Humid Subtropical Forests Constitute a Net Methane Source: A Catchment-Scale Study

Longfei Yu1,2, Jing Zhu1,3, Xiaoshan Zhang4, Zhangwei Wang4, Peter Dörsch1,2, and Jan Mulder1,4

1Faculty of Environmental Sciences and Natural Resource Management, Norwegian University of Life Sciences, Aas, Norway; 2Now at: Laboratory for Air Pollution/Environmental Technology, Empa, Swiss Federal Laboratories for Materials Science and Technology, Duebendorf, Switzerland; 3Department of Environment and Resources, Guangxi Normal University, Guilin, China; 4Research Center for Eco-Environmental Sciences, Chinese Academy of Sciences, Beijing, China

Abstract
Commonly, well-drained forest soils are net methane (CH4) sinks, whereas poorly drained soils in groundwater discharge zones could contribute significant CH4 emissions. Climate change is projected to bring more summer precipitation extremes to sub-tropics, which may affect forest CH4 balance. Chinese forests often have a hilly topography with well-drained hillslopes and pronounced groundwater discharge zones. Although different landscape elements are likely to have different source and sink functions for CH4, the climatic influence on CH4 budget at the catchment scale remains poorly studied. Here, we measured CH4 fluxes over three years along a topographic gradient in a subtropical forested catchment in SW China. CH4 fluxes exhibited a clear spatial pattern indicating moderate CH4 uptake or emission from the well-drained soils on the hillslope (−5.8 to +1.0 kg CH4·C·ha−1·year−1) and significant CH4 emission from the wetter soils in the groundwater discharge zone (94.3 to 479.5 kg CH4·C·ha−1·year−1). Despite its small area contribution to the catchment (0.6%), the groundwater discharge zone emitted substantial amounts of CH4 in monsoonal summers, affecting the whole-catchment budget. Hillslope soils showed weaker CH4 uptake or even turned into a small CH4 source under wet climatic conditions. Estimates of catchment-scale CH4 budgets indicate that sub-tropical forest catchments can tip from a net CH4 sink in drier years to a net CH4 source in wetter years, highlighting the importance of interannual climate variability. Our findings suggest that subtropical forests under projected climate change could contribute a net CH4 source with consequences for the regional CH4 balance.

Plain Language Summary
Forest soils are commonly believed to uptake methane from the atmosphere, which is an important process to counteract the growth of atmospheric methane level. However, sparsely distributed wet soils in forests could contribute transient but large methane emissions to atmosphere. Under climate change, methane emission from wet soils may significantly change the role of forest ecosystems in regional methane budgets. Therefore, for three years, we measured soil-atmosphere exchange of methane in upper drier and lower wetter soils at a subtropical forest in Southwest China. Under the influence of Eastern Asian monsoon, we observed strong methane emissions from the wetter soils of the forest during summers, despite that these areas only account for a small part of the forest. In a wet year, methane uptake in drier soils decreased and methane emission in wetter soils increased. Taking into account the contributions of both wetter and drier soils, estimates of annual methane budgets suggest that the studied subtropical forest contributes a net emission of methane to the atmosphere in a wet year. This work highlights an overlooked source of methane for the sub-tropical region and provides insights into the future role of forest ecosystem in greenhouse gas budgets under climate change.

1. Introduction
Methane (CH4) is an important greenhouse gas, and its global warming potential is 28 times that of carbon dioxide (Ciais et al., 2013). Despite the flattening trend in the late 1990s, atmospheric CH4 concentrations resumed to increase at a rate of 5.7 ppb/year after 2005 (Dlugokencky et al., 2003; Nisbet et al., 2016). At a global scale, CH4 sources comprise natural wetlands, agriculture (ruminants, animal manure, and rice paddies), vegetation, waste, fossil fuel, and biomass burning (Carmichael et al., 2014; Kirschke et al., 2013; Tian et al., 2016). The largest sink of CH4 is its chemical oxidation by OH radicals in the troposphere,
while biological uptake in soils (one third attributed to forest soils) is the second most important sink (Dutaur & Verchot, 2007; Kirschke et al., 2013; Saunois et al., 2016). However, the sink strength of soils for CH₄ varies greatly (Kirschke et al., 2013) and most soils can turn into transient CH₄ sources under warm and wet conditions (Bridgham et al., 2013; Melton et al., 2013), making estimates of global CH₄ budgets highly uncertain.

Regardless of the common understanding of forest soils as net CH₄ sink, CH₄ budgets of forest soils are balanced by two antagonistic biogeochemical processes, CH₄ oxidation, and production (Le Mer & Roger, 2001). Microbial CH₄ oxidation (methanotrophy) occurs in aerobic environments in soils (Conrad, 1996). Hence, methanotrophic activity is often regulated by temperature, moisture, and soil porosity, all of which affect CH₄ and O₂ diffusivity (Le Mer & Roger, 2001; Smith et al., 2003). Nutrient availability may be an additional factor affecting methanotrophy in forest soils (Kolb, 2009). For example, increased N input has been shown to stimulate CH₄ consumption in nitrogen (N)-limited forest soils (Goldman et al., 1995; Veldkamp et al., 2013). However, several studies have pointed out that N enrichment in forest soils inhibits soil CH₄ uptake (Aronson & Helliker, 2010; Liu & Greaver, 2009; Steudler et al., 1989). At the global scale, the rising atmospheric N deposition is likely to suppress the CH₄ sink strength (Zhuang et al., 2013). Conventional methanotrophs are believed to prefer soil pH ~ 7 (Le Mer & Roger, 2001), although the evidence of CH₄ uptake has been reported for a number of acidic forest soils, characterized with “high-affinity” methanotrophs (Kolb et al., 2005).

Methanogenesis (CH₄ production), on the other hand, is responsible for net CH₄ emission observed in wet forest soils (Dutaur & Verchot, 2007). Methanogenesis occurs under anaerobic conditions through microbial reduction of acetate or H₂/CO₂ (Conrad, 1996). Jungkunst et al. (2008) found a clear relationship between groundwater level and CH₄ emission in a temperate forest soil in Germany. Also, soil organic matter content may influence microbial CH₄ production by supplying substrate for methanogenesis and low redox potential in the environment (Le Mer & Roger, 2001). Recent works from boreal forests indicate that carbon-rich soils respond significantly to climate change and can act as hotspots of CH₄ emission during the wet season (Lohila et al., 2016; Shoemaker et al., 2014). By contrast, the presence of nitrate, ferric iron and sulfate is likely to inhibit methanogenesis, due to a competition for acetate and electrons with the corresponding reducers (Chidthaisong & Conrad, 2000).

Whether forest soils act as a net source or sink of CH₄ depends on a number of edaphic factors as described above, which affect both methane consumption and production. The spatial variability of these edaphic factors, in turn, is largely controlled by topography, which also affects hydrological conditions, nutrient transport, and vegetation type (Creed et al., 2013). Several studies have reported topographically regulated patterns of CH₄ fluxes in forest soils (Itoh et al., 2009; Kaiser et al., 2018; Pitz et al., 2018; Sakabe et al., 2016; Warner et al., 2018), mainly driven by topographically related differences in hydrological conditions (Kaisser et al., 2018). For instance, net uptake of CH₄ is often found on hillslopes, which is the dominant landscape element in forests and generally characterized by well-drained soils (Kaiser et al., 2018; Warner et al., 2018). In valley bottoms of forests, which are often water-saturated (e.g., groundwater discharge zone or riparian zone), significant net emissions have been reported (Itoh et al., 2009; O’Connell et al., 2018; Sakabe et al., 2016). Hydrological transport also mediates spatial distribution of soil nutrients which may affect CH₄ fluxes. Warner et al. (2018) identified hotspots of CH₄ uptake at the transitional zone between the hillslope and the valley bottom, where lateral inputs of organic matter, clay particles, and litter accumulated. Possibly, the underlying mechanism is that fine clays provide surface area for methanotrophs to grow and coarse particles promote air diffusion into soil (Saari et al., 1997).

Under global climate change, the thawing of permafrost at high latitudes and high elevations (e.g., on the Tibet-Qinghai plateau) as well as increasing precipitation in the tropics are likely to expand the extent of global natural wetlands, contributing to future increase of atmospheric CH₄ (Wei & Wang, 2016; Zhang et al., 2017). Sparsely distributed CH₄ sources, including wetlands and intermittently water-saturated soils in forested catchments, are commonly overlooked in global modeling estimates of CH₄ budgets (Bridgham et al., 2013; Melton et al., 2013; Zhang et al., 2017). Itoh et al. (2009) and Sakabe et al. (2016) reported that temperate forest soils in warm-humid monsoonal summers in Japan emit significant amounts of CH₄. They also found that wet-season CH₄ emissions to determine the interannual variability of watershed CH₄ budgets. In the monsoonal subtropics and tropics, soil hydrology and thus diffusive
conditions and nutrient availability change rapidly due to the variable volume and frequency of episodic rain events, but the influence of these fluctuating conditions on CH$_4$ exchange is rarely investigated. Most recently, O’Connell et al. (2018) recognized the importance of wet-dry cycles on CH$_4$ cycling in three topographical zones in a Puerto Rican rainforest. They found that post-drought CH$_4$ emission largely offset the CH$_4$ sink during drought, indicating a strong need for multiyear studies investigating climate-driven CH$_4$ cycling patterns. Also, projected increases in precipitation due to global climate change may substantially reduce the CH$_4$ sink in upland forest soils, as indicated by long-term records of CH$_4$ fluxes in two U.S. temperature forests (Ni & Groffman, 2018).

Southern Chinese forests, affected by the East Asian monsoon, are likely to experience increasing air temperature (Yin et al., 2018) and more frequent precipitation extremes (Liu et al., 2014; Xiao et al., 2016) in response to climate change. In addition, increasing atmospheric N input has led to common N saturation in subtropical forests of southern China (Larssen et al., 2011). These changes may weaken CH$_4$ uptake and hence the role of subtropical-tropical forests as a regional CH$_4$ sink (Liu & Greaver, 2009). Previous studies in this region have mostly reported negative net CH$_4$ fluxes from nonmanaged soils (Fang et al., 2009; Tang et al., 2006; Zhang et al., 2008), except for one at an N-saturated subtropical forest (Yu et al., 2017). However, the coarse sampling frequency (monthly) and the short-term observation (<2 years) as reported by Yu et al. (2017) did not allow quantification of episodic CH$_4$ fluxes in monsoonal summers and their interannual variation. In addition, few, if any, studies have focused on the topographic distribution of CH$_4$ fluxes and its influence on the ecosystem CH$_4$ budgets (Fang et al., 2009). These uncertainties in existing field observations have largely restricted nationwide estimates of the CH$_4$ budgets for Chinese subtropical forest soils (Wang et al., 2014).

In the present study, we quantify CH$_4$ fluxes weekly to biweekly in a subtropical, N-saturated forested catchment (Tieshanping, TSP) in SW China over a 3-year period, including wet and dry summers. The catchment mainly consists of hillslopes with well-drained soils, where interflow over the argic horizon is laterally transferred to a small area in the valley bottom (groundwater discharge zone), resulting in water saturation following intensive rain episodes (Zhu et al., 2013). Sampling was conducted along a topographic gradient at four landscape elements, including hillslope, foot of the hillslope, valley bottom, and groundwater discharge zone. The spatiotemporal patterns of net CH$_4$ fluxes were assessed using edaphic and climatic parameters. We hypothesize that (1) well-drained soils on the hillslopes contribute a small CH$_4$ sink or source, similar to the findings at TSP forest by Yu et al. (2017); (2) the wetter soils in the valley bottom and groundwater discharge zone contribute substantial CH$_4$ emissions, especially during monsoonal summers; (3) whole-catchment CH$_4$ budgets of the forested catchment at TSP are strongly influenced by CH$_4$ emissions from the groundwater discharge zone in wet summers, thus acting as a net CH$_4$ source.

2. Materials and Methods

2.1. Site Description

TSP, a 16.2-ha subtropical forest catchment located about 25 km northeast of Chongqing City, SW China, is covered with a secondary mixed coniferous-broadleaf forest, dominated by Masson pine (Pinus massoniana). TSP has a mean annual temperature of 18.2 °C, a mean annual precipitation of 1,028 mm (Chen & Mulder, 2007), and is under the influence of the East Asian monsoon. Intensive precipitation events occur in summer (June to August; Figure 1). The TSP forest receives 40–60 kg N·ha$^{-1}$·year$^{-1}$ N in throughfall which has caused significant N leaching and soil acidification (Huang et al., 2015; Yu et al., 2017).

The TSP catchment is mainly composed of hillslopes, characterized by well-drained soils (Haplic Acrisol; WRB, 2006; Zhu et al., 2013). Water interflow over the argic horizon (which has a high clay content typical for Acrisols) on the hillslope is laterally discharged into the terraced valley bottom of the catchment, where soils are mainly Cambisols (WRB, 2006) with low hydraulic conductivity. Hence, rain episodes often result in water saturation in the valley bottom, in particular, in its outflow area (Sørbotten et al., 2017; Yu et al., 2016; Zhu et al., 2013). For the present study, we categorized the upper part of the valley as “valley bottom” and the lower part in the outflow area as “groundwater discharge zone.” The differentiation is based on the distinct difference in soil moisture (Figure 1).
2.2. Experimental Design and Sample Collection

In this study, we selected a 4.2-ha subcatchment that is categorized into four landscapes elements as hillslope, foot of hillslope, valley bottom, and groundwater discharge zone, following a topographic gradient (Yu et al., 2016). Our field observations covered three full years (September to August) of 2009–2010, 2012–2013, and 2013–2014.

From July 2009 to October 2010, we monitored CH$_4$ fluxes and soil water chemistry at plots similar with the previous projects at TSP (Yu et al., 2016; Zhu et al., 2013). Observations were made at five plots along a transect on the hillslope (T1–T5), one at the foot of the hillslope (B1), three in the valley bottom (B2–B4), and two in the groundwater discharge zone (B5–B6; Figure S1 in the supporting information). The order of the plot numbers is consistent with the hydrological flow path within the catchment. In the warm-humid seasons (April to September), gas and soil water samples were collected at weekly intervals, while the sampling frequency was reduced to biweekly during the cool-dry season. Soil temperature and moisture at 10-cm depth were monitored on the hillslope (T3) and at the foot of the hillslope (B1) since October 2009. Depth of the groundwater table was measured in piezometer tubes, using a measuring tape equipped with an electrical circuit and light, on a daily basis at plots B1–B6 during the same period (Zhu et al., 2013). Total organic carbon (TOC) from the top layers (0–5 cm) of the soils is available from Muzamil (2014). Soil bulk density and dissolved organic carbon (DOC) were obtained from Sørbotten (2011) and Gundersen (2012), respectively.

From August 2012 to September 2014, soil-atmosphere exchange of CH$_4$, soil water chemistry, as well as soil temperature and moisture were determined at fewer plots (plot T1 at the top of hillslope, plot B1 at the foot of
hillslope, plot B2 in the valley bottom, and plot B6 in the groundwater discharge zone). The sampling frequency was weekly throughout these years.

Soil-atmosphere gas exchange was measured in triplicate at each plot with static chambers (30-cm diameter and 30 cm in height; Zhu et al., 2013). Upon sampling, the vented stainless-steel static chambers were deployed on permanently installed frames (stainless-steel) which were water sealed. We collected four 20-ml air samples with a syringe 1, 5, 15, and 30 min after chamber deployment. The samples were injected into 12-ml preevacuated vials crimp sealed with butyl septa (Chromacol, UK), resulting in ~400 hPa over pressure to prevent contamination from ambient air during transport and storage. Flux measurements were mostly conducted between 9 a.m. and 12 a.m., which should represent daily mean fluxes as suggested by Tang et al. (2006). Soil water from T1–T5 and B1 plots was collected in triplicates by ceramic lysimeters (P80; Staatliche Porzellanmanufaktur, Berlin) installed at 5-cm soil depth. For B2–B6, we used triplicate Macrorhizon soil moisture samplers (Rhizophere Research Products, the Netherlands) installed at 30-cm depths. Water samples were kept at 4 °C during transport and storage.

In 2009–2010, soil temperature and moisture at 10-cm depth were measured at plots T3 and B1 by permanently installed time-domain reflectometer probes (Hydra Probe, Stevens Water Monitoring System, USA) with a data logger (Campbell CR200, USA). In 2012–2014, they were measured at all the investigated plots using a hand-held time-domain reflectometer (Hydraprobe; Stevens Water Monitoring System, USA). Throughout the study period, air temperature and precipitation data were obtained from a meteorological station (WeatherHawk 232, USA) located about 1.5 km from the TSP catchment. Due to data logger failure, air temperature data were not available during November 2013 to June 2014.

### 2.3. Chemical Analyses and Data Calculation

Gas samples were measured for CH$_4$ concentrations using a gas chromatograph coupled with a flame ionization detector (Agilent GC-7890A, USA). Exchange rates between soil and atmosphere were calculated from the change of gas mixing ratios over time by linear or polynomial regression.

Soil pH (H$_2$O) was measured with pH electrode (Orion SA720, ThermoFisher, USA), after suspending 10-g dry soil into 50-ml deionized water. To determine exchangeable ammonium (NH$_4^+$) and nitrate (NO$_3^-$), we kept the soils frozen after sampling and extracted the soils after thawing (equivalent to 10-g dry weight) in the laboratory, using 50 ml of 2-M KCl. After filtration of the extracts, the inorganic N concentrations were determined using Flow Injection Analysis (San++, Skalar, the Netherlands). The concentrations of NH$_4^+$ and NO$_3^-$ in soil water were analyzed by ion chromatography (DX-120 for cations and DX-500 for anions).

Soil water-filled pore space (WFPS) was calculated from the measured volumetric soil moisture (VM, cm$^3$/cm$^3$), soil bulk density (BD, g/cm$^3$; Zhu et al., 2013) and soil particle density (PD, 2.65 g/cm$^3$; Linn & Doran, 1984) as

\[
WFPS (\%) = \frac{VM}{(1-BD/PD) \times 100} \tag{1}
\]

### 2.4. Catchment CH$_4$ Budget Estimation

Annual cumulative CH$_4$ fluxes for each landscape element were estimated by linear interpolation, multiplying average measured CH$_4$ fluxes at two sampling dates with time. This approach assumes that our weekly-biweekly measurements are representative of mean fluxes during the period between two nearest sampling days. Uncertainty was estimated based on flux measurements in replicated plots in each landscape element. To upscale the fluxes to the whole catchment, we estimated the areal contributions of the different landscape elements within the TSP catchment based on a digital elevation model. The border of the 4.2-ha catchment has been defined previously by Zhu et al. (2013), also shown in the contour map (Figure S1). Areal contributions were estimated to be 96% for hillslope, 1.8% for foot of hillslope, 1.6% for valley bottom, and 0.6% for groundwater discharge zone (Table 1). Whole-catchment CH$_4$ budgets for different years were then computed based on weighted averages of cumulative annual fluxes from the four landscape elements (Table 1).
### Table 1

| Annual CH₄ budget | Hillslope (96%)ᵃ | Foot of hillslope (1.8%)ᵇ | Valley bottom (1.6%)ᵇ | Groundwater discharge zone (0.6%)ᵇ | Sum by upscaling |
|-------------------|------------------|---------------------------|----------------------|----------------------------------|------------------|
| Year              |                  |                           |                      |                                  |                  |
| 2009–2010         | 1.0 ± 0.5ᵇ       | –1.1 ± 0.5ᵇ               | 21.0 ± 9.8ᵇ          | 479.5 ± 130.9ᵇ                   | 4.2 ± 0.9ᵇ       |
| 2012–2013         | –1.3 ± 0.5ᵇ      | –0.6 ± 0.7ᵇ               | –0.8 ± 1.0ᵇ          | 349.9 ± 105.6ᵇ                   | 0.8 ± 0.8ᵇ       |
| 2013–2014         | –1.7 ± 0.7ᵇ      | –5.8 ± 0.8ᵇ               | 4.6 ± 3.3ᵇ           | 94.3 ± 28.6ᵇ                     | –1.1 ± 0.7**ᵇ    |

ᵃThe percentages in brackets indicate the area contribution by each landscape element. ᵇDifferent remarks (* and **) indicate significant differences of CH₄ fluxes among years at each landscape element (p<0.05).

### 2.5. Statistical Analyses

Statistical analyses were performed with R 3.3.1 (R Core Team, 2016). All data were tested for normality (Kolmogorov-Smirnov’s test) and homoscedasticity (Levene’s test) before further analysis. If not normally distributed, the data were normalized by logarithmic, square root, or reciprocal transformation. To test spatial difference in CH₄ fluxes, we applied linear mixed-effect models to the time-series dataset. In the linear mixed-effect model, plots/landscape elements were considered as fixed effects while sampling time and replicates within plots were included as random effects. Interannual and seasonal comparison of CH₄ fluxes were tested with one-way analysis of variance. Principal component analysis (PCA) was used to examine the relationship between soil factors (pH, WFPS, temperature, NH₄⁺, and NO₃⁻ concentrations in soil water) and CH₄ fluxes. Pearson correlation was applied to further examine the factors influencing CH₄ consumption and emission, respectively. Significance levels were set to p < 0.05, if not specified otherwise.

### 3. Results

#### 3.1. Climatic Conditions, Soil Temperature, and Soil Moisture

Highest temperature and precipitation were recorded from June to August (Figure 1). Annual precipitation at TSP in 2009 and 2010 was higher than in 2012 and 2013, but lower than in 2014 (Figures 1 and S2). If only comparing summer precipitation (June to August; Figure S2), 2009 and 2010 ranked the first and second highest. In 2009, 74% of annual precipitation occurred in the three summer months, mainly due to frequent large precipitation events (Figure 1; Zhu et al., 2013). By contrast, summer precipitation in 2014 (318 mm) was the second lowest despite having the highest annual precipitation.

Soil WFPS was significantly higher in 2009–2010 than in the other periods (Figure 1). In August 2012 and 2013, WFPS on the hillslope and at the foot of the hillslope fell below 20%, indicating relatively dry summers. Along the hydrological continuum, WFPS increased significantly from the hillslope to the valley bottom and the groundwater discharge zone. In the groundwater discharge zone, soil WFPS reached 100% during occasional flooding in summers. Similar to air temperature, soil temperature was highest in summers (Figure 1). Summing up the observed climatic factors, we identified 2009–2010 as wetter years.

#### 3.2. Soil Properties, Soil Water Chemistry, and Groundwater Table

Surface soils at TSP are acidic, with soil pH increasing from ~4.0 on the hillslope to ~5.0 in the groundwater discharge zone (Figure 2b). The bulk density of the surface soil is greatest in the valley bottom (B3) and smallest at the foot of the hillslope (B1; Figure 2c). Along the plots in the valley bottom and groundwater discharge zone, average groundwater table increases gradually from ~130 to ~25 cm (Figure 2d). Soil TOC contents at 0- to 5-cm depths were generally similar across all plots, in a range of 20 to 45 mg/g (Figure 2e).

The DOC concentration in soil water ranged from 8 to 15 mg/L on the hillslope and at the foot of the hillslope and decreased significantly to values <1 mg/L in the valley bottom and in the groundwater discharge zone (Figure 2f). Similarly, concentrations of NH₄⁺ and NO₃⁻ in soil KCl-extracts (October 2009) were generally smaller in the valley bottom and groundwater discharge zone than on the hillslope (Figures 2g and 2h). In 2012–2014, mean inorganic N concentrations in soil water (Figure S3) showed a decrease along the hydrological continuum similar to that observed during 2009–2010.
3.3. Spatial and Temporal Patterns of CH\textsubscript{4} Flux

During the wetter period of 2009–2010, positive CH\textsubscript{4} fluxes at the upper part of the hillslope (T1–T4) indicated net CH\textsubscript{4} production, while negative fluxes from the soils at the lower part (T5) and the foot of hillslope (B1) indicated net CH\textsubscript{4} consumption (Figures 2a and S4). These fluxes were generally smaller than 20 μg C·m\textsuperscript{-2}·hr\textsuperscript{-1}. Net CH\textsubscript{4} emission significantly increased from the lower part of the hillslope to the valley bottom (B2–B4) and reached highest rates in the groundwater discharge zone (B5 and B6), with mean fluxes up to 12,000 μg C·m\textsuperscript{-2}·hr\textsuperscript{-1}.

A similar spatial pattern of CH\textsubscript{4} fluxes was found during the drier period of 2012–2014, with moderate net emissions on the hillslope, moderate net uptake at the foot the hillslope and significant CH\textsubscript{4}
emissions in the valley bottom and the groundwater discharge zone (Figures 3 and 4). Mean CH$_4$ fluxes including all seasons throughout the study period were 0 ± 35, -24 ± 56, 122 ± 483, and 7,000 ± 11,016 μg C·m$^{-2}$·hr$^{-1}$ for hillslope, foot of hillslope, valley bottom, and groundwater discharge zone, respectively.

There was no consistent seasonal pattern of CH$_4$ fluxes on the hillslope (Figures 4, 5, and S4). In 2009, net CH$_4$ emission was only found in winter. In 2010 and 2012, hillslope soils showed net emission of CH$_4$ in the warm seasons and net consumption in the cool seasons (Figure 5). At the foot of the hillslope, the warm-season observations indicated mainly a net CH$_4$ source in 2009–2010 and a net sink in 2012–2014. In the cool seasons (except winter 2012), the foot of the hillslope acted as a net CH$_4$ sink (Figure 5). In the valley bottom and the groundwater discharge zone, we observed significant CH$_4$ emissions during summer and autumn compared to spring and winter (Figures 4, 5, and S4). CH$_4$ emissions were episodic and highly variable, with rates ranging from 0 to 60,000 μg C·m$^{-2}$·hr$^{-1}$. CH$_4$ emission rates in the warm seasons were higher by several folds in 2009–2010 than in 2012–2014. In the valley bottom, moderate CH$_4$ uptake (<50 μg C·m$^{-2}$·hr$^{-1}$) occurred during the cool seasons.

3.4. Relationship Between CH$_4$ Flux and Edaphic Factors

In the PCA score plot, principle component 1 significantly separates landscape elements along the catchment (45.5% explained variance; 2012–2014 data; Figure 6). This is confirmed by the biplots of CH$_4$ flux against WFPS (Figure 7), suggesting topographic control on CH$_4$ flux along the hydrological continuum in the catchment. The loading plot shows positive correlation of soil pH and WFPS with CH$_4$ flux and negative correlation of NO$_3^-$ and NH$_4^+$ concentrations with CH$_4$ flux. By contrast, soil temperature contributed to the spread along the second component that explained 19.2% of the variance.

Pearson correlation test was applied to data sets with positive (net emission) and negative (net uptake) CH$_4$ fluxes, respectively. For the scenario of CH$_4$ emission, we found significant correlation between all soil factors and CH$_4$ flux, except for soil temperature (Table S1). This is consistent with the PCA results. For the scenario of CH$_4$ consumption, CH$_4$ flux seemed to have no clear correlation with any of the soil factors (Table S2).
3.5. Catchment-Scale Estimation of CH$_4$ Budget

Within the TSP catchment, the groundwater discharge zone acted as a significant CH$_4$ source, with significantly larger emissions in 2009–2010 and 2012–2013 than in 2013–2014 (Table 1). Soils in the groundwater discharge zone emitted annually 94 to 480 kg CH$_4$-C/ha. In the valley bottom, soils were net CH$_4$ sources in 2009–2010 and 2013–2014, but their annual emissions per ha were 20 times smaller than in the groundwater discharge zone. In 2012–2013, the valley bottom soils became a small net CH$_4$ sink of 0.8 kg CH$_4$-C/ha. The foot of the hillslope was a permanent moderate CH$_4$ sink, being largest in 2013–2014 (5.8 kg CH$_4$-C/ha). Annual net CH$_4$ fluxes were smallest on the hillslope, with net emission in 2009–2010 and net uptake in 2012–2013 and 2013–2014.

Accounting for the areal coverage of the different landscape elements, which is dominated by hillslopes, catchment-scale CH$_4$ budgets indicate that the forested catchment at TSP was a net CH$_4$ source during wetter years (4.2 and 0.8 kg CH$_4$-C/ha in 2009–2010 and 2012–2013, respectively; Table 1), whereas in the drier year (2013–2014), the catchment acted as a moderate sink of 1.1 kg CH$_4$-C/ha.

4. Discussion

The spatial variability of CH$_4$ emissions in forests has been found to be highly dependent on topographic position, which governs soil moisture content and nutrient availability (Creed et al., 2013; Kaiser et al., 2018; Warner et al., 2018; Zhu et al., 2013). Our observations over a 3-year period show that well-drained
soils on the hillslope at TSP forest constitute a small net sink or source for CH$_4$ on an annual basis, while wetter soils in the valley bottom and the groundwater discharge zone act as significant CH$_4$ sources (Figures 2a and 3 and Table 1). A pronounced spatial pattern of CH$_4$ fluxes was also confirmed by the PCA, which clearly separated landscape elements along the first component (Figure 6).

![Figure 5](image1)

**Figure 5.** Seasonal mean CH$_4$ fluxes from four landscape elements. Red boxes identify warm seasons Error bars refer to 1 SE. March to May refers to Spring, June to August refers to Summer, September to November refers to Autumn, and December to February refers to Winter.

![Figure 6](image2)

**Figure 6.** Principal component analysis for data from 2012–2014, showing plot scores (left) and loading of soil variables relative to CH$_4$ fluxes (right). WFPS = water-filled pore space.
Significant net CH$_4$ emissions, mostly found in the valley bottom and the groundwater discharge zone (Figure 7 and Table S1), were positively correlated with soil water content, suggesting that anaerobic condition supports CH$_4$ production by methanogens at a rate exceeding the CH$_4$ oxidation capacity of the surface soils (Conrad, 1996; Le Mer & Roger, 2001). This suggests a dominant role of lower landscape positions in the catchment for net CH$_4$ production, similar to what has been found for wetlands and riparian zones (Jungkunst et al., 2008; Kaiser et al., 2018; MacDonald et al., 1998). The much higher CH$_4$ emission in the groundwater discharge zone than in the valley bottom (Figures 2a, 3, and 4) could be attributed to differences in anaerobic soil volume controlled by soil WFPS (Figure 1) and groundwater table (Figures 2d and S5). Yet as net CH$_4$ fluxes are controlled by both CH$_4$ oxidation and production (Conrad, 2002), the smaller CH$_4$ emissions in the valley bottom may also indicate a greater role of CH$_4$ oxidation there, as supported by high uptake rates in the drier period 2012–2013. An alternative explanation for the lower CH$_4$ emission in the valley bottom may be the inhibition of methanogenesis by other electron acceptors such as NO$_3^−$ and SO$_4^{2−}$ (Conrad, 2002; Le Mer & Roger, 2001; Veldkamp et al., 2013). Along the TSP catchment, the concentrations of NO$_3^−$ and SO$_4^{2−}$ in soil remain high in the valley bottom (NO$_3^−$; Figures 2h and S3) until significant denitrification (Yu et al., 2016) and sulfate reduction (Yu, Si, et al., 2019) take place in the groundwater discharge zone.

Due to the limited spatial extent of water-saturated forest soils, their contribution to the global CH$_4$ budget for wetlands is often overlooked (Bridgham et al., 2013; Kirschke et al., 2013). Recent studies have reported that CH$_4$ emission in riparian soils could affect forest CH$_4$ budgets significantly (Itoh et al., 2009; Kaiser et al., 2018; Sakabe et al., 2016; Warner et al., 2018). At TSP forest, soils in the groundwater discharge zone emit on average 7,000 μgC m$^{-2}$·hr$^{-1}$ (Figure 3), which is within the range of global averages for wetland CH$_4$ emissions (Turetsky et al., 2014). However, this CH$_4$ emission is higher than the values reported for riparian soils in temperate (Itoh et al., 2009; Kaiser et al., 2018; Warner et al., 2018) and tropical forests (O’Connell et al., 2018). This may be related to the high groundwater tables during monsoonal summer at our site (Figure 2d). In addition, rapid shift between wet and dry conditions as indicated by fluctuations of groundwater tables at TSP forest (Zhu et al., 2013) is likely to play a role on significant CH$_4$ emissions (O’Connell et al., 2018). On the other hand, Segers (1998) suggested that organic matter is a major limiting factor for methanogenesis in anaerobic conditions, as it supplies substrate for CH$_4$ production (acetate or CO$_2$/H$_2$) via degradation and, initially, consumption of other electron acceptors which competes with CH$_4$ production. Previously, Muzamil (2014) reported TOC levels in top soils of the groundwater discharge zone comparable to those on the hillslope (Figure 2e). Since the groundwater discharge zone at TSP receives both seepage water from the valley bottom (upstream) and from interflow from the Acrisols on the surrounding hillslopes (Yu, Mulder, et al., 2019) and because of the large area ratio between the hillslope and groundwater discharge zone in the TSP catchment (160:1), substantial amounts of DOC are expected.
to be laterally transported from the surrounding hillslopes to the groundwater discharge zone (Gunderson,
2012), especially in the rainy seasons. The low DOC concentration in the groundwater discharge zone
seems to contradict with our assumption (Figure 2f; Gunderson, 2012), but it may indicate a rapid decomposition
of DOC in the valley bottom and the groundwater discharge zone. This is expected to drive reductive processes,
as recently shown by the strong denitrification activity in the valley bottom and groundwater discharge zone,
which is indicated by the sharp increase in natural abundance of $^{15}$N and $^{18}$O of NO$_3^-$ (Yu et al.,
2016).

Although well-drained forest soils are commonly considered net CH$_4$ sinks (Dutaur & Verchot, 2007), we
detected periods of net CH$_4$ emissions in the hillslope soils (Figures 1 and 4 and Table 1). During periods
of net CH$_4$ uptake, rates were rather small (15 μg C·m$^{-2}$·hr$^{-1}$ on average; Figures 4 and 5) compared to those
commonly reported for subtropical-tropical forests (Fang et al., 2009; Tang et al., 2006; Werner et al., 2006) or
the nationwide average CH$_4$ uptake by soils in China (Wang et al., 2014). One possible explanation is that in
the aerobic soils on the hillslope (Figure 1), CH$_4$ oxidation is compensated by CH$_4$ production at the same
time, especially during monsoonal summers. Recent studies have proved that methanogens can be active
and contribute to CH$_4$ production in aerated soils (Angel et al., 2012; Angle et al., 2017). von Fischer and
Hedin (2007) proposed that the development of anaerobic “microsites” in soil supports methanogenesis in
aerobic soils. However, under East Asian monsoon, studies at two temperate Japanese forests reported
consistent net sinks of CH$_4$ in the upper dry soils (Itoh et al., 2009; Sakabe et al., 2016). More likely, the small
net CH$_4$ uptake rate found for TSP could point to poor methanotrophic activity. First, this can be attributed
to low soil pH on the hillslope (~4). Hütsch et al. (1994) found that CH$_4$ oxidation significantly declined with
decreasing pH in unmanaged forest soils. Second, N enrichment in forest soil has been found to suppress CH$_4$
uptake (Liu & Greaver, 2009). The forested catchment at TSP receives up to 60 kg N·ha$^{-1}$·year$^{-1}$ from
the atmosphere, resulting in severe N saturation (Huang et al., 2015). Recently, Yu et al. (2017) found
that decreased inorganic N concentration in hillslope soils at TSP, in response to phosphorus addition,
resulted in increased CH$_4$ uptake rates. This was explained by the elimination of N inhibition effects
on methanotrophs after phosphorus addition stimulated N assimilation by the ecosystem. Other N
manipulation studies also demonstrated that aggravated N enrichment could restrict CH$_4$ uptake
(Zhang et al., 2008; Zheng et al., 2016).

At the foot of the hillslope, which is the transitional point between the hillslope and the flattened valley for
the TSP catchment, we found higher net CH$_4$ uptake rates than on the hillslope (Figures 2a and 3). Soil bulk
density at the foot of hillslope was smallest along the catchment (Figure 2c). This could promote CH$_4$
odxidation, as diffusivity of atmospheric CH$_4$ into the soil is one of the major factors determining methano-
trophic activity (Smith et al., 2003). Another difference between the hillslope and the foot of hillslope is soil
pH (Figures 2b and S2). Although methanotrophs tolerate a wide pH range, they are signi-
cantly inhibited under extreme acidity (pH < 4) (Czepiel et al., 1995; Hütsch et al., 1996). Soil pH increases from ~3.5 on the
hillslope to ~4 at the foot of the hillslope, possibly supporting methanotrophic activity in the latter position.
Other studies have also found hotspots of CO$_2$ emission and CH$_4$ uptake at transitional positions between
the upper hillside and valley bottom, where CH$_4$ oxidation is likely to be promoted with lateral inputs of
organic matters and clay from the uplands (Creed et al., 2013; Warner et al., 2018).

The CH$_4$ fluxes observed at TSP were highly episodic (Figure 4). The importance of climatic influence on
CH$_4$ emission in the TSP catchment is reflected by the distinct seasonal pattern shown for the valley bottom
and the groundwater discharge zone, with significant CH$_4$ emissions in warm-humid summers and lower
values in winters (Figures 4 and 5). This finding is supported by the significant positive correlation between
CH$_4$ fluxes and soil WFPS (Figure 7 and Table S1). However, the CH$_4$ fluxes were only weakly correlated
with soil temperature (Figure 6 and Table S1), which is different from the significant effect found in other
studies from wetlands (Conrad, 2002; MacDonald et al., 1998). This may be due to the high mean soil
temperature in the hot subtropical summers at TSP (Figure 1), which appears to limit CH$_4$ production to
a lesser extent than soil water content. At TSP, the negative CH$_4$ fluxes were not correlated significantly
to soil temperature/WFPS (Table S2). For a temperate Japanese forested catchment, Itoh et al. (2009)
reported a similarly nonsignificant relationship between climatic factors and CH$_4$ fluxes in the warm
season. These authors attributed the lack of correlation to a combined effect by increasing CH$_4$ oxidation
and production with increasing temperature. This explanation could also apply to TSP for all landscape ele-
ments except for the groundwater discharge zone, where CH$_4$ production clearly dominates. Le Mer and
Roger (2001) also suggested that CH$_4$ oxidation in soil could be less sensitive to temperature than CH$_4$ production. King and Adamsen (1992) discovered that CH$_4$ oxidation in soil cores from a coniferous forest showed negligible response to temperature changes within the range of 19–38 °C, close to the variations of soil temperature at TSP (Figure 1). At soil WFPS below 30%, a positive correlation was found between WFPS and net CH$_4$ uptake rate (Figure S6). Previous studies have found a similar range of optimum soil moisture content for CH$_4$ oxidation, possibly determined by the trade-off between methanotrophic growth and CH$_4$/O$_2$ diffusion (Czepiel et al., 1995; Dijkstra et al., 2013).

The strong influence of soil moisture on CH$_4$ emission (Figure 7) translates into an interannual CH$_4$ flux pattern (Figures 4 and 5). Based on cumulative fluxes and areal contributions of each landscape elements, we estimated catchment-scale net annual CH$_4$ budgets, showing that the TSP forested catchment was a net CH$_4$ source (0.8–4.2 kg CH$_4$-C/ha) during wet years and a net CH$_4$ sink (1.1 kg CH$_4$-C/ha) during dry years (Table 1). The switch between CH$_4$ source and sink functions for the whole catchment is primarily sensitive to CH$_4$ fluxes from the groundwater discharge zone, despite its small areal contribution (0.6%). Hence, the accuracy of CH$_4$ flux estimates for the whole catchment depends primarily on sampling frequency and replicate measurements of CH$_4$ fluxes in the groundwater discharge zone, in addition to a precise estimate of its areal contributions (Sakabe et al., 2016). The catchment-scale assessment and upscaling as done for TSP in this study is of relevance for the subtropical region of South China at large, where topography and landscape elements are similar to that found at TSP (Yu, Mulder, et al., 2019). Hillslopes, which account for 96% of the total catchment area, played a secondary role in determining the interannual variability of whole-catchment CH$_4$ budgets (Table 1). A recently reported long-term study in two temperate forests in Maine, USA, found a dramatic decline in forest soil CH$_4$ uptake throughout the past three decades, presumably due to increased precipitation (Ni & Groffman, 2018). In the wetter years 2009–2010, hillslope soils even turned into a net CH$_4$ source, although this contribution to CH$_4$ emission is small compared with upland carbon-rich soils from a boreal forest during a wet year (Lohila et al., 2016). Our findings indicate the vulnerability of subtropical forests to become net CH$_4$ sources under future climate change. It is therefore strongly recommended that interannual variability of CH$_4$ fluxes in subtropical forests under monsoonal climate should be taken into consideration when estimating ecosystem-scale CH$_4$ budgets.

5. Conclusion

Multiyear observations of CH$_4$ fluxes at the TSP forested catchment in South China revealed pronounced topographic patterns of soil-atmosphere CH$_4$ exchange. While small fluctuating CH$_4$ fluxes at the well-drained hillslope and foot of hillslope indicated a balance between moderate CH$_4$ uptake and production, significant CH$_4$ emissions were found in the wetter valley bottom and water-saturated groundwater discharge zone. In wet summers, increased net CH$_4$ emission was even observed in well-drained hillslope soils. The seasonal patterns of CH$_4$ fluxes mainly seen for the valley bottom and the groundwater discharge zone reflected a strong response of CH$_4$ production to increasing precipitation and consequently in soil moisture content, whereas the relationship between CH$_4$ flux and temperature seemed to be obscured by the generally high temperature in the warm subtropics. Based on annual cumulative fluxes and areal contribution of landscape elements, we show that the TSP catchment acts as a net CH$_4$ sink in drier years and as a net CH$_4$ source in wetter years. Such interannual variations in the CH$_4$ source/sink function is largely attributed to the contribution of summer emissions in the groundwater discharge zone, even though its area only occupies a small proportion of the catchment. Under global climate change, Subtropical China receives increasing precipitation extremes in summers (Liu et al., 2014; Xiao et al., 2016). Therefore, we expect that future environmental change may further weaken the role of southern Chinese forests as a CH$_4$ sink, and turn them into a regionally significant CH$_4$ source which should not be overlooked.

References

Angel, R., Claus, P., & Conrad, R. (2012). Methanogenic archaea are globally ubiquitous in aerated soils and become active under wet anoxic conditions. The ISME Journal, 6, 847–862. https://doi.org/10.1038/ismej.2011.141

Angle, J., Morin, T. H., Solden, L. M., Narrowe, A. B., Smith, G. J., Horton, M. A., et al. (2017). Methanogenesis in oxygenated soils is a substantial fraction of wetland methane emissions. Nature Communications, 8(1), 1567. https://doi.org/10.1038/s41467-017-0153-4

Aronson, E. L., & Helliker, B. R. (2010). Methane flux in non-wetland soils in response to nitrogen addition: A meta-analysis. Ecology, 91(11), 3242–3251. https://doi.org/10.1890/09-2185.1
Global Biogeochemical Cycles

Biology and Fertility of Soils

Le Mer, J., & Roger, P. (2001). Production, oxidation, emission and consumption of methane by soils: A review. *Soil Biology and Biochemistry*, 33(1), 37–38. https://doi.org/10.1016/S0038-0717(00)00067-9

Dijkstra, F. A., Morgan, J. A., Follett, R. F., & Lecain, D. R. (2013). Climate change reduces the net sink of CH4. *Global Change Biology*, 19(2), 571–583. https://doi.org/10.1111/gcb.12061

Jungkunst, H. F., Flessa, H., Scherber, C., & Fiedler, S. (2008). Groundwater level controls CO2 emission in forest soils. *Soil Biology and Biochemistry*, 40(8), 2372–2381. https://doi.org/10.1016/j.soilbio.2008.02.016

Hütsch, B., Webster, C., & Powlson, D. (1994). Methane oxidation in soil as affected by land use, soil pH and N fertilization. *Soil Biology and Biochemistry*, 26(12), 1613–1622. https://doi.org/10.1016/0038-0717(94)90313-1

Kolb, S. (2009). The quest for atmospheric methane oxidizers in forest soils. *Environmental Microbiology Reports*, 1(5), 336–346. https://doi.org/10.1111/j.1758-2229.2009.00047.x

Kolb, S., Nien, E., Dunfield, P. F., & Conrad, R. (2005). Abundance and activity of uncultured methanotrophic bacteria involved in the consumption of atmospheric methane in two forest soils. *Environmental Microbiology*, 7(8), 1150–1161. https://doi.org/10.1111/j.1462-2920.2005.00791.x

Larsen, T., Duan, L., & Mulder, I. (2011). Deposition and leaching of sulfur, nitrogen and calcium in four forested catchments in China: Implications for acidification. *Environmental Science & Technology*, 45(4), 1192–1198. https://doi.org/10.1021/es103426p

Le Mer, J., & Roger, P. (2001). Production, oxidation, emission and consumption of methane by soils: A review. *European Journal of Soil Biology*, 37(1), 1–10.

Linn, D. M., & Doran, J. W. (1984). Effect of water-filled pore space on carbon dioxide and nitrous oxide production in tilled and nontilled soils. *Soil Science Society of America Journal*, 48(6), 1267–1272. https://doi.org/10.2136/sssaj1984.03615995004800012x

Liu, L., & Greaver, T. L. (2009). A review of nitrogen enrichment effects on three biogenic GHGs: The CO2 sink may be largely offset by stimulated N2O and CH4 emission. *Ecology Letters*, 12(10), 1103–1117. https://doi.org/10.1111/j.1461-0266.2009.01351.x

Liu, M., Xu, X., Sun, A. Y., Wang, K., Liu, W., & Zhang, X. (2014). Is southwestern China experiencing more frequent precipitation extremes? *Environmental Research Letters*, 9(6), 064002. https://doi.org/10.1088/1748-9326/9/6/064002

Lohila, A., Aalto, T., Aurela, M., Hatakka, J., Tuovinen, J. P., Kilkki, J., et al. (2016). Large contribution of boreal upland forest soils to a catchment-scale CH4 balance in a wet year. *Geophysical Research Letters*, 43, 2946–2953. https://doi.org/10.1002/2016GL067718

MacDonald, J. A., Fowler, D., Hargreaves, K. J., Skiba, U., Leith, I. D., & Murray, M. B. (1998). Methane emission rates from a northern wetland; Response to temperature, water table and transport. *Atmospheric Environment*, 32(19), 3219–3227. https://doi.org/10.1016/S1352-2310(97)00464-0

MacDonald, J. A., Fowler, D., Skiba, U., Leith, I. D., & Murray, M. B. (1998). Methane emission rates from a northern wetland; Response to temperature, water table and transport. *Atmospheric Environment*, 32(19), 3219–3227. https://doi.org/10.1016/S1352-2310(97)00464-0
Melton, J. R., Melton, J. R., Hodson, E. L., Poulter, B., Ringeval, B., Sparnh, R., et al. (2013). Present state of global wetland extent and wetland methane modeling: Methodology of a model inter-comparison project (WETCHIMP). Geoscientific Model Development, 6(3), 617–641. https://doi.org/10.5194/gmd-6-617-2013

Muzamil, B. (2014). Abundance of functional groups of nitrogen transforming microorganisms potentially involved in N₂O emissions from a subtropical forested watershed in China, Master Thesis. Nor. Univsity Life Sci.

Ni, X., & Groffman, P. M. (2018). Declines in methane uptake in forest soils. Proceedings of the National Academy of Sciences, 115(34), 8587–8590. https://doi.org/10.1073/pnas.1807377115

Nisbet, E. G., Bonnet, S., Hernández, N., Martínez-Pérez, A. M., Nieto-Cid, M., Álvarez-Salgado, X. A., et al. (2016). Rising atmospheric methane: 2007–2014 growth and isotopic shift. Global Biogeochemical Cycles, 30, 952–961. https://doi.org/10.1002/2015GB005326

O’Connell, C. S., Ruan, L., & Silver, W. L. (2018). Drought drives rapid shifts in tropical rainfall soil biogeochemistry and greenhouse gas emissions. Nature Communications, 9(1), 1348. https://doi.org/10.1038/s41467-018-03352-3

Pitz, S. L., Megonigal, J. P., Chang, C. H., & Szlavecz, K. (2018). Methane fluxes from tree stems and soils along a habitat gradient. Biogeochemistry, 137(3), 307–320. https://doi.org/10.1007/s10533-017-0409-3

Saari, A., Martikainen, P. J., Fern, A., Ruuskanen, J., de Boer, W., Troelstra, S. R., & Laanbroek, H. J. (1997). Methane oxidation in soil profiles of Dutch and Finnish coniferous forests with different soil texture and atmospheric nitrogen deposition. Soil Biology and Biochemistry, 29(11-12), 1625–1632. https://doi.org/10.1016/S0038-0717(97)00085-0

Sakabe, A., Kosugi, Y., Okumi, C., Itoh, M., & Takahashi, K. (2016). Impacts of riparian wetlands on the seasonal variations of watershed-scale methane budget in a temperate monsoonal forest. Journal of Geophysical Research: Biogeosciences, 121, 1717–1732. https://doi.org/10.1002/2015JG003292

Sørbotten, L. (2011). Hill slope unsaturated flowpaths and soil moisture variability in a forested catchment in southwest China, Master Thesis. Nor. Univsity Life Sci.

Sørbotten, L., Bousquet, P., Poulter, B., Peregon, A., Ciais, P., Canadell, J. G., et al. (2016). The global methane budget: 2000-2012. Earth System Science Data Discussions, 8, 697–751. https://doi.org/10.5194/essd-2016-25

Segers, R. (1998). Methane production and methane consumption: A review of processes underlying wetland methane fluxes. Biogeochemistry, 41, 23–51. https://doi.org/10.1023/A:1005929032764

Shoemaker, J., Keenan, T., Hollinger, D., & Ricardou, A. (2014). Forest ecosystem changes from annual methane source to sink depending on late summer water balance. Geophysical Research Letters, 41, 673–679. https://doi.org/10.1002/2013GL058691

Smith, K. A., Ball, T., Conen, F., Dobbe, K. E., Massheder, J., & Rey, A. (2003). Exchange of greenhouse gases between soil and atmosphere: Interactions of soil physical and biological processes. European Journal of Soil Science, 54(4), 779–791. https://doi.org/10.1046/j.1365-2389.2003.00567.x

Serbott, L. (2011). Hill slope unsaturated flowpaths and soil moisture variability in a forested catchment in southwest China, Master Thesis. Nor. Univsity Life Sci.

Serbott, L., Stolte, J., Wang, Y., & Mulder, J. (2017). Hydrological response and flow pathways in acrisols on a forested hillslope in monsoonal sub-tropical climate, Chonqing, Southwest China. Porphysphere, 27(6), 1037–1048. https://doi.org/10.1111/s1090-0139.00447-8

Steudler, P. A., Bowden, R. D., Melillo, J. M., & Aber, J. D. (1989). In soil carbon and nitrogen cycling and dynamics. Journal of Geophysical Research: Biogeosciences, 121, 2386–2403. https://doi.org/10.1029/97JG002687

Thom, C.R. (2005). A language and environment for statistical computing. Vienna, Austria: R Foundation for statistical computing, 2015.

von Fisher, J.C., & Hedin L.O. (2007). Controls on soil methane fluxes: Tests of biophysical mechanisms using table isotope tracers. Global Biogeochemical Cycles, 21, GB2007. https://doi.org/10.1029/2006GB002687

Veldkamp, E., Koehler, B., & Corre, M. D. (2013). Indications of nitrogen-limited methane uptake in tropical forest soils. Biogeochemistry, 108(6), 5367–5379. https://doi.org/10.1002/2013GB004189

von Fischer, J.C., & Hedin L.O. (2007). Controls on soil methane fluxes: Tests of biophysical mechanisms using table isotope tracers. Global Biogeochemical Cycles, 21, GB2007. https://doi.org/10.1029/2006GB002687

Wei, D., & Wang, X. (2016). CH₄ uptake by grasslands and forests in China. Soil Biology and Biochemistry, 70, 74–81. https://doi.org/10.1016/j.soilbio.2014.02.023

Warner, D. L., Vargas, R., Seyfferth, A., & Inamdar, S. (2018). Transitional slopes act as hotspots of both soil CO₂ emission and CH₄ uptake in a temperate forest landscape. Biogeosciences, 15(2), 121–135. https://doi.org/10.5194/bg-15-121-2018

Wei, D., & Wang, X. (2016). CH₄ exchanges of the natural ecosystems in China during the past three decades: The role of wetland extent and its dynamics. Journal of Geophysical Research: Biogeosciences, 121, 2445–2463. https://doi.org/10.1002/2016JG003418

Werner, C., Zheng, X., Tang, J., Xie, B., Liu, C., Kiese, R., & Butterbach-Bahl, K. (2006). N₂O, CH₄ and CO₂ emissions from seasonal tropical rainforests and a rubber plantation in Southwest China. Plant and Soil, 289(1–2), 335–353. https://doi.org/10.1007/s11104-006-9143-y

WRB (2006). World reference base for soil resources (pp. 67–97). Rome: FAO.

Xiao, C., Wu, P., Zhang, L., & Song, L. (2016). Robust increase in extreme summer rainfall intensity during the past four decades observed in China. Scientific Reports, 6(1), 1–9. https://doi.org/10.1038/srep38506

Yin, Y., Ma, D., & Wu, C. (2018). Climate change risk to forests in China associated with warming. Scientific Reports, 8(1), 1–13. https://doi.org/10.1038/s41598-017-18798-6

Yu, L., Mulder, J., Zhu, J., Zhang, X., Wang, Z., & Dörsch, P. (2019). Denitrification as a major regional nitrogen sink in subtropical forest catchments: Evidence from multi-site dual nitrate isotopes. Global Change Biology, 25(5), 1765–1778. https://doi.org/10.1111/gcb.14596

Yu, L., Wang, Y., Zhang, X., Dörsch, P., & Mulder, J. (2017). Phosphorus addition mitigates N₂O and CH₄ emissions in N-saturated subtropical forest, SW China. Biogeosciences, 14(12), 3097–3109. https://doi.org/10.5194/bg-14-3097-2017

Yu, L., Zhu, J., Mulder, J., & Dörsch, P. (2016). Multicyear dual nitrate isotope signatures suggest that N-saturated subtropical forested catchments can act as robust N sinks. Global Change Biology, 22(11), 3662–3674. https://doi.org/10.1111/gcb.13333

Yu, Q., Si, G., Zong, T., Mulder, J., & Duan, L. (2019). High hydrogen sulfide emissions from subtropical forest soils based on field measurements in south China. The Science of the Total Environment, 657, 1302–1309. https://doi.org/10.1016/j.scitotenv.2018.09.301

Zhang, W., Mo, J., Zhou, G., Granderse, P., Fang, Y., Lu, X., et al. (2008). Methane uptake responses to nitrogen deposition in three tropical forests in southern China. Journal of Geophysical Research, 113, D11116. https://doi.org/10.1029/2007JD009195
Zhang, Z., Zimmermann, N. E., Stenke, A., Li, X., Hodson, E. L., Zhu, G., et al. (2017). Emerging role of wetland methane emissions in driving 21st century climate change. *Proceedings of the National Academy of Sciences, 114*(36), 9647–9652. https://doi.org/10.1073/pnas.1618765114

Zheng, M., Zhang, T., Liu, L., Zhang, W., Lu, X., & Mo, J. (2016). Effects of nitrogen and phosphorus additions on soil methane uptake in disturbed forests. *Journal of Geophysical Research: Biogeosciences, 121*, 3089–3100. https://doi.org/10.1002/2016JG003476

Zhu, J., Mulder, J., Wu, L. P., Meng, X. X., Wang, Y. H., & Dörsch, P. (2013). Spatial and temporal variability of N$_2$O emissions in a subtropical forest catchment in China. *Biogeosciences, 10*(3), 1309–1321. https://doi.org/10.5194/bg-10-1309-2013

Zhuang, Q., Chen, M., Xu, K., Tang, J., Saikawa, E., Lu, Y., et al. (2013). Response of global soil consumption of atmospheric methane to changes in atmospheric climate and nitrogen deposition. *Global Biogeochemical Cycles, 27*, 650–663. https://doi.org/10.1002/gbc.20057