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Responses of CO_2, N_2O and CH_4 fluxes between atmosphere and forest soil to changes in multiple environmental conditions

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Abstract

To investigate the effects of multiple environmental conditions on greenhouse gas (CO_2, N_2O, CH_4) fluxes, we transferred three soil monoliths from Masson pine forest (PF) or coniferous and broadleaved mixed forest (MF) at Jigongshan to corresponding forest type at Dinghushan. Greenhouse gas fluxes at the *in situ* (Jigongshan), transported and ambient (Dinghushan) soil monoliths were measured using static chambers. When the transported soil monoliths experienced the external environmental factors (temperature, precipitation and nitrogen deposition) at Dinghushan, its annual soil CO_2 emissions were 54% in PF and 60% in MF higher than those from the respective *in situ* treatment. Annual soil N_2O emissions were 45% in PF and 44% in MF higher than those from the respective *in situ* treatment. There were no significant differences in annual soil CO_2 or N_2O emissions between the transported and ambient treatments. However, annual CH_4 uptake by the transported soil monoliths in PF or MF was not significantly different from that at the respective *in situ* treatment, and was significantly lower than that at the respective ambient treatment. Therefore, external environmental factors were the major drivers of soil CO_2 and N_2O emissions, while soil was the dominant controller of soil CH_4 uptake. We further tested the results by developing simple empirical models using the observed fluxes of CO_2 and N_2O from the *in situ* treatment and found that the empirical models can explain about 90% for CO_2 and 40% for N_2O of the observed variations at the transported treatment. Results from this study suggest that the different responses of soil CO_2, N_2O, CH_4 fluxes to changes in multiple environmental conditions need to be considered in global change study.

Keywords: greenhouse gas, nitrogen deposition, soil moisture, soil monolith, soil temperature, subtropical forest

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Introduction

CO_2, N_2O, CH_4 are three major greenhouse gases in the atmosphere, and increases in the concentrations of these and other greenhouse gases are predicted to cause global warming that will have significant impact on the Earth's environment (Lashof & Ahuja, 1990). Previous studies have shown that forest soil is a source for CO_2 and N_2O, and a sink for CH_4 (Keller & Reiners, 1994; Kiese *et al*., 2003; Tang *et al*., 2006; Luo *et al*., 2012). The rates of soil CO_2 and N_2O emissions and CH_4 uptake are highly variables, depending on the key biophysical processes in the soil, such as root respiration, decomposition, microbial activities (Shaver *et al*., 2000; Davidson & Janssens, 2006; Wu *et al*., 2010a) and their responses to external environmental factors, such as soil temperature, moisture and so on.

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Over the last two decades, experiments along climate gradients or with environment modifications, such as soil warming, precipitation manipulation, nitrogen (N) addition, have been used to study the effects of different ecosystem processes or their responses to single or multiple environmental factors on the exchange rates of CO_2, N_2O and CH_4. More recently soil monoliths have been used as an experimental system to study the responses of soil CO_2 emission and species composition to multiple environmental conditions (Hart, 2006; Breeuwer *et al*., 2010). Many of these studies showed that altering temperature or changing in rainfall pattern (naturally or artificially) significantly changed soil emissions of CO_2 and N_2O or uptake of CH_4 (Peterjohn *et al*., 1994; Davidson *et al*., 2008; Deng *et al*., 2012).

The responses of ecosystem processes to changes in multiple environmental conditions can be very complex. For example, the responses of ecosystem net primary production to multifactor changes cannot be fully explained by the response to each individual factor

because of the strong interactive effects of different factors (Shaw *et al*., 2002; Luo *et al*., 2008). The effects of diurnal warming on soil respiration or ecosystem carbon exchange were not equal to the separate effects of day and night warming in a temperate steppe (Xia *et al*., 2009). However, studies of soil CO_2 emission to multiple environmental conditions found that response to temperature was by far the most dominant one (Edwards & Norby, 1998; Lin *et al*., 2001; Niinistö *et al*., 2004; Zhou *et al*., 2006). Soil CO_2 emission increased with temperature, largely independent of the changes of other factors. Previous experimental studies also found that soil temperature and moisture were good predictors of CO_2, N_2O and CH_4 fluxes at forest floor (Raich & Schlesinger, 1992; Keller & Reiners, 1994; Dobbie *et al*., 1999; Luo *et al*., 2012), which is the basis of many ecosystem models for simulating fluxes of CO_2, N_2O and CH_4 at forest floor. Some of those models were used to predict changes in soil CO_2, N_2O and CH_4 fluxes under future climate scenarios (Parton *et al*., 1996; Potter *et al*., 1996a, b; Del Grosso *et al*., 2000; Kiese *et al*., 2005; Hashimoto *et al*., 2011; Tian *et al*., 2011), only limited number of experiments have been carried out to test these predictions under changes in multiple environmental conditions in the field.

To study the responses of soil emissions of CO_2 or N_2O and uptake of CH_4 to changes in multiple environmental conditions, we transported intact cylindrical soil monoliths from Jigongshan to Dinghushan. Both sites are strongly influenced by the Asian monsoon and have similar seasonal variations in soil temperature and precipitation. Previous studies at the two sites found that soil temperature was the most dominant environmental factor influencing the seasonal variations in soil CO_2, N_2O and CH_4 fluxes (Tang *et al*., 2006; Zhang *et al*., 2008; Luan *et al*., 2012). Including soil moisture as a second independent variable in an empirical model would not significantly improve the accuracy by that model as compared with using soil temperature alone (Yan *et al*., 2009). This has yet to be tested in the field.

In this study, we measured the soil CO_2, N_2O and CH_4 fluxes at all soil monoliths at Jigongshan (*in situ* treatment) and Dinghushan (transported and ambient treatments) from October 2010 to September 2011. Data collected from the three treatments of the *in situ*, transported and ambient were analysed in this study. The differences between the *in situ* and transported treatments (ΔE) were considered to be caused by changes in external environmental factors (temperature, precipitation and N deposition) as the same soil was used. The differences between the transported and ambient treatments (ΔS) were considered to be caused by the differences in soil because they experienced the same external environmental factors, such as temperature, precipitation, N deposition and so on. The differences between the *in situ* and ambient treatments (ΔES) were considered to be caused by the differences in both the external environmental factors and soil. The objectives of this study are: (i) to quantify the relative effects of changes in external environmental factors (ΔE) and soil (ΔS) on the observed soil CO_2, N_2O and CH_4 fluxes; and (ii) if the effects of environmental changes on the fluxes are greater than soil, can we predict the fluxes under a different external environment using an empirical model developed from the observations at the *in situ* treatment?

Materials and methods

Site descriptions

The Nature Reserve of Jigongshan (31°46′–31°52′N, 114°01′–114°06′E) is located in southern Henan Province, central China with a total area of about 3000 ha on a hilly terrain. It is located within a transitional region from northern subtropical climate to warm temperate climate. The mean annual surface air temperature at the reserve is 15.3 °C with the highest and lowest monthly mean air temperatures being 27.5 °C in July and 1.9 °C in January respectively. The mean annual rainfall was 1108 mm. Two forest types, Masson pine forest (PF) and coniferous and broadleaved mixed forest (MF) are dominant in the region. The rock formations of Jigongshan are composed of migmatitic granite and gneiss belonging to Early Precambrian Period. The soil type belongs to the yellow–brown soil.

The Nature Reserve of Dinghushan (23°09′–23°12′N, 112°31′–112°34′E) is located in central Guangdong Province, southern China. The total area of the reserve is 1156 ha. The terrain is quite hilly with an altitude varying from 100 to 700 m in most areas. The region is characterized by a typical subtropical monsoon humid climate, with a mean annual temperature of 21.4 °C. The highest and lowest monthly mean air temperatures were 28.1 °C in July and 12.5 °C in January respectively. The mean annual rainfall was 1700 mm. Three forest types are dominant in the region: PF, MF and monsoon evergreen broadleaved forest, representing forest types at early, middle and late succession. The bedrocks of Dinghushan are sandstone and shale belonging to the Devonian Period. The predominant soil type is lateritic red earth, between the elevations of 400–500 m, followed by yellow earth, which is found between the elevations of 500–800 m.

The Transported soil monolith experiment

At the PF or MF at Jigongshan, we marked six circular ground blocks (diameter = 1 m) on surface soil under forest gaps, then carefully excavated a trench vertically just outside the marked circle to a depth of 1.2 m, and then removed sufficient amount of soil on one side just outside the circle for separating the base of the soil monolith from the soil underneath using a chain saw. Before the base separation, the soil monoliths were covered by an open cylindrical box made from Polyvinyl chlo-

ride (diameter = 1 m; depth = 1 m) to avoid disturbing the soil column. Three soil monoliths were removed and transported from Jigongshan to the corresponding forest type at Dinghushan. The remaining three were kept in the *in situ* (*in situ* treatment). In the PF or MF at Dinghushan site, we placed each of the three transported soil monoliths to a hole (diameter = 1.2 m; depth = 1 m) freshly dug under the forest gap (transported treatment), where we also obtained three ambient cylindrical soil monoliths covered by the same open cylindrical box, and then backfilled (ambient treatment).

Greenhouse gas fluxes measurements

Greenhouse gas fluxes at each of three soil monoliths in each of the three treatments were measured using a static chamber system. In total, we have 18 soil monoliths with three replicates for each of three treatments at two forest types. The system consisted of a circular base (diameter = 0.25 m) with an annular collar on which a cylindrical chamber with height of 0.30 m was placed. The circular base was permanently pushed 5 cm deep into each of soil blocks. The chamber was made from polyvinyl chloride with a small electric fan installed for air mixing. The sample tube was connected to the chamber through a hole on the chamber wall. During measurements, the chamber was sealed by filling water into the base's trough where the chamber sat. All soil blocks were established in April 2010. Measurements of greenhouse gas fluxes at soil monoliths were conducted from October 2010 to September 2011.

Gas samples were taken using a gastight syringe (100 ml) at 0, 15, 30, 45 min after chamber closure. Four gas samples at each soil block were collected between 9:00 and 11:00 hours, once per week for laboratory analysis. Samples were analysed for CO_2, CH_4 and N_2O concentrations using an HP4890D gas chromatograph (Agilent, Wilmington, DE, USA) equipped with flame ionization detectors (Wang & Wang, 2003). The rates of gas exchange were calculated from the rate of change in gas concentration within the chamber with time after chamber closure. For further details about the calculation, see Yan *et al.* (2006). Positive regression indicates an emission from soil to the atmosphere. Negative regression indicates a net uptake by soil from the atmosphere. Previous studies demonstrated that greenhouse gas fluxes measured from 09:00 to 11:00 hours were representative of the daily mean flux (Tang *et al.*, 2006). Monthly gas fluxes were estimated from four measurements within that month.

Measurements of environmental factors and soil physiochemical properties

Daily total rainfall and mean air temperature at 2 m above ground were obtained from the Jigongshan and Dinghushan weather stations. Soil temperature (Thermistor, TES-1310; TES Electrical Electronic Corp., Taipei, China) at 10 cm and moisture (ICT; ICT International, Armidale, NSW, Australia) at 5 cm below ground surface were monitored at each chamber while gas samples were collected. N deposition above the forest was measured by ion-exchange resin during the study period.

We used a 4.5 cm diameter stainless-steel corer to collect three soil samples (0–10 cm depth) from each of the soil monoliths in July 2010 and July 2011. The three soil samples were mixed, then divided into three portions for measuring fine root biomass (diameter ≤ 2 mm), extractable dissolved organic carbon (DOC) and mineral N (NH_4^+ and NO_3^-). Fine roots were separated by washing and sieving, then dried at 60 °C for 48 h and weighed (Cleveland & Townsend, 2006). After removing large roots, wood and litter, samples were passed through a 2-mm-mesh sieve. DOC was extracted with 1 M K_2SO_4 from soils. Extractable DOC in the K_2SO_4 extracts was analysed using a total carbon analyser (Shimadzu model TOC-500, Kyoto, Japan). Extractable NH_4^+ content was determined using the indophenol blue method, followed by colorimetric analysis. NO_3^- content was determined after cadmium reduction to NO_2-N, followed by sulphanilamide-NAD reaction.

Data analysis

Three-way ANOVAs were used to examine effects of treatment, forest type, year and their possible interactions on soil carbon ($R_{biomass}$ and DOC) and mineral N (NH_4^+ and NO_3^-). Two-way ANOVAs were used to examine effects of environmental condition (site or soil) and forest type on greenhouse gas fluxes from soil monoliths. One-way ANOVA with Tukey's HSD test was used to examine the differences in $R_{biomass}$, DOC, NH_4^+ and NO_3^- between the *in situ* and transported treatments. All statistical analyses were performed using SAS (version 9.1, Cary, NC, USA). The differences in the measured fluxes between the *in situ* and transported treatments represent the effects of different external environmental factors (ΔE), and the differences in the measured fluxes between the transported and ambient treatments represent the soil effects (ΔS). If ΔE > ΔS, external environmental factors are considered to be the major drivers of the fluxes at forest soil. If ΔE < ΔS, soil is the dominant factor to control the fluxes at forest soil.

Results

Rainfall, temperature and nitrogen deposition at Jigongshan and Dinghushan

Seasonal variations of monthly rainfall or mean air temperature were similar between Jigongshan and Dinghushan (see Fig. 1). Total rainfall from October 2010 to September 2011 was 724.1 mm at Jigongshan and 1203.2 mm at Dinghushan. Amount of rainfall during wet season (April–September) accounted for more than 80% of annual total rainfall at the both sites. Annual mean air temperature during the study period was 15.8 °C at Jigongshan and 22.2 °C at Dinghushan. The difference in the mean air temperature in summer between the two sites was much smaller than that in winter (Fig. 1). During the study period, the total N deposition (wet and dry deposition) was 19.7 ± 0.8 at

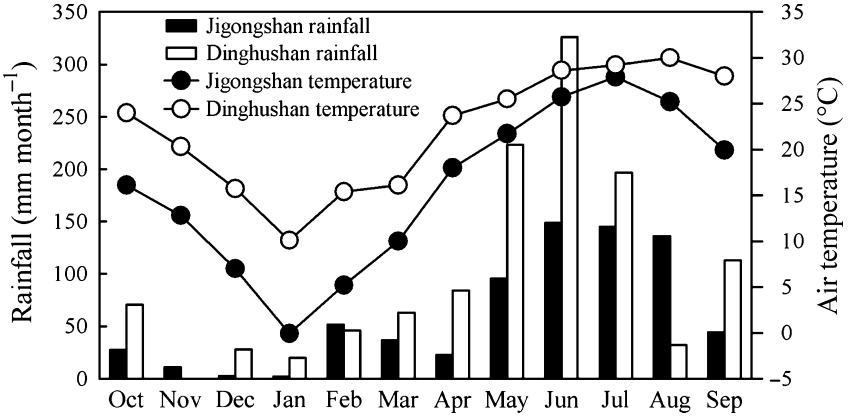

Fig. 1 Monthly rainfall (mm $month^{-1}$) and mean monthly air temperature (°C) over the study period (October 2010–September 2011) at Jigongshan or Dinghushan.

Jigongshan and 38.9 ± 2.3 kg ha^{-1} yr^{-1} at Dinghushan. N input in the form of NH_4^+ accounted for 71% of the total N deposition on average at Jigongshan, and only 56% at Dinghushan. Overall, the transported or ambient soil monoliths at Dinghushan experienced much warmer and wetter conditions, and higher N deposition than the *in situ* soil monoliths at Jigongshan.

Root biomass, DOC and mineral N in different treatments

Root biomass ($R_{biomass}$), DOC and total mineral N (NH_4^+ and NO_3^-) varied significantly ($P < 0.000$) among the *in situ*, transported and ambient treatments (Table 1). Both forest type ($P < 0.000$) and year ($P < 0.000$) had significant effects on $R_{biomass}$ and DOC. The difference in the amount of soil mineral N between PF and MF was significant in NH_4^+ ($P = 0.009$) but not significant in NO_3^- ($P = 0.207$). Over the period of measurements, the amount of NO_3^- ($P < 0.000$) but not NH_4^+ ($P = 0.125$) in soil increased significantly in all the 18 soil monoliths (Table S1). Results of ANOVA analysis showed that there was significant interaction between treatment and forest type on $R_{biomass}$ and DOC, but not for NH_4^+ or NO_3^-. In addition, no interaction was found between year and treatment, forest type or their combination on $R_{biomass}$, NH_4^+ and NO_3^- (Table 1).

About 1 year after the transported soil monoliths from Jigongshan experienced the environmental conditions at Dinghushan, $R_{biomass}$ did not change significantly in PF or MF. Extractable soil DOC increased significantly in PF, but decreased significantly in MF. Mineral N in the form of NO_3^- but not NH_4^+ in both forests increased significantly because of the high NO_3^- deposition at Dinghushan (Table S1). The measured $R_{biomass}$, DOC and soil mineral N in both the *in situ* and transported soil monoliths were quite variable and the differences in their mean values between those two treatments were not significant (Table S1). Therefore, the most differences in greenhouse gas fluxes between the *in situ* and transported treatments were likely to be caused by the differences in external environmental factors between Jigongshan and Dinghushan.

Seasonal variations of greenhouse gas fluxes at two forest types

The seasonal variations of greenhouse gas fluxes from the soil monoliths in each of the three treatments at two

Table 1 Results (*P*-value) of statistical analysis (three-way ANOVAs) on the effects of treatment (*in situ*, transported and ambient treatments), forest type (Masson pine forest and coniferous and broadleaved mixed forest), year (2010 and 2011) and their interactions on fine root biomass ($R_{biomass}$), soil extractable dissolved organic carbon (DOC) and soil mineral nitrogen (NH_4^+ and NO_3^-). The effect is significant only if $P < 0.05$

	Treatment	Forest type	Year	Treatment* Forest type	Treatment*Year	Forest type*Year	Treatment* Forest type*Year
$R_{biomass}$	0.000	0.000	0.000	0.001	0.444	0.194	0.736
DOC	0.000	0.000	0.000	0.001	0.010	0.014	0.005
NH_4^+	0.000	0.009	0.125	0.048	0.975	0.871	0.900
NO_3^-	0.000	0.207	0.00	0.270	0.011	0.862	0.800

forest types are shown in Fig. 2. Mean monthly soil CO_2 emission at all soil monoliths in the wet season was much higher than that for the dry season (Fig. 2) because of the wetter and warmer conditions in the wet season (Fig. 1). The amplitude of seasonal variation in soil CO_2 emission at MF was greater than that for PF. Similar to the difference in soil temperature between the two sites, mean monthly soil CO_2 emission from the *in situ* treatment at Jigongshan was much lower than that from the transported or ambient treatment at Dinghushan during the dry season, but it was quite similar during the wet season (Fig. 1 and 2). Therefore, the

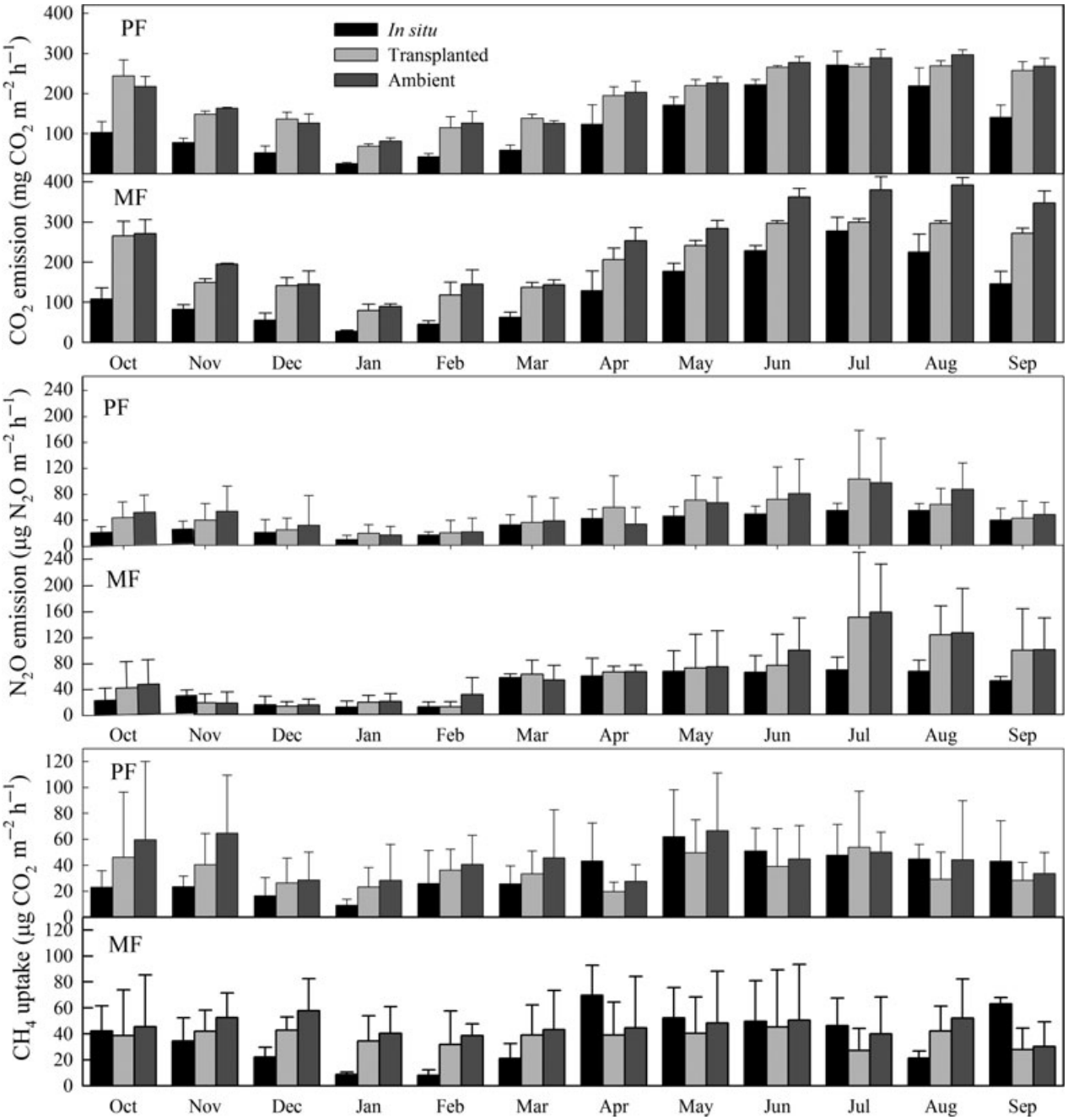

Fig. 2 Monthly mean soil CO_2 emission rate (mg CO_2 m^{-2} h^{-1}), soil N_2O emission rate (μg N_2O m^{-2} h^{-1}) or soil CH_4 uptake rate (μg CH_4 m^{-2} h^{-1}) at the *in situ* (Jigongshan), transplanted or ambient (Dinghushan) soil monoliths in Masson pine forest (PF), or coniferous and broadleaved mixed forest (MF) from October 2010 to September 2011. Number of samples in each treatment is 3 and number of measurements is 4 in each month. The error bar in the plot represents 1 SE of the mean of the four measurements in each month.

difference in the mean annual soil CO_2 emission between the *in situ* treatment and the transported or ambient treatment was mainly contributed by their difference during the dry season.

N_2O emission from the soil monoliths in all treatments varied seasonally, being greater in the wet season than in the dry season (Fig. 2). The seasonal variations in rainfall and temperature played an important role in the variation in soil N_2O emission between the wet and dry seasons. In PF, total soil N_2O emission during the wet season accounted for about 70%, 70% and 66% of annual total for the *in situ*, transported and ambient treatments, respectively. In MF, the wet season emission contributed about 72%, 78% and 77% to the annual total for the *in situ*, transported and ambient treatments, respectively.

The observed soil CH_4 uptake was quite variable in PF or MF (Fig. 2). Soil CH_4 uptake at the *in situ* treatment in the wet season was higher than that for the dry season. When the transported soil monoliths experienced environmental factors at Dinghushan, its CH_4 uptake was higher during the dry season but lower during the wet season than that during the same season at the *in situ* treatment. As a result, the seasonal variation in soil CH_4 uptake at the transported treatment was smaller than that at the *in situ* treatment. Our results showed that the seasonal variation in soil CH_4 uptake at the ambient treatment was quite weak, as found previously (Tang *et al.*, 2006).

Differences in greenhouse gas fluxes between in situ and transported treatments: the effect of external environmental factors

In PF, the annual mean rate of soil CO_2 emission from all measurements was 125.8 mg CO_2 m^{-2} h^{-1} at the *in situ* treatment and 193.7 mg CO_2 m^{-2} h^{-1} at the transported treatment. In MF, it was 130.4 mg CO_2 m^{-2} h^{-1} at the *in situ* treatment and 208.7 mg CO_2 m^{-2} h^{-1} at the transported treatment. Although soil CO_2 emission from each of the three treatments in PF was smaller than the corresponding treatment in MF (Fig. 3), no significant effects of forest type ($P = 0.476$) or its interaction with site ($P = 0.696$) were found on soil CO_2 emission (Table 2). However, the external environmental factors at Dinghushan, such high air temperature, significantly ($P < 0.000$) stimulated soil CO_2 emission. When the transported soil monoliths experienced the environmental factors at Dinghushan, the mean rate of soil CO_2 emission

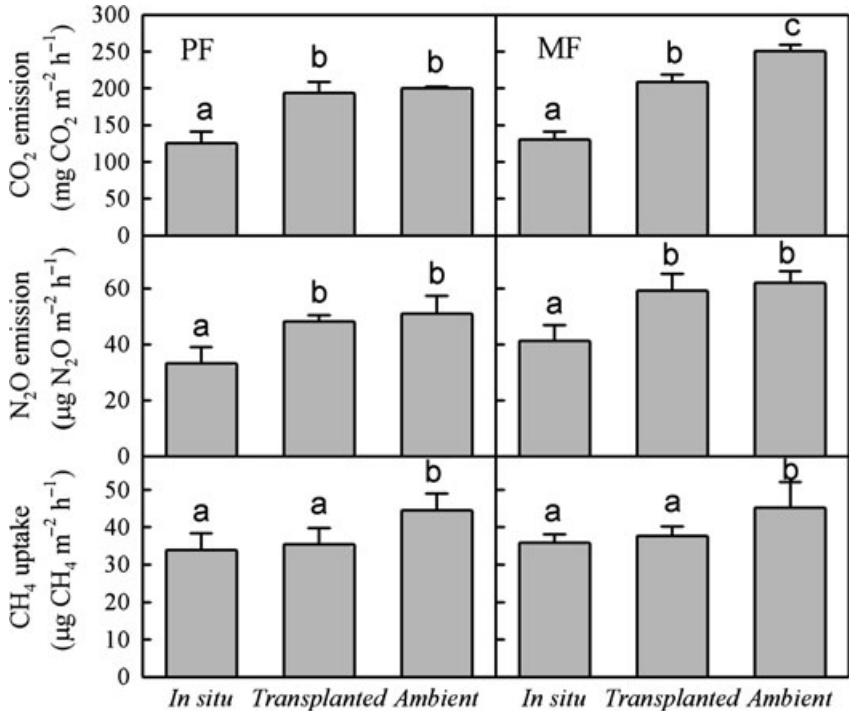

Fig. 3 Annual mean soil CO_2 emission rate (mg CO_2 m^{-2} h^{-1}) and soil N_2O emission rate (μg N_2O m^{-2} h^{-1}) or soil CH_4 uptake rate (μg CH_4 m^{-2} h^{-1}) at the *in situ* (Jigongshan), transplanted or ambient (Dinghushan) treatments in Masson pine forest (PF), or coniferous and broadleaved mixed forest (MF). The annual mean rate was estimated as the mean of 48 measurements from October 2010 to September 2011. The error bar represents 1 SE of the mean of measurements from all three soil monoliths in each of the three treatments in PF or MF. Different letters indicate significant differences at 5% level among treatments.

Table 2 Results (*P*-value) of two-way ANOVAs on the effects of site (Jigongshan and Dinghushan) and forest type (Masson pine forest and coniferous and broadleaved mixed forest) and their interactions on soil CO_2, N_2O or CH_4 fluxes between the *in situ* and transported treatments

Source of variance	Site	Forest type	Site*Forest type
CO_2	0.000	0.476	0.696
N_2O	0.006	0.061	0.753
CH_4	0.641	0.572	0.985

The effect is significant only if $P < 0.05$.

increased significantly, by 54% in PF and 60% in MF, as compared to the rates at the *in situ* treatment.

The mean rate of soil N_2O emission was 31.4 μg N_2O m^{-2} h^{-1} for the *in situ* treatment and 48.3 μg N_2O m^{-2} h^{-1} for the transported treatment in PF, and 37.1 μg N_2O m^{-2} h^{-1} for the *in situ* treatment and 59.3 μg N_2O m^{-2} h^{-1} for the transported treatment in MF (Fig. 3). The mean annual soil N_2O emission from each of the three treatments in PF was smaller than the same treatment in MF (Fig. 3). However, neither the effect of forest type nor the interaction of forest and site were statistically significant ($P = 0.061$ for forest, and $P = 0.753$ for the interaction between forest type and site). The effects of the external environmental factors on soil N_2O emission were significant (Table 2). Soil N_2O emission increased significantly ($P = 0.006$) after the transported soil monoliths experienced the environmental factors at Dinghushan, as compared with the observed soil N_2O emission from the *in situ* treatment at Jigongshan.

The mean annual soil CH_4 uptake was 33.8 μg CH_4 m^{-2} h^{-1} for the *in situ* treatment and 35.5 μg CH_4 m^{-2} h^{-1} for the transported treatment in PF (Fig. 3). Mean soil CH_4 uptake at MF was slightly higher than at PF, with 35.8 μg CH_4 m^{-2} h^{-1} for the *in situ* treatment and 37.6 μg CH_4 m^{-2} h^{-1} for the transported treatment at MF (Fig. 3). The difference was not statistically significant either between PF and MF ($P = 0.572$), or between the *in situ* and transported treatments ($P = 0.641$). In addition, no significant interactions between site and forest type ($P = 0.985$) were found on soil CH_4 uptake (Table 2).

Differences in greenhouse gas fluxes between transported and ambient treatments: the effect of soil

The rates of CO_2 and N_2O emissions at the transported treatment were slightly smaller than those for the corresponding ambient treatment in PF or MF (Fig. 3). Soil was found to have no significant effect on soil CO_2 or N_2O emission, as the rates of soil CO_2 emission ($P = 0.076$) or soil N_2O emission ($P = 0.538$) were not significantly different between the transported and ambient treatments (Table 3). However, the rates of CH_4 uptake at the transported treatment were 20–30% smaller than those for the corresponding ambient treatment in PF or MF (Fig. 3). Soil had significant effect ($P = 0.045$) on soil CH_4 uptake, but the effects of external environmental factors, such as temperature, precipitation, N deposition and so on were not significant (Table 2).

Comparison of the effect of forest type on the three gas fluxes at the same site (Dinghushan), the significant effect of forest type was found for soil CO_2 emission ($P = 0.024$) and soil N_2O emission ($P = 0.036$), but not for soil CH_4 uptake ($P = 0.695$). There was no significant interactive effect between soil and forest type on the observed CO_2, N_2O and CH_4 fluxes (Table 3).

Major driver of CO_2, N_2O and CH_4 fluxes at soil monoliths

Table 4 showed the differences in greenhouse gas fluxes from the soil monoliths between any two of the three treatments (*in situ*, transported and ambient). The results show that the external environmental factors were the main drivers of soil CO_2 or N_2O emission because the effects of external environmental factors (ΔE) were much greater than the effects of soils (ΔS) (Table 4). When the measurements were divided into wet season and dry season, we also found that ΔE in the wet season was greater than that in the dry season on soil CO_2 emission but smaller on soil N_2O emission (Table 4). However, soil had greater effect on annual soil CH_4 uptake than external environmental factors ($\Delta E < \Delta S$) (Table 4). Furthermore, the effects of external environmental factors on soil CH_4 uptake were positive in the wet season, and negative in the dry season (Table 4). As a result, the effects of external environmental factors on annual soil CH_4 uptake were small and statistically not significant.

Analysing the dependence of soil CO_2 or N_2O emissions from the *in sit*u treatment at Jigongshan on various

Table 3 Results (*P*-value) of two-way ANOVAs on the effects of soil (transported soil from Jigongshan and ambient soil at Dinghushan) and forest type (Masson pine forest and coniferous and broadleaved mixed forest) and their interactions on soil CO_2, N_2O or CH_4 fluxes between the transported and ambient treatments

Source of variance	Soil	Forest type	Soil*Forest type
CO_2	0.076	0.024	0.171
N_2O	0.538	0.036	0.997
CH_4	0.045	0.695	0.847

The effect is significant only if $P < 0.05$.

environmental factors, we found that soil CO_2 emission increased exponentially with soil temperature and soil N_2O emission increased linearly with soil temperature. An exponential model explains 91% ($P < 0.001$) of the temporal variations in soil CO_2 emission for PF and 83% ($P < 0.001$) for MF (Fig. 4). A linear model explains

Table 4 Effects of external environmental factors (ΔE) or soil (ΔS) on the observed fluxes of CO_2, N_2O or CH_4. Where ΔE is calculated from the differences in the measured fluxes between the *in situ* and transported treatments and ΔS from the differences in the measured fluxes between the transported and ambient treatments. ΔES is the combined effect of external environmental factors and soil (ΔES = ΔE + ΔS). All effects were calculated using the observed fluxes for the year, wet or dry season for Masson pine forest (PF) and coniferous and broadleaved mixed forest (MF)

		Annual mean			Wet season mean			Dry season mean		
Flux	Forest type	ΔE	ΔS	ΔES	ΔE	ΔS	ΔES	ΔE	ΔS	ΔES
CO_2 emission (mg CO_2 m^{-2} h^{-1})	PF	67.9	6.4	74.3	81.8	−1.7	80.1	54.2	14.5	68.7
	MF	78.3	42.1	120.4	85.0	16.4	101.4	71.7	67.8	139.5
N_2O emission (μg N_2O m^{-2} h^{-1})	PF	15.1	2.8	17.9	9.6	4.8	10.4	20.7	0.5	21.2
	MF	18.0	2.8	20.8	3.3	2.9	6.2	34.6	6.1	40.7
CH_4 uptake (μg CH_4 m^{-2} h^{-1})	PF	1.7	9.0	10.7	13.7	10.3	24.0	−12.0	7.9	−4.1
	MF	1.8	7.7	9.5	15.4	8.2	23.6	−13.3	7.2	−6.2

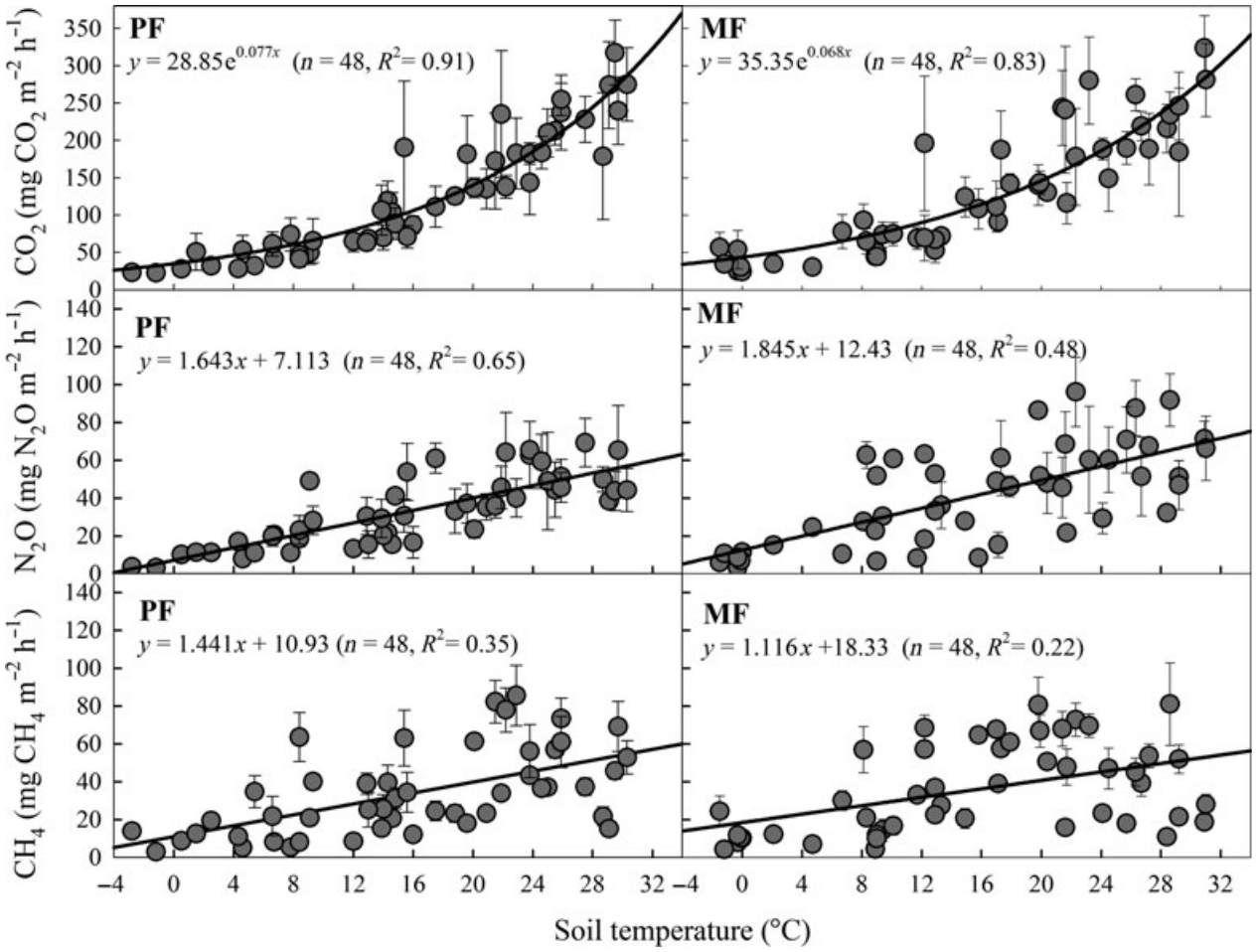

Fig. 4 Responses of soil CO_2 emission rate (mg CO_2 m^{-2} h^{-1}), soil N_2O emission rate (μg N_2O m^{-2} h^{-1}) or soil CH_4 uptake rate (μg CH_4 m^{-2} h^{-1}) to soil temperature for Masson pine forest (PF), or coniferous and broadleaved mixed forest (MF) at the *in situ* (Jigongshan) treatment. The best fit empirical equations are also shown for each plot. The error bar for each data point represents 1 SE of the mean of measurements from three soil monoliths in PF or MF.

65% ($P < 0.001$) of the temporal variations in soil N_2O emission from PF and 48% ($P < 0.001$) from MF (Fig. 4). Consistent with previous statistical analysis, we found the correlation between soil CH_4 uptake and soil temperature or any other (data not shown) environmental factors to be insignificant (Fig. 4).

Comparison of simple model prediction with observation

To confirm the dominant effect of environmental conditions on the observed soil CO_2 and N_2O emissions, we used the empirical relationships derived in the previous section from the observations at the *in situ* treatment to predict the CO_2 or N_2O fluxes from the transported treatment and then compared the predicted fluxes with the observed.

As shown in Fig. 5, all observed soil CO_2 emissions from the transported treatment at Dinghushan can be reliably predicted using the empirical model, as almost all data points lie within the 95% CI of model predictions at PF or MF. Soil temperature explains about 88% of variation in soil CO_2 emission in PF and 92% in MF. However, the model tends to underpredict the soil CO_2 emission observed at the transported treatment. At the annual scale, the predicted rate of soil CO_2 emission is about 6% lower for PF and 9% lower for MF than the estimated annual mean rate from the observations at the transported treatment.

As compared with the observed soil N_2O emissions from the transported treatment, the empirical model overestimates soil N_2O emission when the observed soil N_2O emission was low (<40 μg N_2O m^{-2} h^{-1}) or underestimates soil N_2O emission when the observed soil N_2O emission was high (>60 μg N_2O m^{-2} h^{-1}) (Fig. 6). The empirical model explains 36% of the variance of the observed N_2O emission from the transported treatment in PF and 39% in MF. As a result, the predicted seasonal soil N_2O emission is weaker than the observed at the transported treatment for both forest types. On average, the predicted annual soil N_2O emission is about 9% in PF and 8% in MF lower than those from the observations at the transported treatment.

Discussion

Response of soil CO_2 emission

The rate of CO_2 emission between soil and atmosphere depends on CO_2 production, transport and interactions between physical and biological processes in the soil. Numerous field studies across different forest types (Saiz *et al.*, 2007; Graf *et al.*, 2008; Wang *et al.*, 2010;

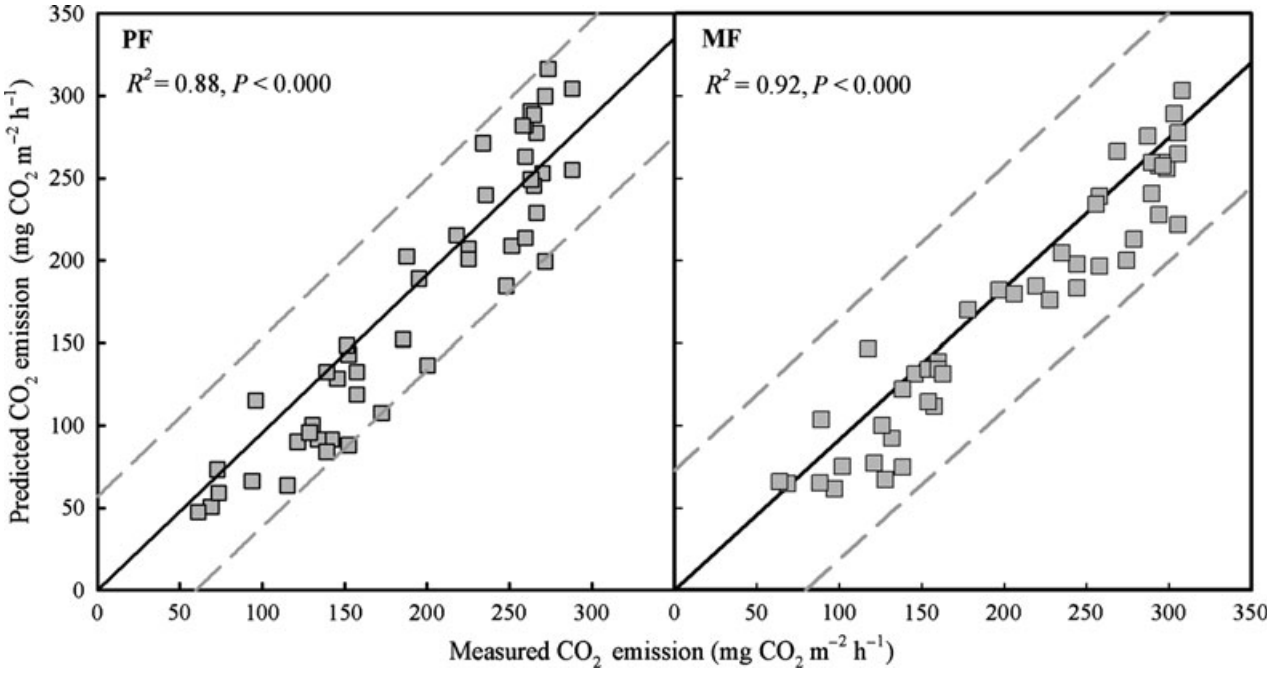

Fig. 5 Comparison of the predicted soil CO_2 emission rates (mg CO_2 m^{-2} h^{-1}) by the empirical model with the observed fluxes at the transported treatment. PF represents Masson pine forest and MF represents coniferous and broadleaved mixed forest. Solid line is a linear regression passing through origin. Ninety-five per cent CI of the empirical model predictions are indicated by the grey dash curves.

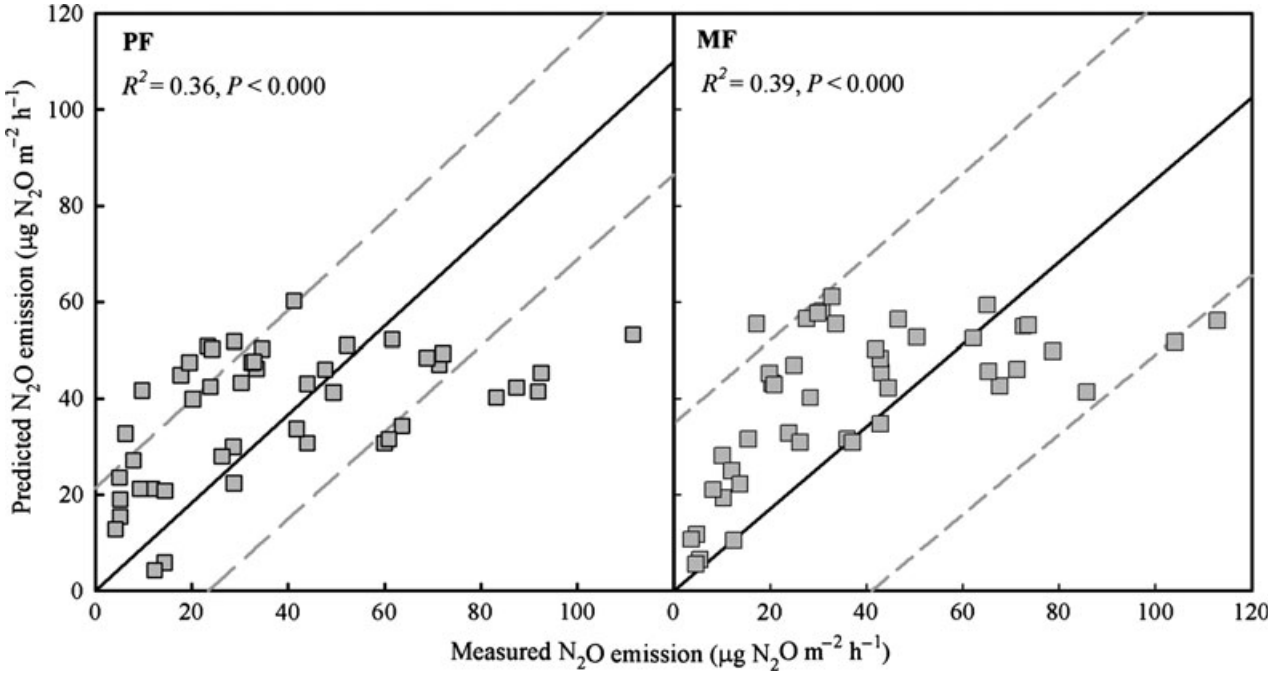

Fig. 6 Comparison of the predicted soil N_2O emission rates ($\mu g\ N_2O\ m^{-2}\ h^{-1}$) by the empirical model with the observed fluxes at the transported treatment. PF represents Masson pine forest and MF represents coniferous and broadleaved mixed forest. Solid line is a linear regression passing through origin. Ninety-five per cent CI of the model predictions are indicated by the grey dash curves.

Wu *et al.*, 2010b) showed a significant and positive correlation between soil temperature and CO_2 emission. In this study, soil temperature explains about 91% variation in soil CO_2 emission in PF and 83% in MF at Jigongshan. Therefore, soil temperature is the major driver of CO_2 emission from soil monoliths, as found previously in subtropical forests in China (Yan *et al.*, 2009).

The influence of soil moisture on CO_2 emission was more variable at our sites. In general, gas transport within the soil is not a significant limiting factor for soil CO_2 emission, because most emitted CO_2 is produced in top 10–20 cm soil that is quite porous (Borken *et al.*, 2002; Subke *et al.*, 2003; Elberling & Ladegaard-Pdersen, 2005). Severe drought can lower CO_2 production mainly by reducing the base rate (the coefficient of the exponential function), but not the temperature coefficient (the exponent of the exponential function) (Epron *et al.*, 2004; Davidson & Janssens, 2006). Because of a strong influence of Asian monsoon on the seasonal climate at both sites, soil moisture and temperature covaried within a year. A previous study in the PF and MF at Dinghushan also found that change in soil moisture was not an important factor influencing soil CO_2 emission (Yan *et al.*, 2009). Therefore, soil temperature alone can be used to predict soil CO_2 emission under different climate conditions (Fig. 5). At annual scale, the predicted soil CO_2 emission is slightly lower than that observed at the transported treatment. This may be related to the effect of environmental changes on soil nutrient supply. This is supported by the observed increase in $R_{biomass}$ and DOC when the soil monoliths were transported from Jigongshan to Dinghushan. Furthermore, the higher N deposition at Dinghushan also contributed to the underestimation of CO_2 emission by the empirical model derived from the observation at Jigongshan.

Response of soil N_2O emission

Previous studies found that the correlation between soil temperature and N_2O emission was strong and positive in temperate forests (Papen & Butterbach-Bahl, 1999; Schindlbacher *et al.*, 2004; Wu *et al.*, 2010a), but quite weak in tropical forests (Breuer *et al.*, 2000; Kiese & Butterbach-Bahl, 2002; Werner *et al.*, 2007). The weak correlation in the tropical forests probably resulted from small variation in seasonal soil temperature or the interactions between soil temperature and moisture. The effect of soil moisture on soil N_2O emission is rather complicated. Increasing soil moisture can increase soil microbial activities and therefore N_2O production. On the other hand, increased soil moisture under warm conditions, such as during wet seasons in the subtropical climate zone, can increase denitrification exponentially (Arah & Smith, 1989). Under highly

anaerobic conditions, most soil NO_3^- is lost as N_2 rather than N_2O, therefore soil N_2O emission may not increase with the increased soil moisture (Riley & Vitousek, 1995; Kiese & Butterbach-Bahl, 2002). At Jigongshan site, where climate was relatively cooler and drier than that at Dinghushan, the effects of soil moisture on soil N_2O emission were also weak. Soil temperature was the most dominant environmental factor on soil N_2O emission. Using dependence of soil temperature to predict soil CO_2 emission under Dinghushan climate conditions, the empirical model overestimated the observed soil CO_2 emissions when the observed soil CO_2 emission was low, and underestimated the observed soil CO_2 emissions when the observed was high (Fig. 5). As a result, the predicted annual soil N_2O emission agreed well with the observed at the transported treatment at Dinghushan.

Previous studies found that soil N_2O emission increased significantly with N addition for N-rich forests (Gundersen *et al.*, 1998; Gasche & Papen, 1999; Lohse & Matson, 2005; Zhang *et al.*, 2008), but did not change significantly for N-limited ecosystems (Magill *et al.*, 2000; Zhang *et al.*, 2008). Some evidence suggests that the carbon production at Dinghushan is phosphorus limited (Huang *et al.*, 2013). The high NO_3^- deposition at Dinghushan provided additional substrate for denitrification at the transported soil monoliths, and therefore increased the soil N_2O emission. Result from this study is consistent with the findings from other studies (Venterea *et al.*, 2003; Ambus & Robertson, 2006). That is soil inorganic N availability as a key factor controlling N_2O emission rate, as reported from previous studies in temperate or tropical forests (Bowden *et al.*, 1991; Sitaula *et al.*, 1995; Hall & Matson, 1999). However, the effect of soil inorganic N was not included in our model because soil samples were collected twice only from soil monoliths to avoid significant disturbance to the soil. Additional studies are needed to quantify the effect of soil mineral N including high N deposition on soil N_2O emission in subtropical forests.

Response of soil CH_4 uptake

Many factors can affect CH_4 uptake by soil (Barber *et al.*, 1988; Joabsson *et al.*, 1999; Joyce & Jewell, 2003; Baird *et al.*, 2004), such as soil temperature, carbon substrate, water regime, soil redox potential etc. (Segers, 1998; Wang *et al.*, 1999; Le Mer & Roger, 2001). Previous studies showed that soil CH_4 uptake increased with soil temperature at a temperate forest (Butterbach-Bahl *et al.*, 1998), and decreased with soil moisture in tropical or temperate forests (Castro *et al.*, 2000; Verchot *et al.*, 2000). Contrary to these previous studies, Hart (2006) found that soil CH_4 uptake was negatively correlated with soil temperature, but uncorrelated with soil moisture based on a soil transfer study. In this study, we did not find any significant difference in CH_4 uptake between the wet and dry seasons, or between the transported and ambient treatments. Our finding here is consistent with a previous study at Dinghushan (Tang *et al.*, 2006). The cause for the relative insensitive response of soil CH_4 uptake to environmental conditions probably resulted from the opposing effect of soil temperature and moisture on CH_4 uptake.

In PF or MF at Jigongshan, soil CH_4 uptake was greater in the wet season than in the dry season (Fig. 2). Two points should be noted here. First, average rainfall at Jigongshan was much lower than at Dinghushan (Fig. 1). Soil moisture in the wet season was often below the water-holding field capacity, therefore did not significantly affect the activities of CH_4 consuming microbes. Second, the difference in temperature between Jigongshan and Dinghushan was greater in the dry season than that in the wet season. Soil temperature at Jigongshan occasionally during the dry cold period fell below 0 °C, which decreased the activities of CH_4-consuming microbes in forest soil. Therefore, the relative difference of CH_4 uptake between the wet and dry seasons at Jigongshan was much larger than that at Dinghushan. This has not been found before at Jigongshan.

The rate of CH_4 uptake at the transported soil monoliths was also quite insensitive to changes in multiple environmental factors including high N deposition at Dinghushan. N fertilization studies in temperate forests (Steudler *et al.*, 1989) or grasslands (Mosier *et al.*, 1991) showed that soil CH_4 uptake was sensitive to rates of soil net mineralization and nitrification. An increase in soil NH_4^+ concentration can weaken CH_4 uptake, as the increased soil NH_4^+ concentration can inhibit the activity of CH_4-oxidizing bacteria (Whittenbury *et al.*, 1970; O'Neill & Wilkinson, 1977). Although an increase in net N mineralization was found at the transported treatment, this increase was likely caused by the increased nitrification. We did not find a significant increase in available soil NH_4^+ at the transported treatment, as compared with at the *in situ* treatment (Table S1). Therefore, a measurable but small increase in CH_4 uptake rate was found at the transported soil monoliths (Fig. 4).

The models developed by Potter *et al.* (1996a, b) and Del Grosso *et al.* (2000) have been widely used to simulate soil CH_4 uptake. The performance of their models is quite consistent with our finding that environmental factors were not major controllers of soil CH_4 uptake. Soil processes, such as substrate dynamics and variations in other biogeochemical processes were the major

factors influencing soil CH_4 uptake at the two forest types. This study therefore suggested that soil parameters relating to soil biophysical or chemical properties should be considered during the future development of soil CH_4 uptake model.

The projected climate change by the end of this century will significantly alter soil temperature and moisture and soil carbon and nitrogen cycling, therefore soil emissions of CO_2 and N_2O. This may not the case for soil CH_4 uptake based on our study here. Our results suggest that the responses of soil CO_2 and N_2O emissions and CH_4 uptake to the projected future climate change can be quite different because of different controlling factors. A simple model can be used to predict the response of annual soil CO_2 emission and its seasonal variation at Jigongshan under a different climate conditions quite accurately. The predicted annual soil N_2O emission using our empirical model is also quite accurate. Differences in soils between the two sites were identified as the major contributing factors for the observed variation in soil CH_4 uptake among different treatments in two forest types. Therefore, additional studies are urgently needed on the processes of CH_4 consumption and substrate dynamics and on their dependence on different biophysical properties.

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Supporting Information

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

Table S1. Values of fine root biomass ($R_{biomass}$, g dry matter m^{-2}), soil extractable dissolved organic carbon (DOC, mg C kg^{-1}) and soil mineral nitrogen (NH_4^+ and NO_3^-, mg N kg^{-1}) in the 18 soil monoliths at Jigongshan (*in situ*), transported, and Dinghushan (ambient). Soil samples (0–10 cm depth) were collected in July 2010 and July 2011 respectively. Sn represents the soil sample from soil monolith 1, 2 or 3 in each treatment by two forest types (PF represents Masson pine forest and MF represents coniferous and broadleaved mixed forest).