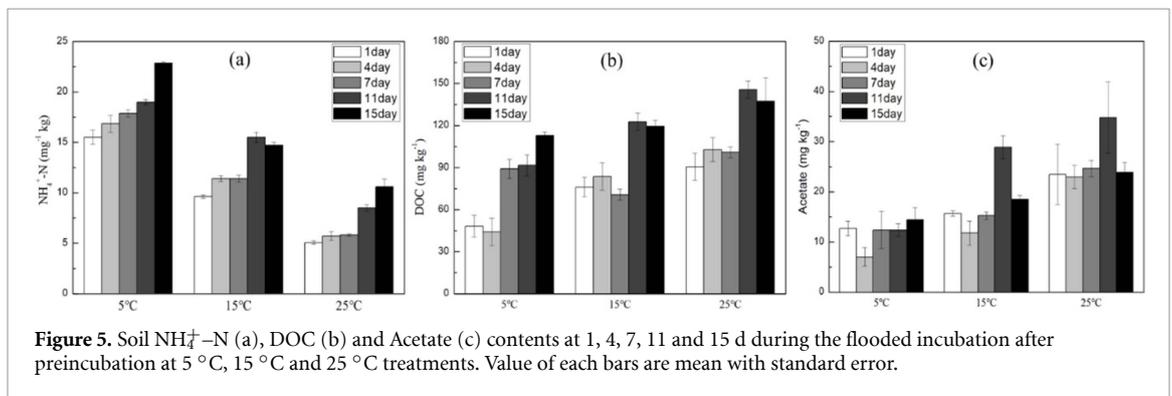
During the incubation experiments. After soil flooding, all treatments were conducted under the same temperature conditions. In the flooded period, soil NH<sub>4</sub><sup>+</sup>-N and DOC maintained the same difference between treatments as in the aerobic incubation (figures 5(a) and (b)). Soil NH<sub>4</sub><sup>+</sup>-N was lower after pre-incubation at 25 °C where soil DOC was higher. In addition, the concentration of acetate showed the same trend as soil DOC, the 15 °C and 25 °C treatments had higher contents of acetate (figure 5(c)).

### 3.5. CH<sub>4</sub> flux in rice growing season

In field experiment, CH<sub>4</sub> emissions increased by 35% in 2014 and by 192% in 2015 compared to 2013 (figures 6(a) and (b)). The main difference of CH<sub>4</sub> emissions occurred in early rice season whereas the late rice season had no significant difference (figure 6(b)). In early rice season, the peak CH<sub>4</sub> fluxes were 23.50, 36.33 and 59.83 for 3 years, respectively. What is more, the peak value appeared at the day 22, 35 and 44 after rice planting in 3 years, respectively. Path analyses identified potential causal relationships between WSTV and CH<sub>4</sub> fluxes during the growing season by combining data from the two seasons (figure 7). WSTV affected CH<sub>4</sub> emissions indirectly



**Figure 4.** Initial soil DOC (a) and NH<sub>4</sub><sup>+</sup>-N (b) contents after flooding for the 2013, 2014 and 2015 rice growing season. Value of each bars are mean with standard errors. Letters indicate significant differences between years ( $p < 0.05$ ).



**Figure 5.** Soil NH<sub>4</sub><sup>+</sup>-N (a), DOC (b) and Acetate (c) contents at 1, 4, 7, 11 and 15 d during the flooded incubation after preincubation at 5 °C, 15 °C and 25 °C treatments. Value of each bars are mean with standard error.

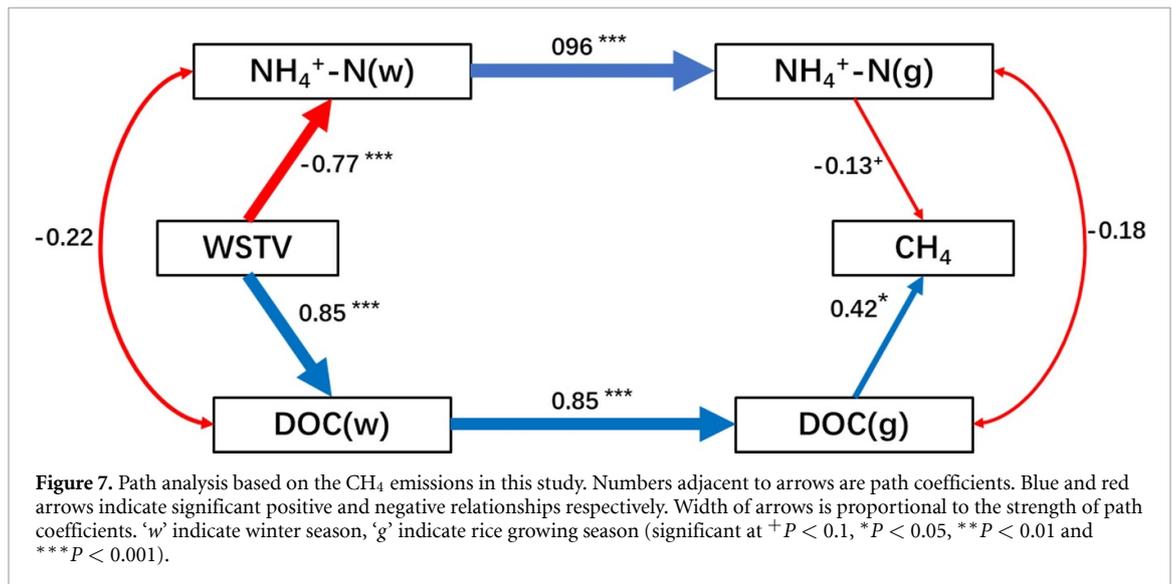
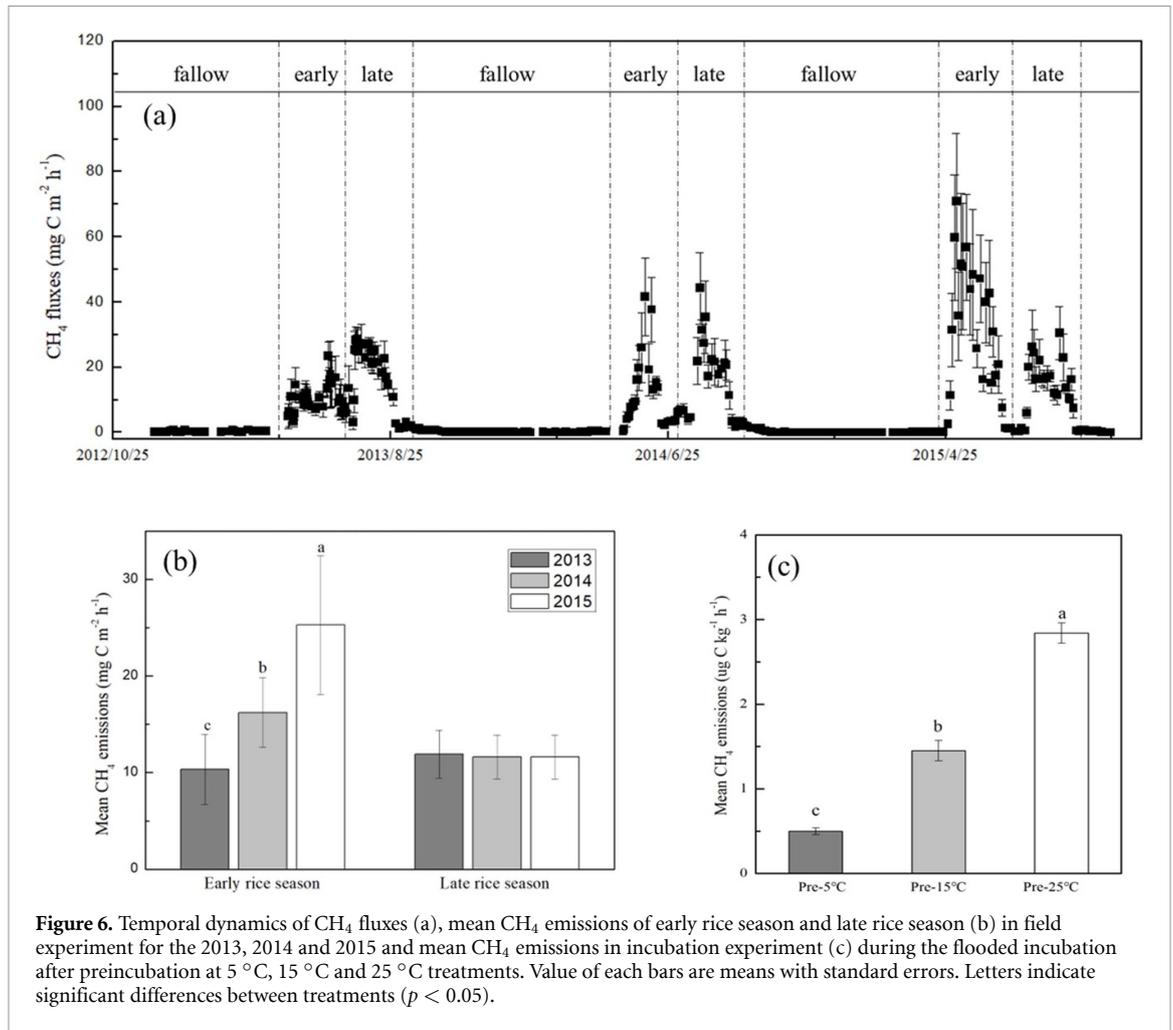
via changes in DOC and NH<sub>4</sub><sup>+</sup>-N concentrations. There was a statistically significant positive relationship between the initial soil DOC after flooding and mean CH<sub>4</sub> emissions (figure 7). In contrast, the initial soil NH<sub>4</sub><sup>+</sup>-N during the growing season had a significant negative relationship with CH<sub>4</sub> emissions (figure 7). Similarly, higher temperature during ‘fallow season’ in incubation experiment stimulated CH<sub>4</sub> emissions during the following flooded period, CH<sub>4</sub> emission increased by 190% and 468% when preincubation temperature increased 10 °C and 20 °C (figure 6(c)).

#### 4. Discussion

Our field and incubation experiments consistently demonstrated that warming in winter enhanced the CH<sub>4</sub> emissions during the growing season. These results suggest that most warming studies have ignored the legacy effects of winter warming on seasonal CH<sub>4</sub> emissions in rice cropping systems, considering only the influence of temperature change during the growing season.

##### 4.1. Winter soil temperature change

The winter temperature increases faster than in other seasons, especially at latitudes of 30–90°N (IPCC 2013). Most studies have focused on relatively cold regions with long winters (such as the High Arctic) relative to temperate regions (Kreyling 2010), which may disguise some key aspects of winters. In our field experiment, the increase in mean winter temperature was due to the decrease in the temperature variability and the minimum temperature days (figures 1(a)–(c)), whereas the soil temperature remained stable during the growing season (figures 1(d)–(f)). This result is agreed with previous studies, the low-latitude temperate region was predicted with ‘vanishing winters’ (Kreyling and Henry 2011). Seasonal warming is a complex concept, the increase in temperature during a season is not simply an increase in the mean temperature. In our investigation, the winter fallow period lasted 4–5 months, and its warming came from fewer cold days and higher minimum temperatures (figure 1(a)). Temperature is projected to continue increasing in this region, which will have a shorter and warmer winter (Kunkel 2004),



but overall, this means that the days of minimum temperatures have reduced (Easterling 2000, Caprio et al 2009).

Higher temperatures and smaller temperature variations could increase microbial activity and substrate availability (Xia et al 2014), which indirectly affects ecological processes in the following seasons.

Although field experiments provided an opportunity to explore the relationships between winter temperature change and CH<sub>4</sub> emissions during the growing season, the results from year-to-year comparisons are not completely straightforward, since there are other factors affecting CH<sub>4</sub> emissions except winter temperature. However, controlled, replicated

soil incubation experiments have provided important confirmation from field observations. In lab experiment, we created three temperature treatments (5 °C, 15 °C and 25 °C) to simulate different temperature segments in winter. Although the magnitude of winter warming was weak (<2 °C), it was just a change of mean temperature. The real effect of winter warming was the duration of the different temperature segments, not the mean value (Xia *et al* 2014).

The results from the warming stages of rice paddy soil (fallow season in winter and growing season in spring and summer) strongly support the idea that warming winter has a strong influence on microbial, soil, and other ecosystem processes for the following growing season (Durán *et al* 2013, Blanc-Betes *et al* 2016).

#### 4.2. Dynamic of soil C and N in winter

In the field experiment, the rice paddy was left fallow without flooding, the higher soil temperature increased the flux of CO<sub>2</sub> from the SOM and residual rice stubble (figure 3). After the rice was harvested, the majority of the straw was removed from the field, SOM and little residual stubble was the primary substrates of heterotrophic respiration in the soil. Under the same substrate supply and water condition (figure S4), soil temperature was the main factor controlling SOM mineralization and rice straw decomposition to CO<sub>2</sub> (Amelung *et al* 1997, Peng *et al* 2015, Zhang *et al* 2015). The main reason for the increase in SOM mineralization with increasing temperature is that high temperatures accelerate the rate of enzyme-mediated reactions, especially in the cold winter (Davidson and Janssens 2006, Lawrence *et al* 2009, Wallenstein *et al* 2010). According to previous studies (Fang *et al* 2005, Davidson and Janssens 2006, Ågren 2000), labile and resistant organic matter has a similar response to soil warming; higher CO<sub>2</sub> fluxes indicate a higher accumulation of DOC from insoluble organic matter (figure 2(a)). The same result was obtained in the incubation experiment (figure 2(c)). Additionally, SOM decomposition can serve as an additional available N source because of the coupling of soil C and N cycles (Maljanen *et al* 2003, Harrison-Kirk *et al* 2015). However, in the field study, the NH<sub>4</sub><sup>+</sup>-N content decreased with increasing temperature, and the NO<sub>3</sub><sup>-</sup>-N content and N<sub>2</sub>O emissions were negligible (figure 2(b)), indicating that the warmer winter had less inorganic N supplies, consistent with the hypothesis of Melillo *et al* (2011). There was a slight difference in the incubation experiment, and the NH<sub>4</sub><sup>+</sup>-N content had the same variation as the field experiment (figures 2(b) and (d)), whereas the NO<sub>3</sub><sup>-</sup>-N content and N<sub>2</sub>O fluxes increased with increasing temperature (figures S2 and S3(b)). This result may be due to the fact that higher temperatures reinforce nitrification and nitrification-induced N<sub>2</sub>O emissions (Wang *et al* 2010). The difference between

the two experiments was that the incubation experiment was strictly controlled, and the field experiment had many other uncontrollable factors that could lead to other N loss pathways (Maljanen *et al* 2003, Harrison-Kirk *et al* 2015). The result of incubation experiment explained the accumulation of DOC and NH<sub>4</sub><sup>+</sup>-N of different temperature segments during winter in field experiment. In winter season, extended period of warmth and decreased cold days lead to higher contents of DOC in the soil. In addition, the smaller soil temperature variability in the field experiment (figure 1(c)), due to the increase in minimum temperature, is likely to have a significant impact on soil biogeochemical properties (Schimel and Clein 1996, Kreyling *et al* 2012). The smaller soil temperature variability may have relieved the stress on microbial populations, thereby increasing organic matter decomposition (Stuanes *et al* 2008, Brooks *et al* 2011). Moreover, the change in winter soil temperature variability may further influence the following growing season. It is likely that microbial populations recover more easily at the beginning of the growing season (Brooks *et al* 1998).

#### 4.3. Legacy effects of warming winter on CH<sub>4</sub> emissions

In warm winter year, the cumulative CH<sub>4</sub> in growing season was higher (figure 6(a)). Comparing the CH<sub>4</sub> emissions from two growing period of double cropping rice, we found that the increase in CH<sub>4</sub> emissions was mainly caused by the early rice period (figure 6(b)). Under the same conditions of field management, rainfall and temperature, there were changes in the early rice period but no difference in the late rice stage. It was clear that this effect came from the previous fallow season. Soils from the beginning of flooding in early rice period had similar inorganic N and DOC concentrations with the winter period (figures 4 and 5). The warming winter or high temperature during the previous aerobic incubation provided more DOC and less NH<sub>4</sub><sup>+</sup>-N, which contributed to more CH<sub>4</sub> emissions in the submerged growing season. Especially, the increase of CH<sub>4</sub> emissions in early rice period was caused by higher and earlier emission peaks (figure 6(a)). This result can be explained by the difference in the response of methanogens and methanotrophs to previous soil warming without flooding. CH<sub>4</sub> emissions from rice paddies are controlled by coupling CH<sub>4</sub> production and oxidation (Conrad 2007). CH<sub>4</sub> is the terminal product of organic matter produced by methanogens under anaerobic conditions, and this process is determined by C availability (Conrad 2007). It has been demonstrated that warming could increase methanogen abundance and CH<sub>4</sub> emissions through more substrates (Yang *et al* 2015). In both experiments, more DOC stimulated CH<sub>4</sub> production from submerged rice paddy soil. In

the field experiment, the earlier CH<sub>4</sub> emission peak of warm winter year showed soil C was the main substrate for microbial processes, because there was few available DOM from root secretion in seeding stage. Furthermore, in the incubation experiment, not only the DOC but also the concentration of acetate was significantly higher in the previous high-temperature treatment (figure 5(c)). In paddy fields, acetate fermentation and H<sub>2</sub>/CO<sub>2</sub> reduction are the main production pathway of CH<sub>4</sub> (Sugimoto and Wada 1993, Conrad and Klose 1999). Notionally, more than 67% of the total CH<sub>4</sub> production is determined by methanogenesis that uses acetate (Conrad and Klose 1999). The results of the soil incubation experiment showed a consistent significant relationship between previous temperature and acetate concentrations, which improved CH<sub>4</sub> production.

Path analysis also showed that winter soil temperature variability had a positive influence on CH<sub>4</sub> emissions during the growing season. Winter warming affected CH<sub>4</sub> indirectly via impacts on DOC and NH<sub>4</sub><sup>+</sup>-N accumulation. Although methanogenesis has a higher temperature sensitivity than methanotrophs (Dunfield et al 1993), the warming winter may indirectly stress methanotrophs due to the lack of NH<sub>4</sub><sup>+</sup>-N. Some studies found that methanogenesis and CH<sub>4</sub> emissions were inhibited by N fertilizer, especially ammonium fertilizers (Banik et al 1996, Singh and Singh 1996). In addition to the field experiment (Krüger et al 2001), microcosm incubation (Eller and Frenzel 2001) supported that more NH<sub>4</sub><sup>+</sup>-N increased methanotrophic activity in rice paddy soil. Methanotrophic bacteria are nitrogen-hungry microorganisms (Anthony 1982), the demand for ammonium from methanotrophic bacteria restricts ammonium oxidation (Megraw and Knowles 1987). However, the mechanism by which ammonium stimulates CH<sub>4</sub> oxidation not only relieves the N limitation for methanotrophic bacteria growth but also oxidizes methane (Chan and Parkin 2001). In the incubation experiment, soil inorganic N was the only source after flooding, and the lower ammonium in the previous high-temperature treatment (figure 5(a)) suppressed CH<sub>4</sub> oxidation, which in turn stimulated CH<sub>4</sub> emissions. Although the field experiment had a large amount of nitrogen fertilizer applied for crop growth after flooding, the soil NH<sub>4</sub><sup>+</sup>-N still played an important role, which might reduce the competition between crops and methanotrophs. Our measurements were limited by the absence of microbial research, but the significant change in CH<sub>4</sub> fluxes suggests that future work needs to better capture the changes in soil microbial communities associated with C and N cycles in response to climate change. Some studies have found that microbial processes are more susceptible and may be key regulators of C and N cycles to global warming (Gubry-Rangin et al 2011, Durán et al 2013).

## 5. Conclusion

Winter warming significantly increased the contribution of rice paddies to CH<sub>4</sub> emissions during the subsequent growing season. The influence of global warming on these ecosystems is highly uncertain, as changes in soil carbon and nitrogen dynamics by soil temperature affect CH<sub>4</sub> fluxes in the growing season beyond the direct effects on winter processes. We show strong and clear links between winter warming and CH<sub>4</sub> emissions in the subsequent growing season for the first time. In our study area, the change in soil temperature may be more important than that in other winter climate conditions. Overall, our results suggest that winter climate change may be the key driver of CH<sub>4</sub> release from rice paddies in low-latitude regions and may increase uncertainties in climate predictions. When assessing the response of CH<sub>4</sub> emissions from paddy soil to global warming, special attention should be paid to the impact of seasonal differences in temperature rise. The effect of temperature change in winter fallow season on CH<sub>4</sub> emission from paddy fields should not be ignored. It indicates that the impact of climate warming on CH<sub>4</sub> emission from paddy soil may be higher than the current model prediction.

## Data availability statement

All data that support the findings of this study are included within the article (and any supplementary files).

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