

# CH<sub>4</sub> and N<sub>2</sub>O dynamics in the boreal forest-mire ecotone

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## Abstract

In spite of advances in greenhouse gas research, the spatio-temporal CH<sub>4</sub> and N<sub>2</sub>O dynamics of boreal landscape remain challenging e.g. we need clarification of whether forest-mire transitions are occasional hotspots of landscape CH<sub>4</sub> and N<sub>2</sub>O emissions during exceptionally high and low ground water level events.

In our study, we tested the differences and drivers of CH<sub>4</sub> and N<sub>2</sub>O dynamics of forest/mire types in field conditions along the soil moisture gradient of the forest-mire ecotone. Soils changed from podzols to histosols and ground water rose downslope from the depth of 10 m in upland sites to 0.1 m in mires. Yearly meteorological conditions changed from being exceptionally wet to typical and exceptionally dry for the local climate. The median fluxes measured with a static chamber technique varied from -51 to 586  $\mu\text{g m}^{-2} \text{h}^{-1}$  for CH<sub>4</sub> and from 0 to 6  $\mu\text{g m}^{-2} \text{h}^{-1}$  for N<sub>2</sub>O between forest/mire types throughout the entire wet-dry period.

In spite of the highly dynamic soil water fluctuations in carbon rich soils in forest-mire transitions, there were no large peak emissions in CH<sub>4</sub> and N<sub>2</sub>O fluxes and the flux rates changed minimally between years. Methane oxidations were significantly lower in poorly drained transitions than in the well-drained uplands. Water saturated mires showed large CH<sub>4</sub> emissions, which were reduced entirely during the exceptional summer drought period. Near zero N<sub>2</sub>O fluxes did not differ significantly between the forest/mire types probably due to their low nitrification potential. When upscaling boreal landscapes, pristine forest-mire transitions should be considered as CH<sub>4</sub> oxidation types and background N<sub>2</sub>O emission types instead of CH<sub>4</sub> and N<sub>2</sub>O emission hotspots.

## 1 Introduction

Soil fertility, soil water content and soil carbon storage of boreal forest varies between well drained mineral soils mainly found in uplands and poorly drained organic soils mainly found in peatlands (Seibert et al. 2007, Weishampel et al. 2009). The CH<sub>4</sub> and N<sub>2</sub>O fluxes from mineral and organic soils are impacted by varying soil moisture conditions (Solondz et al. 2008, Pihlatie et al. 2004). Typical mineral soil forests are small sinks of CH<sub>4</sub> and small sources or sinks of N<sub>2</sub>O (Moosavi and Crill 1997, Pihlatie et al. 2007). Sparsely forested peatlands are typically large or small sources of CH<sub>4</sub> and small sources or sinks of N<sub>2</sub>O (Martikainen et al. 1995, Nykänen et al. 1995, D'Angelo and Reddy, 1998). Field CH<sub>4</sub> and N<sub>2</sub>O studies of natural boreal forest-mire ecotones are rare (e.g. Ullah et al. 2009, Ullah and Moore 2011) in comparison to those of typical forests or peatlands. However, the forest-mire ecotone “the lagg transitional zone” collects nutrients from the adjacent mineral soil runoff and is often more minerotrophic, biologically diverse, and productive than open mires or bogs (Howie and Meerveld 2011). Furthermore, ecotones between forests and mires are ecological switches (Agnew et al. 1993), where the vegetation of forests and mires coincide and soils frequently undergo fluctuations in water level position and chemistry (Hartshorn et al. 2003, Howie and Meerveld 2011), and where the CH<sub>4</sub> and N<sub>2</sub>O dynamics of forest-mire transitions may be expected to differ generally and on a year-to-year basis from those of typical forests and mires.

The CH<sub>4</sub> uptake of forest soils is a result of CH<sub>4</sub> oxidizing aerobic methanotrophs sensitive to water saturation, soil porosity, moisture, temperature, pH, and ammonium (Moosavi and Crill 1997, Saari et al. 2004, Jaatinen et al. 2004). Unsaturated upland forest soils oxidize CH<sub>4</sub> at higher rates than more water saturated, acidic, and ammonium rich forested peat soils (Saari et al. 2004). In contrast to the CH<sub>4</sub> sinks of upland forest soils, and drained peatlands, natural mires emit CH<sub>4</sub> to the atmosphere (Bubier et al. 1995, Nykänen et al. 1998, Kettunen et al. 1999). CH<sub>4</sub> production in peat soil is a result of methanogenic and methanotrophic active bacteria, whose activity depends on anoxic and oxic conditions below and above the water level, temperature and availability of carbon substrate (Kettunen et al. 1999). Increasing soil moisture increases anoxic conditions favorable for increased methanogenesis (Juottonen et al. 2005), and as a result increases CH<sub>4</sub> emissions (Saarnio et al. 1997, Ojanen et al. 2010, Yrjälä et al. 2011).

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2 N<sub>2</sub>O emissions in well-drained boreal forest soils are controlled by soil moisture, pH,  
3 available nitrate, ammonium, oxygen, and carbon concentrations (Regina et al. 1996, Ullah et  
4 al. 2008). N<sub>2</sub>O production is limited by the amount of nitrogen and is subject to denitrification  
5 and nitrification processes (Ambus et al. 2006). In well-drained soils NO<sub>3</sub> limitation, anoxic  
6 microsites, and larger soil porosity may also promote N<sub>2</sub>O consumption (Frasier et al. 2010).  
7 N<sub>2</sub>O consumption of soils correlates with dehydrogenase activity, which is affected by  
8 oxidation-reduction status and possibly controlled by soil moisture (Włodarczyk et al. 2005).  
9 The N<sub>2</sub>O consumption by soils is attributed to respiratory reduction (Conrad 1996) caused by  
10 denitrifiers and nitrifiers (Rosenkranz et al. 2006). N<sub>2</sub>O emissions increase during drier  
11 periods through increased ammonification and nitrification (Regina et al. 1996, Nykänen et al.  
12 1995, von Arnold et al. 2005). In water saturated minerotrophic peatlands nitrification  
13 supplies nitrate (Wrage et al. 2001) for denitrification, which is the main but small N<sub>2</sub>O  
14 source (Wray et al. 2007, Frasier et al. 2010).

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16 Our aims were 1) to test whether forest floor CH<sub>4</sub> and N<sub>2</sub>O fluxes of the forest-mire transition  
17 differ from the typical upland forests and lowland mires of natural boreal landscape and 2)  
18 how meteorologically different years, i.e., exceptionally wet (2004), typical (2005), and  
19 exceptionally dry (2006), affect the fluxes.

20  
21 We addressed the question, if in forest-mire transitions increasing wetness promote CH<sub>4</sub>  
22 production, and whether dry conditions reduce CH<sub>4</sub> production and increase N<sub>2</sub>O emissions.  
23 We hypothesized that forest/mire types exhibit distinct levels of CH<sub>4</sub> and N<sub>2</sub>O fluxes due to  
24 the changing soil structure from podzols to histosols and due to increasing soil water content  
25 from xeric to saturated. We expected that the occasionally saturated organo-mineral soils of  
26 forest-mire transitions are variable sources of CH<sub>4</sub> and N<sub>2</sub>O fluxes.

## 2 Material and methods

### 2.1 Study site characteristics

The Vatiharju-Lakkasuo ecotone of nine forest and mire study sites forms a gradient in vegetation communities, soil moisture and nutrient conditions in Central Finland (61° 47', 24° 19') (Tūpek et al. 2008). Forest/mire types were classified using the Finnish classification systems (Cajander 1949, Laine et al., 2004) based on soil fertility reflected by the composition and abundance of forest floor vegetation, and by the site location on the slope. The ecotone study sites are situated along a 450 m transect on a hillslope with a relative relief of 15 meters and a 3.3% slope facing NE (Figure 1a). The fertility of the forest/mire sites increase from the poorly fertile sites at the xeric and saturated edges of the ecotone towards the most fertile *Oxalis-Myrtillus* type forest (OMT) in the middle of the hillslope (Figure 1b).

Dominant vegetation composition changes with increasing soil moisture down the slope. Xeric Scots pine forest (CT – *Calluna* Type) on the summit of glacial sandy esker gives way to subxeric Scots pine Norway spruce forest (VT – *Vaccinium Vitis Idea* Type) on the shoulder, and mesic and herb-rich Norway spruce dominated types on the backslope and footslope (MT – *Vaccinium Myrtillus* Type, OMT – *Oxalis-Myrtillus* Type). The toeslope contains forest-mire transitions of paludified mixed spruce-pine-birch forests (OMT+ – *Oxalis-Myrtillus* Paludified, KgK – *Myrtillus* Spruce Forest Paludified). There is a permanently wet mixed spruce-pine-birch swamp (KR – Spruce Pine Swamp) at the mire edge of the forest-mire transitions. On the level of the hillslope there are birch-pine fen mires with open tree canopies (VSR1 – and VSR2 – Tall Sedge Pine Fen) (Figure 1b). The forest floor vegetation is composed of site-specific mosses and vascular plants (Figure 1c).

Soils are formed by well-drained haplic podzols on the hillslope, intermediately drained histic and gleyic-histic podzols in the forest-mire transitions on the toe of the slope, and permanently wet hemic histosols downslope (Figure 1d).

We measured pH during the 2005 summer campaign from soil water data collected on all sites by suction-cup lysimeters. Three lysimeters were installed at 10 cm and one at depth of 30 cm below the soil surface in each site. A detailed description of the lysimeters and sampling procedure can be found in Starr (1985). The pH was measured on the day of water sampling in the laboratory by a pH meter equipped with a glass electrode. The mean acidity

level of the sites of forest-mire ecotone was gradually increasing from pH 5.6 in uplands (CT) to 4.4 in transitions (KR), whereas the mires were less acidic than the transitions with pHs of 5.1 and 4.8 (VSR1 and VSR2 respectively) (Table 1). Collected soil water from a depth of 30 cm generally showed a higher pH than soil water pH from a depth of 10 cm. Three soil cores for each plot were taken in July 2006 from the top soil (0-10 cm) in upland forests and from the two profile depths (0-10 cm, 10-30 cm) in forest mire transitions and in peatlands. The volume of samples was measured before the oven drying at 70 °C to determine the bulk density. The bulk density of the upper organic layer ranged from 0.24 gcm<sup>-3</sup> (KR) to 0.48 gcm<sup>-3</sup> (MT) and was approximately half of the bulk density of the organic layer from depths of 10-30 cm (mean of transitions and mires 0.77 gcm<sup>-3</sup>) (Table 1). The C/N ratio was determined once for each plot from the soil organic matter analysed by dry combustion with Leco CNS-1000 (Leco Corp., USA). The C/N ratio was wider in the 0-10 cm profile (mean 37) than in the 10-30 cm profile (mean 27). The highest N content and lowest C/N ratio along the ecotone was found in forest-mire transitions OMT+ and KgK (Table 1). A more detailed forest/mire type characterization is given by Ľupek et al. (2008).

## **2.2 Micrometeorological conditions**

The micrometeorological measurements along the Vatiharju - Lakkasuo forest-mire ecotone were taken weekly during the summers of 2004 (July-November), 2005 (May-November), 2006 (May-September), and monthly during the winters (December-April). The forest floor soil temperatures (°C) at depths of 5, 15, and 30 cm (T<sub>5</sub>, T<sub>15</sub>, and T<sub>30</sub>) were measured using a portable thermometer connected to thermocouples installed permanently in the soil. The volumetric soil moisture (%) at depths of 5, 10, and 30 cm (SWC<sub>5</sub>, SWC<sub>10</sub>, and SWC<sub>30</sub>) was measured by a portable ThetaProbe (Delta-T Devices Ltd.) in diagonally installed perforated PVC tubes, to ensure the same compactness of the soil. The depth of water table was measured inside PVC tubes (ø 30 mm) installed at each site. Precipitation was measured by an automated bucket system at a station for monitoring forest – atmosphere relations, SMEARII (Hari and Kulmala, 2005), located 6km north - west from the forest-mire ecotone. Missing soil temperature and moisture data of ecotone were gap filled by linear regression between continuous measurements of soil temperature and moisture at SMEARII.

## 2.3 CH<sub>4</sub> and N<sub>2</sub>O fluxes

The field gas sampling was conducted weekly in the 2004 and 2005 seasons, bi-weekly during the 2006 season, and monthly during the winters. The gas sampling was done the same day  $\pm$  one day as the micrometeorological measurements. If there was packed snow on the ground the gas samples were taken from the top and bottom layers; and the CH<sub>4</sub> ( $\mu\text{g m}^{-2} \text{ h}^{-1}$ ) and N<sub>2</sub>O ( $\mu\text{g m}^{-2} \text{ h}^{-1}$ ) fluxes were calculated by the snowpack diffusion method using each gas concentration difference, snow depth, porosity and temperature, and gas diffusion coefficients as in Sommerfeld et al. (1993). Otherwise if there was no snowpack, the samples were taken from 3 opaque, vented, closed, static chambers ( $\varnothing$  315 mm, h 295 mm) placed air tightly on preinstalled collars. On each measuring occasion a sample of ambient gas and four 15 ml samples from each of the three chambers were drawn in syringes at intervals of 5, 10, 15, 20 min from chamber closure, totaling 13 samples for each site. Chamber temperature was monitored during the sampling. After the sampling event, the gas samples were stored in coolers at +4°C and analyzed within 36 hours in a laboratory with a gas chromatograph. The gas chromatograph (Hewlett-Packard, USA) model number HP-5890A was fitted with a flame ionization detector (FID) for CH<sub>4</sub> and an electron capture detector (ECD) for N<sub>2</sub>O detection. The gas chromatograph was also equipped with a moisture trap. Prior to analysis of field samples and after each set of 13 samples a reference gas sample of known CH<sub>4</sub> and N<sub>2</sub>O concentration was analyzed. The CH<sub>4</sub> ( $\mu\text{g m}^{-2} \text{ h}^{-1}$ ) and N<sub>2</sub>O ( $\mu\text{g m}^{-2} \text{ h}^{-1}$ ) fluxes were calculated from the slope of linear regression between the set of 4 gas concentrations and sampling time, time elapsed after the chamber closure, and by applying temperature correction. For the flux calculation we used a MATLAB (The Mathworks Inc.) script developed at the Dept. of Physics, University of Helsinki.

The quantification limit of the gas chromatograph (MQL) was based on 100 subsequently analyzed samples of reference gas of known CH<sub>4</sub> and N<sub>2</sub>O concentrations (mean  $\pm$  two SD: 1.837  $\pm$  0.055 and 0.295  $\pm$  0.023 ppm respectively) and reference gas samples analyzed before the set of field samples for each site. The MQL was a gas specific standard deviation of the random fluxes derived from 1000 random sets of 4 CH<sub>4</sub> or N<sub>2</sub>O concentrations of reference gas samples (22  $\mu\text{g m}^{-2} \text{ h}^{-1}$  for CH<sub>4</sub> and 18  $\mu\text{g m}^{-2} \text{ h}^{-1}$  for N<sub>2</sub>O). In order to minimize the random error related to gas sampling in the field, fluxes were verified using the ambient field air sample analyzed before each sequence of chamber samples adopting similar

criteria as used in Alm et al. (2007). Due to gas sampling disturbances in the field and poor gas chromatograph accuracy 17% of CH<sub>4</sub> and 49% of N<sub>2</sub>O fluxes were discarded.

## 2.4 Statistical analysis

Two-way analysis of variance (ANOVA) was used to test whether CH<sub>4</sub> and N<sub>2</sub>O fluxes of forest/mire types have common means in wet, typical, and dry years. Post-hoc Tukey HSD tests were used to test the pairwise differences between the forest/mire types and years changing from wet to dry. For CH<sub>4</sub> fluxes we ran ANOVA tests twice, first on the whole dataset including nine forest/mire types and then on a subset of data including upland forests and forest-mire transitions, and excluding mires. For testing significant differences between the two groups of data we performed Welch's Two Sample t-test e.g. between the N<sub>2</sub>O fluxes from the snow on the ground season (January-April in 2006) and the N<sub>2</sub>O fluxes from the snowless seasons (May-November in 2005 and May-September in 2006).

In addition to ANOVA, we tested the dependence between the measured CH<sub>4</sub> (μg m<sup>-2</sup> h<sup>-1</sup>) and the gap filled half-hourly environmental variables in separate models for: a) the upland forests on mineral soils (VT, VT, MT, OMT) and b) forest-mire transitions on organo-mineral soils and (OMT+, KgK, and KR), and c) mires (VSR1, VSR2).

CH<sub>4</sub> fluxes (μg m<sup>-2</sup> h<sup>-1</sup>) of uplands and transitions were fitted by two linear mixed-effects regression models with a random effect for forest types (Pinheiro et al. 2013). For both groups of forest types, we evaluated the effect of all our environmental variables on CH<sub>4</sub> together and their combinations iteratively by selecting the model combination of variables that were significant.

The CH<sub>4</sub> fluxes for upland forests and transitions included soil moisture at 10 cm (%) (SWC<sub>10</sub>) and soil temperature at 5 cm (°C) (T<sub>5</sub>) as predictors in separate models (Eqs. (1) and (2)):

$$yu_{ij} = \beta_{CT} SWC_{10} + \beta_{VT} SWC_{10} + \beta_{MT} SWC_{10} + \beta_{OMT} SWC_{10} + \beta_{CT} T_5 + \beta_{VT} T_5 + \beta_{MT} T_5 + \beta_{OMT} T_5 + b_{CT} + b_{VT} + b_{MT} + b_{OMT} + \epsilon_{ij}, \quad (1)$$

$$yt_{ij} = \beta_{OMT} SWC_{10} + \beta_{KgK} SWC_{10} + \beta_{KR} SWC_{10} + \beta_{OMT} T_5 + \beta_{KgK} T_5 + \beta_{KR} T_5 + b_{OMT+} + b_{KgK} + b_{KR} + \epsilon_{ij}, \quad (2)$$

where  $y_{uij}$  and  $y_{tij}$  is the CH<sub>4</sub> flux ( $\mu\text{g m}^{-2} \text{h}^{-1}$ ) for upland forests or transitions and for a particular  $i^{\text{th}}$  forest type and the  $j^{\text{th}}$  observation,  $\beta_{\text{CT}}$  through  $\beta_{\text{KR}}$  are the fixed effect coefficients for a particular  $i^{\text{th}}$  forest type (CT, VT, MT, OMT Eq. (1), or OMT+, KgK, and KR Eq. (2)),  $\text{SWC}_{10}$ , and  $T_5$  are the fixed effect variables (predictors) for observation  $j$  in forest type  $i$  where each forest type's predictor is assumed to be multivariate normally distributed,  $b_{\text{CT}}$  through  $b_{\text{KR}}$  are intercepts for the random effect for a particular  $i^{\text{th}}$  forest type and  $\varepsilon_{ij}$  is the error for case  $j$  in forest type  $i$  where each forest type's error is assumed to be multivariate normally distributed (Table 2).

The CH<sub>4</sub> fluxes ( $\mu\text{g m}^{-2} \text{h}^{-1}$ ) of mires were fitted by using a multiplicative non-linear regression model with a combined response to water table depth and soil temperature at 5 cm Eq. (3):

$$y_{ij} = a_0 e^{\left(-0.5 \left(\frac{WT - WT_{\text{opt}}}{WT_{\text{tol}}}\right)^2\right)} e^{\left(-0.5 \left(\frac{T_5 - T_{\text{opt}}}{T_{\text{tol}}}\right)^2\right)} + \varepsilon_{ij}. \quad (3)$$

where  $y_{ij}$  is the CH<sub>4</sub> flux ( $\mu\text{g m}^{-2} \text{h}^{-1}$ ) for the  $i^{\text{th}}$  mire (VSR1, VSR2) and for the  $j^{\text{th}}$  case,  $WT$  (cm) is water table depth,  $T_5$  ( $^{\circ}\text{C}$ ) is soil temperature at 5 cm, and  $a_0$ ,  $WT_{\text{opt}}$ ,  $WT_{\text{tol}}$ ,  $T_{\text{opt}}$ ,  $T_{\text{tol}}$  are parameters (Table 3).

The N<sub>2</sub>O fluxes ( $\mu\text{g m}^{-2} \text{h}^{-1}$ ) of all forest/mire types were fitted by using one multiplicative non-linear regression model with a combined response to soil moisture and soil temperature at 5 cm Eq. (4):

$$z_{ij} = a_0 \text{SWC}_5 e^{\left(-0.5 \left(\frac{T_5 - T_{\text{opt}}}{T_{\text{tol}}}\right)^2\right)} + \varepsilon_{ij}, \quad (4)$$

where  $z_{ij}$  is the N<sub>2</sub>O flux ( $\mu\text{g m}^{-2} \text{h}^{-1}$ ) for the  $i^{\text{th}}$  mire (VSR1, VSR2) and for the  $j^{\text{th}}$  case,  $\text{SWC}_5$  (%) is soil moisture at 5 cm, and  $T_5$  ( $^{\circ}\text{C}$ ) is soil temperature at 5 cm, and  $a_0$ ,  $T_{\text{opt}}$ ,  $T_{\text{tol}}$  are parameters (Table 4).

To illustrate the sensitivity of CH<sub>4</sub> and N<sub>2</sub>O flux response to environmental factors we performed a residual analysis by simulating a value for each data point with only one factor allowed to vary and the other set to its mean level. To examine correlations between CH<sub>4</sub> and N<sub>2</sub>O fluxes and pH, and soil properties we performed Pearson's correlation tests. The



1 statistical analyses were performed in MATLAB R2012a (The Mathworks Inc.) and in R (R  
2 Core Team 2013) software environments.

### 3 **3 Results**

#### 5 **3.1 Micrometeorological conditions**

6 The largest differences between years 2004, 2005, and 2006 were seen in changing summer  
7 precipitation patterns (measured nearby the SMEARII station). The average June-August  
8 monthly precipitation was reduced from 94 to 44 mm from a wet 2004 to a dry 2006, while  
9 ambient temperature increased from 14 °C to 17 °C. In the coldest summer (2004) the average  
10 precipitation in June and July was over 117 mm, and dropped to 47 mm in August. In the  
11 typically warm summer of 2005 the monthly precipitation gradually increased up to 123 mm  
12 in August, and dropped to 58 mm in September. However, in the warmest summer (2006) the  
13 monthly precipitation never reached more than 48 mm. In July 2006, two rainless weeks  
14 induced a drought. By drought we mean that the soil water content in the upper soil layer (in  
15 mineral soils) was so low that mosses wilted and dried (all along the ecotone). The drought  
16 conditions lessened in mid-August and ended in September with increasing rains towards  
17 autumn. Late autumn was exceptionally warm and snowless.

19 Monthly median soil temperatures at 5 cm ( $T_5$ ) ranged from around 5 °C in May, culminated  
20 to around 15-16 °C in July and August and subsided again to around 5 °C in October. The  
21 non-vegetative season  $T_5$  minimum was close to 0 °C. The warmest  $T_5$  was in upland forest  
22 1CT and the coldest was in upper forest-mire transition 5 OMT+. Soil temperature slightly  
23 increased from forest-mire transitions towards mires. In spite of the ambient air temperature  
24 difference throughout all the months in the 3 years, we detected differences mainly during  
25 early and late season in 2004, 2005, and 2006  $T_5$  (Figure 2a).

26 The median water table (WT) showed the obvious rise from 10 m at the summit of the hill, to  
27 around 1 m in the mid-slope, between 0.5 and 0.1 m at the toe-slope and close to 0.01 m on  
28 the level (Figure 2b). The seasonal WT rise in 2005 was observed between the July and  
29 August medians. During the drought of 2006, the WT values dropped less than 0.1 m for the

uppermost forest sites, but dropped heavily by ~1 m in the forest-mire transitions, and more than 0.5 m in the lowermost peatland sites.

Volumetric soil water content (SWC) in 10 cm depth ranged from a dry value of around 10% in the mineral soils to a water-saturated value of around 80% in swamp and mires (Figure 2c). The largest drought reduction of SWC was in August 2006 on the well-drained sandy podzol at the summit of the hill, and also on the poorly drained histic podzol on the toe slope.

### 3.2 CH<sub>4</sub> fluxes

The median fluxes from the forest floor varied from -51 to 586  $\mu\text{g m}^{-2} \text{h}^{-1}$  for CH<sub>4</sub> among individual forest/mire types (CT, VT, MT, OMT, OMT+, KgK, KR, VSR1, VSR2) during the entire period (Figure 3a). The small negative CH<sub>4</sub> fluxes associated with prevailing oxidation were mostly observed in uplands and in transitions while mires typically showed large positive higher CH<sub>4</sub> fluxes associated with prevailing production. The CH<sub>4</sub> dynamics changed exponentially with increasing levels of the ground water table from small consumptions to large productions (Figure 2, Figure 3). The median CH<sub>4</sub> fluxes of uplands (CT, VT, MT, OMT), transitions (OMT+, KgK, KR), and mires (VSR1, VSR2) varied from -38, -8, and 392  $\mu\text{g m}^{-2} \text{h}^{-1}$  respectively (Figure 3b). Momentary CH<sub>4</sub> fluxes of uplands and transitions ranged from -342 to 143  $\mu\text{g m}^{-2} \text{h}^{-1}$ , whereas in mires the fluxes ranged from -12 to 6808  $\mu\text{g m}^{-2} \text{h}^{-1}$  (Figure 3b). The median CH<sub>4</sub> fluxes for one upland (VT) and all the transitions (OMT+, KgK, KR) were found inside the range of the gas chromatograph detection limits ( $\text{MQL}_{\text{CH}_4} = 22 \mu\text{g m}^{-2} \text{h}^{-1}$ ). In forest-mire transitional types the ground water level in August 2005 increased towards the surface and approached the levels typically found in mires (Figure 2b), but the soil water saturation in transitions was not followed by CH<sub>4</sub> emissions such as those found in mires.

A two-way analysis of variance (ANOVA) showed that forest floor CH<sub>4</sub> fluxes differed significantly for the nine forest/mire types of the ecotone  $F(8, 1252) = 108, p < 0.001$  and for the wet, typical, and dry years  $F(2, 1252) = 10, p < 0.001$ . There was a significant interaction between CH<sub>4</sub> fluxes of forest/mire types and wet, typical, and dry years  $F(16, 1252) = 5, p < 0.001$ . Tukey post-hoc comparison of the nine forest/mire types indicated that mires (VSR1, VSR2) gave significantly higher CH<sub>4</sub> fluxes than the other forest types. Differences in means (M) and 95% confidence limits (CI) ranged from minimum VSR2-KgK (M = 481, 95% CI

[352, 610]) to maximum VSR1-OMT ( $M = 793$ , 95% CI [668, 918]) at  $p < 0.001$ . Also the  $\text{CH}_4$  fluxes of the mires were significantly different from each other VSR2-VSR1 ( $M = -260$ , 95% CI [-384, -137]),  $p < 0.001$ . Differences between the years were significant at  $p < 0.001$  for dry-typical ( $M = -96$ , 95% CI [-149, -43]) when  $\text{CH}_4$  fluxes of mires were highly reduced. The comparison of mean  $\text{CH}_4$  fluxes of typical-wet ( $M = 51$ , 95% CI [-6, 108]),  $p = 0.089$  and dry-wet years did not show a significant difference ( $M = -45$ , 95% CI [-111, 20]),  $p = 0.237$ .

Differences between the other forest types (transitions, uplands) were not significant when analyzed together with the  $\text{CH}_4$  fluxes of mires. The  $\text{CH}_4$  fluxes for the seven transitional and upland forest types were significantly different  $F(6, 976) = 71$ ,  $p < 0.001$  when ANOVA was run without mires. Though unlike the nine forest/mire type dataset, for the group of uplands with transitions there was no difference between wet, typical, and dry years  $F(2, 976) = 1$ ,  $p = 0.292$  or their interactions  $F(12, 976) = 1$ ,  $p = 0.135$ . The mean  $\text{CH}_4$  oxidation of the upland forests ( $-42.9 \mu\text{g m}^{-2} \text{h}^{-1}$ ) was for the whole period significantly larger than the mean  $\text{CH}_4$  oxidation of the forest-mire transitions ( $-12.8 \mu\text{g m}^{-2} \text{h}^{-1}$ ) according to Welch's two sample t-test  $t(994) = 15.56$ ,  $p < 0.001$ . Tukey post-hoc comparison of the differences in the mean  $\text{CH}_4$  fluxes for 21 pairs of seven upland and transitional forest types was significant for 17 pairs at  $p < 0.001$  and ranged from OMT-VT ( $M = -35$ , 95% CI [-45, -25]) to KR-OMT ( $M = 51$ , 95% CI [41, 61]). Tukey post-hoc comparisons showed non-significant  $p$  values for 4 of the 21 pairs of  $\text{CH}_4$  fluxes of transitional and upland forest types (MT-CT 0.056, OMT+-VT 0.965, OMT-MT 0.431, and KR-KgK 0.999).

### 3.3 Factors controlling $\text{CH}_4$ fluxes

The mean level of  $\text{CH}_4$  fluxes of upland and transitional forests differed (Table 2, parameter "group bi"), though the sensitivity response to environmental factors was similar (Figure 4). The largest part of the  $\text{CH}_4$  fluxes remained unexplained with our models, as the proportion of explained variance was relatively low for uplands (10%) and transitions (15%) and slightly higher for mires (22%). The modeled  $\text{CH}_4$  flux response for the upland and transitional forest types to soil moisture at 10 cm was nearly flat, although the soil moisture parameter was significant ( $p = 0.011$ , Table 2). In the transitional *Oxalis-Myrtillus* Paludified forest type OMT+, where the soil moisture at 10 cm ranged from 20% (in the uplands) to over 70% (in the mires), the modeled  $\text{CH}_4$  flux response between dry and water saturated soil differed by

50  $\mu\text{g m}^{-2} \text{h}^{-1}$ . A stronger gradient than that in the soil moisture was detected by modeling stronger temperature responses of  $\text{CH}_4$  fluxes for the uplands and the nearly flat response for the transitions (Figure 4). The model parameter to soil temperature at 5 cm in the uplands was highly significant at  $p < 0.001$ , in contrast to transitions where the temperature parameter was insignificant  $p = 0.629$  (Table 2). In the mires the observed range of water level during wet, typical, and dry years spanned from the surface to a depth of 54 cm and showed a sigmoidal response with lower  $\text{CH}_4$  fluxes towards the extreme ends. The optimum water level for  $\text{CH}_4$  effluxes was at 18 cm (se 2.2) below the surface with 16.6 cm tolerance which is a deviation of the water level up to 60% of  $\text{CH}_4$  flux maximum (Figure 4,  $p < 0.001$ ,  $\text{WT}_{\text{opt}}$  and  $\text{WT}_{\text{tol}}$  in Table 3). Optimum near surface peat temperature for the  $\text{CH}_4$  emissions was found at 13.9 °C (se 1.4) with 6.4 °C tolerance (Figure 4,  $p < 0.001$ ,  $T_{\text{opt}}$  and  $T_{\text{tol}}$  in Table 3).

### 3.4 $\text{N}_2\text{O}$ fluxes

During the typical and dry years the momentary forest floor  $\text{N}_2\text{O}$  fluxes of forest/mire types ranged from -107 to 248  $\mu\text{g m}^{-2} \text{h}^{-1}$ . The median  $\text{N}_2\text{O}$  fluxes were similar for the forest/mire types and ranged only from 0 to 6  $\mu\text{g m}^{-2} \text{h}^{-1}$  (Figure 5). The median  $\text{N}_2\text{O}$  fluxes of all forest/mire types were found inside the range of the method quantification limits ( $\text{MQL}_{\text{N}_2\text{O}} = 18 \mu\text{g m}^{-2} \text{h}^{-1}$ ). The  $\text{N}_2\text{O}$  fluxes of the snow on the ground period were significantly lower than the  $\text{N}_2\text{O}$  fluxes of the snowless period according to Welch's two sample t-test  $t(297) = 5.094$ ,  $p < 0.001$ . Forest floor  $\text{N}_2\text{O}$  fluxes did not differ significantly for the nine forest/mire types of the ecotone for the snowless periods  $F(8, 284) = 0.708$ ,  $p = 0.684$ . Though, the momentary  $\text{N}_2\text{O}$  fluxes were significantly different in typical and dry snowless seasons  $F(1, 284) = 6.157$ ,  $p < 0.014$ .  $\text{N}_2\text{O}$  fluxes were lower during dry snowless seasons and a small increase was observed only in one forest-mire transition (KR – Spruce Pine Swamp) and in one mire (VSR2 - Tall Sedge Pine Fen) (Figure 6).

In general  $\text{N}_2\text{O}$  fluxes were low and did not show clear spatial differences in relation to increasing soil moisture from xeric uplands to water saturated mires, but the  $\text{N}_2\text{O}$  fluxes were lower in the dry than in the typical years. The post-hoc Tukey tests of means and 95% confidence limits of  $\text{N}_2\text{O}$  fluxes for all pairs (except one) showed insignificant forest/mire type pair-wise differences during the whole period and also during the snowless periods of wet or dry years (Figure 6). The significant  $\text{N}_2\text{O}$  flux difference for VSR2-OMT in a dry year

(M = 35, 95% CI [3, 68],  $p = 0.02$ ) was caused by a small decrease in OMT and increase in VSR2 fluxes.

### 3.5 Factors controlling N<sub>2</sub>O fluxes

The sensitivity response of fluxes was weak in relation to soil moisture at 5 cm and had a somewhat clearer and significant relation with soil temperature at 5 cm ( $p < 0.001$ , Table 4, Figure 7). The modeled Gaussian type response showed optimum N<sub>2</sub>O production at 11.3 (°C) soil temperature at a depth of 5 cm with a very narrow temperature range increasing from 7 °C and subsiding at 14 °C.

### 3.6 Effects of pH and soil properties on CH<sub>4</sub> and N<sub>2</sub>O flux

The site specific momentary CH<sub>4</sub> and N<sub>2</sub>O fluxes did not show significant correlation with varying soil water pH (except for one correlation coefficient  $r = -0.45$ ,  $p = 0.02$  on MT for N<sub>2</sub>O and pH at 10 cm). No correlation was found between CH<sub>4</sub> momentary data on the ecotone level. Although, for the CH<sub>4</sub> data including that for a group of upland forest and forest-mire transitions (excluding mires) Pearson correlation between momentary CH<sub>4</sub> fluxes and soil water pH was significant ( $r = -0.32$ ,  $p < 0.001$ ). Mean fluxes of summer 2005 CH<sub>4</sub> ( $\mu\text{g m}^{-2} \text{h}^{-1}$ ) of upland forests and forest-mire transition were negatively correlated with mean pH ( $\text{CH}_4 = 129.35 - 33.36 \cdot \text{pH}$ ,  $r^2 = 0.49$ , Fig. 8a). The ecotone N<sub>2</sub>O fluxes ( $\mu\text{g m}^{-2} \text{h}^{-1}$ ) of the summer 2005 pH campaign were significantly correlated with pH ( $r = 0.174$ ,  $p = 0.004$ ). The mean N<sub>2</sub>O fluxes ( $\mu\text{g m}^{-2} \text{h}^{-1}$ ) of sites increased with mean pH ( $\text{N}_2\text{O} = -117.07 + 27.33 \cdot \text{pH}$ ,  $r^2 = 0.32$ , Fig. 8b). However, the post-hoc Tukey differences of mean N<sub>2</sub>O fluxes from the forest floor for the pair-wise comparisons of forest/mire types were not significant for 31 pairs and mean N<sub>2</sub>O flux differences were significant only for 5 pairs (KgK-CT, VSR1-KgK, VSR1-KR, VSR1-MT, VSR1-OMT, Figure 9). We did not find significant correlation between site specific mean CH<sub>4</sub> and N<sub>2</sub>O flux and bulk density and/or C/N ratio.

## 4 Discussion

### 4.1 CH<sub>4</sub> dynamics

The forest/mire types significantly differ in forest floor CH<sub>4</sub> fluxes and between wet, typical and dry years. As expected, the largest difference was found between emissions of mires and the small oxidation of other forest types. However, CH<sub>4</sub> oxidation also showed significant differences between the forest types on mineral soil (uplands) and organo-mineral soil (transitions). Our study demonstrated that the CH<sub>4</sub> flux response to soil moisture changes with the relatively small mesoscale levels of a forest-mire ecotone (450 m long transect) (Figure 4). The CH<sub>4</sub> flux sensitivity to soil moisture showed a positive linear response to CH<sub>4</sub> oxidation for the drier soils of transitions and uplands. Alternatively CH<sub>4</sub> emission in mires showed a Gaussian form response with a reduction of the optimum under saturated or drier surface peat conditions. We have complemented the few studies on forest-mire gradients (e.g. Moosavi and Crill 1997, Ullah et al. 2009, Ullah and Moore 2011) and have lowered the likelihood of forest-mire transitions being biogeochemical hotspots of CH<sub>4</sub> emissions during short-term water level fluctuations.

The lack of an increase in CH<sub>4</sub> emissions during increased ground water levels in the transitions in our study could be attributed more to the relatively slow response of CH<sub>4</sub> producing bacteria than to the effectiveness of CH<sub>4</sub> oxidation which was reduced by a reduction in the aerated soil layer. Mäkiranta et al. (2009) showed that in forested peatlands the highest abundance of respiratory microbes could be found in the zone around the average water level. It is also known that the depth of maximum CH<sub>4</sub> production and oxidation is strongly related to 30-day average water level depth with time lag differences between the drier and wetter microsites (Kettunen et al. 1999). The duration of exceptionally increased high water levels was probably too short for CH<sub>4</sub> producing bacteria to relocate and/or adapt to water saturated conditions. Temporally water saturated soil layers of pristine forest-mire transitions had low CH<sub>4</sub> production partly due to highly acidic pH levels imposing physiological restrictions on soil microbial communities. Methanogenic activity in water saturated organic soils can be reduced by high acidity (e.g. Ye et al. 2012). Small momentary CH<sub>4</sub> emissions (Supplement Fig. 3a) observed in forest-mire transitions also indicated potential for occasionally higher production than consumption/oxidation. Beside microsite

1 differences in soil saturation and microbial populations also plant communities (Fig. 1c) could  
2 play an important role in explaining enhanced emissions (e.g. Saarnio et al., 1997, Riutta et  
3 al., 2007). For example, sedges through aerenchymatic transport interplay with microbes by  
4 providing recently photosynthesized carbon downwards and transporting CH<sub>4</sub> from microbial  
5 populations upwards (Alm et al., 1997).

6  
7 Small CH<sub>4</sub> emissions as observed in relatively dry Scots pine dominated forests (VT –  
8 *Vaccinium Vitis idea* type) (Figure 3) with sandy podzol soil and ground water depths around  
9 two meters, have been occasionally found in mineral soil forests in other studies. This implies  
10 that plants' deepest roots play a role in CH<sub>4</sub> transport via the transpiration stream (Megonigal  
11 and Guenther 2008). Ullah et al. (2009) found that Spruce forest soils produced CH<sub>4</sub> only  
12 during the spring thaw season but later under drier summer conditions soils switched to CH<sub>4</sub>  
13 consumption. In our study the rare occurrence of small CH<sub>4</sub> emissions from forest soils  
14 differed between forest types and cannot only be attributed to increased soil moisture levels of  
15 microsites or transport from deep ground water sources. Small CH<sub>4</sub> emissions could be also  
16 partly attributed to the random noise in measurements. However, all the data showed a  
17 significant reduction of CH<sub>4</sub> uptake with increasing soil moisture at 10 cm, this may be  
18 associated with oxidation processes.

19  
20 The form of CH<sub>4</sub> flux – soil moisture sensitivity is better known from soil incubation studies  
21 (Pihlatie et al. 2004, Ullah et al. 2007) than from field studies, as field soil moisture ranges  
22 may be narrow (e.g. Nakamo et al. 2004). In order to describe the sensitivity of CH<sub>4</sub> uptake to  
23 moisture in the field we need a large amount of data covering a wide range of soil conditions  
24 (e.g. Hashimoto et al. 2011). In our study soil moisture varied between xeric and saturated  
25 conditions both spatially along the ecotone and temporally between years. Temporal soil  
26 water saturation in transitional forest-mire sites rather reduced CH<sub>4</sub> oxidations than promoted  
27 such CH<sub>4</sub> emissions as found in nearby permanently saturated mires. Beside the sensitivity of  
28 CH<sub>4</sub> fluxes to moisture we also observed sensitivity to soil temperature (Figure 4) possibly  
29 also reflecting the role of soil physiochemical properties and/or the activity of methanogens.  
30 The positively increasing CH<sub>4</sub> oxidation rates with temperature in upland forest types could  
31 reflect the importance of soil physiochemical properties e.g. bulk density, whereas the  
32 Gaussian form may also reflect a biological driven response in mires.

1  
2 In our upland forests the role of soil physiochemical and microbiological drivers may have  
3 contributed to the fact that the temperature and moisture significantly explained just 10% of  
4 the variation. Although our mean CH<sub>4</sub> data did not show significant correlations with bulk  
5 density, the porous organic horizon is known to enable larger diffusion and CH<sub>4</sub> oxidation  
6 (Nakamo et al. 2004, Ullah and Moore 2011). It was difficult to assess the differences in  
7 sensitivity of CH<sub>4</sub> oxidation because of poor MQL and low fluxes of CH<sub>4</sub> oxidation. The  
8 absolute levels of the temperature effect on CH<sub>4</sub> fluxes in forest-mire transitions caused part  
9 of the signal to be mixed with variable sources of sampling errors and gas chromatograph  
10 precision errors. Though, in transitions both soil physiochemical and microbiological drivers  
11 may be important for CH<sub>4</sub> oxidations, as our forest-mire transitions showed a significant  
12 relation to soil moisture but not to temperature. The weak response of CH<sub>4</sub> oxidation to  
13 temperature was in contrast to the strong response to moisture and bulk density found in  
14 forests growing on mineral soils (Hashimoto et al. 2011). However, Nakamo et al. (2004)  
15 reported a clear relation with temperature but not with moisture for boreal birch forest (similar  
16 to our KR – Spruce Pine Swamp).

17  
18 In mires, the form of temperature and moisture CH<sub>4</sub> sensitivity may be also determined by  
19 differences in the composition of microbial (Saari et al. 2004, Jaatinen et al. 2004) and plant  
20 functional communities (Bubier et al. 1995, Riutta et al. 2007, Saarnio et al. 1997). For  
21 example in the study by Saarnio et al. (1997) the CH<sub>4</sub> flux response to water level would be  
22 exponential if it accounted only for emissions from hummock and *Carex* lawn microsites, but  
23 the response was Gaussian for flark, hummock, *Eriophorum* lawn and *Carex* lawn microsites  
24 taken together. The CH<sub>4</sub> emissions in VSR1 - Tall Sedge Pine Fen were larger than in VSR2 -  
25 Tall Sedge Pine Fen (Figure 4). In VSR1 the water level was closer to the surface, and the  
26 lawn microsites had a greater abundance of *Menyanthes* species, which are known to mediate  
27 higher CH<sub>4</sub> transport (Bubier et al. 1995, Macdonald et al. 1998).

## 28 **4.2 N<sub>2</sub>O dynamics**

29 The momentary N<sub>2</sub>O fluxes in the range from -107 to 248 (µg m<sup>-2</sup> h<sup>-1</sup>) and median emissions  
30 close to 0 (µg m<sup>-2</sup> h<sup>-1</sup>) for forest/mire types (Figure 5) were in the proximity of values for  
31 soils in similar climates (von Arnold et al. 2005a, Von Arnold et al. 2005b, Pihlatie et al.



2007, Matson et al. 2009, Ullah et al. 2009, Ojanen et al. 2010). Forest floor N<sub>2</sub>O fluxes did not differ significantly for the nine forest/mire types of the ecotone  $p = 0.637$  for the whole period from May 2005 to September 2006 probably due to the low nitrification potential of boreal forest in natural conditions (Regina et al. 1996). Low N<sub>2</sub>O fluxes of different natural forests or wetlands sometimes do not show statistically significant difference (Matson et al. 2009, Ullah et al. 2009) e.g. due to the skewedness of data around zero with few seasonal peak events. However, statistically significant differences may be found between drained and undrained forests growing on organic soils and between evergreens and deciduous plants (Arnold et al. 2005a, Arnold et al. 2005b). Our drainage class of forest/mire types ranged from well drained to poorly drained, and our forest stands changed from pine and spruce dominated (uplands) to pine-spruce-birch mixed forests (transitions). Ullah and Moore (2009, 2011) found that soil drainage and dominant tree species strongly control net nitrification rates, and that N<sub>2</sub>O emissions from poorly drained soils can be three times larger than those from well drained soils due to slower denitrification than nitrification activity.

Soil incubation studies under various moisture and temperature regimes (Pihlatie et al., 2004, Szukics et al., 2010) imply that our higher forest floor N<sub>2</sub>O emissions during the typical 2005 summer than during the dry 2006 summer (Supplement Fig. 3b) were probably induced by stimulated N turnover through the soil wetting and drying cycle at a favorable temperature. During conditions with intermediate moisture (July-September 2005) we observed also mean N<sub>2</sub>O flux of dry pine forest significantly larger than that of the paludified spruce forest (larger CT than KgK), whereas mean N<sub>2</sub>O flux of the water saturated mire was larger than four sites (VSR1-KgK, VSR1-KR, VSR1-MT, VSR1-OMT) (Fig. 8, Fig. 9). Therefore during fluctuating soil moisture, we could expect increased N<sub>2</sub>O fluxes for the normally xeric (CT) and water saturated (VSR1) site due to stimulated nitrification (CT in the rewetting phase, and VSR1 in the drying phase). During July-September in 2005, CT and VSR1 sites were also least acid along the ecotone which could favor nitrification and consequently N<sub>2</sub>O emissions through denitrification (Regina et al., 1996, Ste-Marie and Pare', 1999, Paavolainen et al., 2000). These studies reported that increasing pH by rewetting could initiate nitrification. In contrast to the less acid CT and VSR1, highly acid forest-mire transitions with the widest ranges of water level fluctuations along the forest-mire ecotone ranked into a group of sites with lower N<sub>2</sub>O fluxes. Highly acid conditions prevent the development of nitrifiers, substrate

1 affinity and nitrification, even if ammonium is available (Ste-Marie and Pare', 1999,  
2 Paavolainen et al., 2000). The fact that the net nitrification of acid sensitive nitrifiers  
3 positively increases with forest floor pH, whereas acidification reduces it, suggests that the  
4 nitrifiers in our sites were acid sensitive and not acid tolerant. The lack of nitrate renders any  
5 denitrification potential to be negligible. Although, if nitrate had been present the low pH  
6 would enhance N<sub>2</sub>O emissions due to inhibiting di-nitrogenoxide reductase and increasing  
7 N<sub>2</sub>O/N<sub>2</sub> ratio of denitrification (e.g. Weslien et al., 2009).

8  
9 In pristine peatlands nitrification positively depends on pH and negatively on water level  
10 (Regina et al., 1996) for the supply of nitrate for denitrification, as the main source of N<sub>2</sub>O  
11 emissions (Regina et al., 1996; Nykänen et al., 1995; Wray et al., 2007). Thus, during drying-  
12 rewetting periods as in July-September 2005 our sites could initiate short-term significant  
13 differences, but for the whole measurement period the lack of a statistically significant  
14 difference in N<sub>2</sub>O fluxes was probably due to its low nitrification potential. Generally the low  
15 pH and the high C/N ratios of our forest floors suggest conditions of low nitrification  
16 potential. Thus, the lack of a statistically significant difference in N<sub>2</sub>O fluxes was probably  
17 due to low nitrification potential. Other reasons could be the low field sampling frequency  
18 and relatively high noise in the data (MQL compared to low fluxes). Measuring three  
19 microsites per site could lead to missing some peak N<sub>2</sub>O emission events due to a large  
20 microscale spatial variation (von Arnold et al. 2005a). With our weekly or bi-weekly  
21 sampling frequency we could not identify larger microsite specific peak events possibly  
22 occurring after N was mobilized from e.g., fast decomposition of deciduous foliage during the  
23 drought related early peak in litterfall or during sudden soil freeze-thaw cycles (Pihlatie et al.  
24 2007). However, these events might be rare in typical boreal conditions where plants are  
25 adapted to a rapid uptake of limited rates of soil N mineralization (Hikosaka 2003, Korhonen  
26 et al. 2013, Lupi et al. 2013).

27  
28 Several studies (Martikainen et al. 1995, Regina et al. 1996) reported that peatlands in a  
29 pristine state showed small N<sub>2</sub>O emissions, but when drained nitrification rates were  
30 enhanced and N<sub>2</sub>O emissions increased depending on nutrient status (a large increase for rich  
31 sites and no increase for poor sites). The limited increase in N<sub>2</sub>O emissions during the  
32 summer drought in our mires may be therefore attributed to low nutrient levels, a low supply

of nitrate and/or low nitrification potential. Relatively low fertility may also be expected to limit the N<sub>2</sub>O emissions during the dry season of our forests and forest-mire transitions as the N<sub>2</sub>O emissions are also known to correlate with site fertility e.g., expressed as C/N ratio (Klemetsson et al 2005, Ojanen et al. 2010, Hashimoto et al. 2011).

The N<sub>2</sub>O fluxes of forest/mire types fitted by nonlinear regression models showed positive linear response to soil moisture at a depth of 5 cm and significant Gaussian type response to temperature at depths of 5 cm (Table 4, Figure 7). Although, the residuals of the moisture and temperature model were large (Figure 7) and R<sup>2</sup> was only 10%. Luo et al. (2012) demonstrated for temperate forests that N<sub>2</sub>O emissions depended nonlinearly on the soil moisture and positively on soil temperature. In our study, the weak linear response of soil moisture to N<sub>2</sub>O fluxes could be an artifact of fitting several N<sub>2</sub>O processes of different sensitivity to different forest/mire types. For example in well drained uplands the N<sub>2</sub>O fluxes may be mainly due to processes of ammonification and nitrification while in mires nitrification in the drier surface layer may be coupled with denitrification in deeper water-saturated layers (Ambus et al. 2006, Regina et al. 1996). The soil moisture and temperature from deeper layers did not significantly explain the N<sub>2</sub>O fluxes (results not shown). An active depth of 5 cm corresponding to the top of the organic layer is in agreement with Pihlatie et al. (2007) who demonstrated that N turnover in poor boreal forest soil takes place in the litter layer and that N<sub>2</sub>O emissions originate mainly from the top soil. The N<sub>2</sub>O production in our study, increased with rising soil temperature of the humus layer from 7 °C typically found after the soil thawed during spring warming and in autumn during soil cooling. These could be the periods when the nitrification potential increased; in spring probably due to mobilization of nitrogen during freeze-thaw cycles and in autumn probably due to mobilization of nitrogen from the quickly decomposing foliar litterfall (Pihlatie et al. 2007, Pihlatie et al. 2010, Luo et al. 2012).

## 5 Conclusions

The CH<sub>4</sub> fluxes of forest-mire ecotone were significantly different not only between sources or sink type forests, but also between sinks (upland and transitional types) and between sources (mires). The forest-mire transitions showed CH<sub>4</sub> oxidation rather than emission with very small sensitivity to wet and dry events. The N<sub>2</sub>O fluxes of forest mire types were

generally low. Despite small N<sub>2</sub>O peaks in spring and autumn, the N<sub>2</sub>O fluxes showed low sensitivity to soil moisture probably due to poor soil nitrogen content and the low nitrification potential of the forest/mire types in pristine conditions. Our pristine forest-mire transitions did not act as biogeochemical hotspots for CH<sub>4</sub> and N<sub>2</sub>O emissions. The organo-mineral soils of pristine forest-mire transitions should be considered as CH<sub>4</sub> oxidation types and background N<sub>2</sub>O emission types rather than landscape peak emission types.

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23

1 Table 1. Site soil water solution pH and soil properties.

2

	CT		VT		MT		OMT		OMT+		KgK		KR		VSR1		VSR2	
	mean	SE	mean	SE	mean	SE	mean	SE	mean	SE	mean	SE	mean	SE	mean	SE	mean	SE
pH 10 cm	5.57	0.36	5.14	0.42	5.24	0.08	4.68	0.39	4.58	0.30	4.46	0.14	4.37	0.22	5.06	0.39	4.80	0.44
pH 30 cm	6.20	0.06	6.18	0.02	5.91	0.13	5.30	0.11	5.53	0.04	4.91	0.10	4.55	0.08	5.32	0.15	4.79	0.19
Bulk density 0-10 cm	0.37	0.09	0.28	0.04	0.48	0.03	0.27	0.09	0.31	0.13	0.33	0.05	0.24	0.02	0.40	0.12	0.40	0.12
Bulk density10-30cm									0.92	0.07	0.31	0.12	0.85	0.03	0.90	0.07	0.90	0.07
Tot C (%) 0-10 cm	43.17		24.22		49.63		47.09		45.36		48.68		50.30		45.76		48.20	
Tot C (%) 10-30 cm									21.76		53.31		48.33		47.70		49.97	
Tot N (%) 0-10 cm	1.02		0.61		1.18		1.59		2.19		1.47		1.12		1.29		0.96	
Tot N (%) 10-30 cm									0.96		1.95		1.45		1.87		1.81	
C/N 0-10 cm	42.32		39.70		42.06		29.62		20.71		33.12		44.91		35.47		50.21	
C/N 10-30 cm									22.67		27.34		33.33		25.51		27.61	

3

4

Table 2. Parameter estimates and their standard errors for trend coefficients of CH<sub>4</sub> fluxes (μg m<sup>-2</sup> h<sup>-1</sup>) of the upland forest types (CT, VT ... OMT (Eq. (1)), and for the forest-mire transitions (OMT+, KgK, and KR (Eq. (2))). Both equations are functions of volumetric soil moisture at 10 cm (%) and soil temperature at a depth of 5 cm (°C).

Eq. (1)	bi	group bi	group bi SE	βi1	βi1 SE	βi2	βi2 SE	N	RMSE
CT	-39.345							137	35.2
VT	-26.213							143	25.1
MT	-50.984	-43.632	9.102	0.762 <sup>a</sup>	0.299	-1.249	0.223	139	25.2
OMT	-57.985							144	32.1
Eq. (2)									
OMT+	-49.898							139	22.3
KgK	-48.216	-50.248	7.507	0.638	0.105	-0.109 <sup>b</sup>	0.226	146	17.9
KR	-52.630							149	31.5
Eq. (2) soil temperature excluded from fitting									
OMT+	-51.799							139	22.3
KgK	-50.404	-52.466	6.341	0.660	0.099			146	17.9
KR	-55.196							149	31.5

p < 0.001 for all parameters, except <sup>a</sup> p = 0.011, <sup>b</sup> p = 0.629

βi1 - soil moisture at 10 cm, βi2 - soil temperature at 5 cm

Table 3. Parameter estimates and their standard errors for trend coefficients of CH<sub>4</sub> fluxes (μg m<sup>-2</sup> h<sup>-1</sup>) of the mires (VSR1, VSR2 (Eq. (3)). The Eq. 3 is a function of water table depth (cm) and soil temperature at a depth of 5 cm (°C).

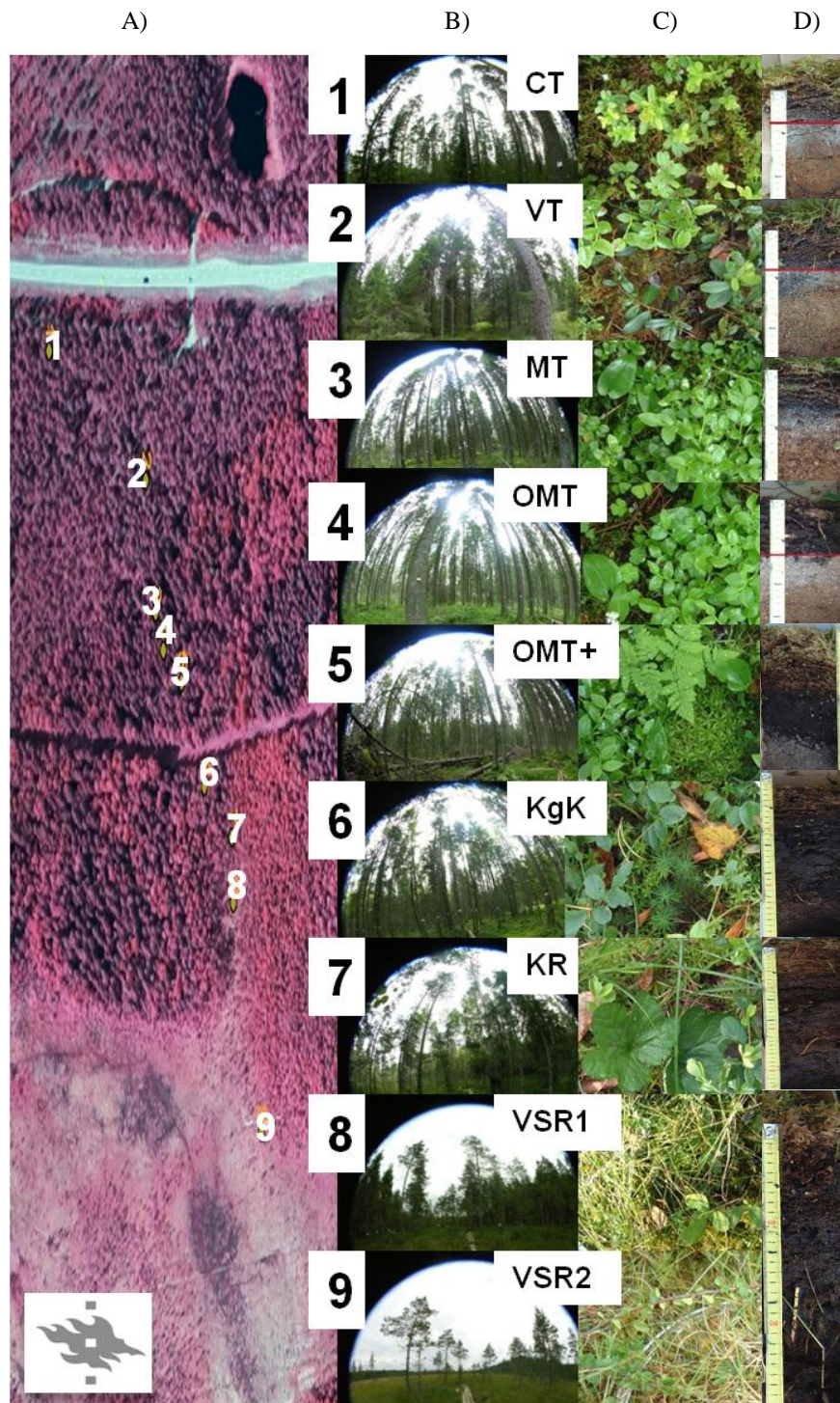
Eq. 3)	a0	a0 SE	T <sub>opt</sub>	T <sub>opt</sub> SE	T <sub>tol</sub>	T <sub>tol</sub> SE	WT <sub>opt</sub>	WT <sub>opt</sub> SE	WT <sub>tol</sub>	WT <sub>tol</sub> SE	N	RMSE
mires	1207.1	126.7	13.9	1.4	6.4	1.3	-18.0	2.2	16.6	2.8	324	656
VSR1	1570.3	155.1	13.0	0.8	5.8	0.8	-18.6	1.6	15.5	1.7	162	424
VSR2	801.3	190.8	16.6 <sup>a</sup>	6.8	8.7 <sup>b</sup>	4.5	-17.3 <sup>c</sup>	5.3	20.7 <sup>d</sup>	9.7	162	558

p values < 0.001, except <sup>a</sup> p = 0.016, <sup>b</sup> p = 0.053, <sup>c</sup> p = 0.002, <sup>d</sup> p = 0.035

Table 4. Parameter estimates and their standard errors for forest floor N<sub>2</sub>O fluxes ( $\mu\text{g m}^{-2} \text{ h}^{-1}$ ) of all forest/mire types (CT, VT ... VSR2) in one group Eq. (4). The Eq. (4) is function of volumetric soil moisture at 5 cm (%) and soil temperature at a depth of 5 cm (°C).

Eq. 4)	a0	a0 SE	T <sub>opt</sub>	T <sub>opt</sub> SE	T <sub>tol</sub>	T <sub>tol</sub> SE	N	RMSE
forests/mires	4.034	0.635	11.268	0.183	1.414	0.181	400	36.2

p < 0.001 for all parameters



3 Figure 1. A) Airborne infrared photograph shows a 450 m long boreal forest-mire ecotone located on the NE  
 4 slope of the glacial Vatiharju - Lakkasuo esker in Finland (61° 47', 24° 19'). B) The fisheye photographs show  
 5 tree stands of xeric (1), subxeric (2), mesic (3), herb-rich (4), paludified (5-7), and saturated (8-9) forest/mire  
 6 types. C) Photographs show ground vegetation and D) soil profiles of 9 forest/mire types. \*Upland forests: 1 CT –  
 7 *Calluna*, 2 VT – *Vaccinium Vitis Idea*, 3 MT – *Vaccinium Myrtillus*, 4 OMT – *Oxalis-Myrtillus*; paludified forest-mire  
 8 transition types (5 OMT+ – *Oxalis-Myrtillus* Paludified, 6 KgK – *Myrtillus* Spruce Forest Paludified, 7 KR – Spruce Pine  
 9 Swamp); sparsely forested wet mire types: 8 VSR1 and 9 VSR2 – Tall Sedge Pine Fen.



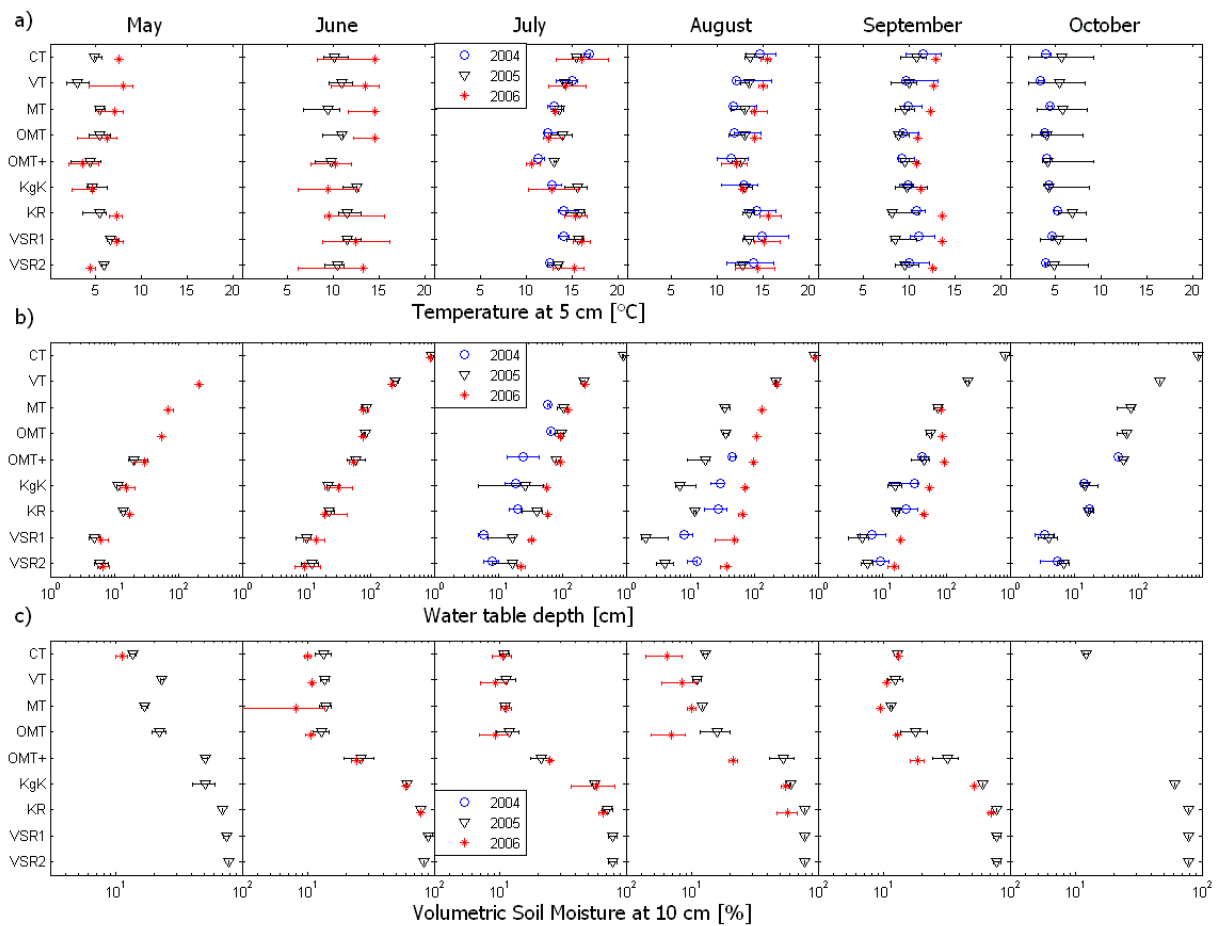


Figure 2. The panel a, b, c shows the monthly medians of environmental variables: a) soil temperature at a depth of 5 cm, b) ground water level, and c) volumetric soil moisture at 10 cm depth observed along the forest/mire ecotone during wet (2004), intermediate (2005), and dry year (2006). The top-down arrangement of sites mimics the locations on the slope (see Fig. 1). The error bars represent the 25th and 75th percentiles.

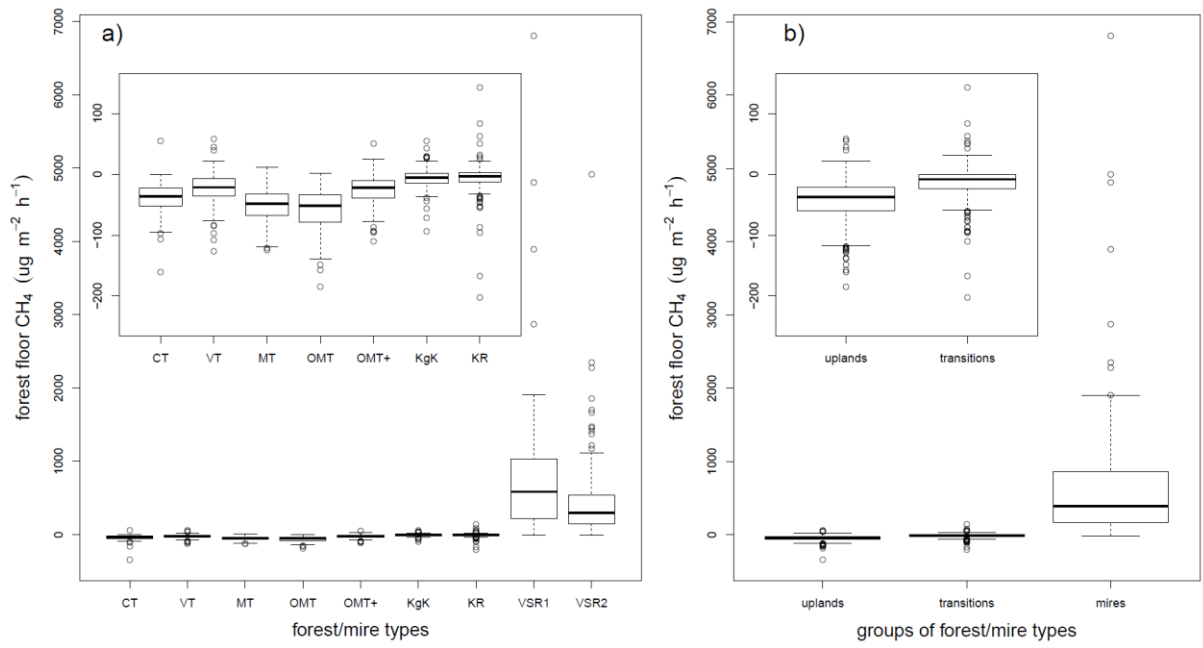
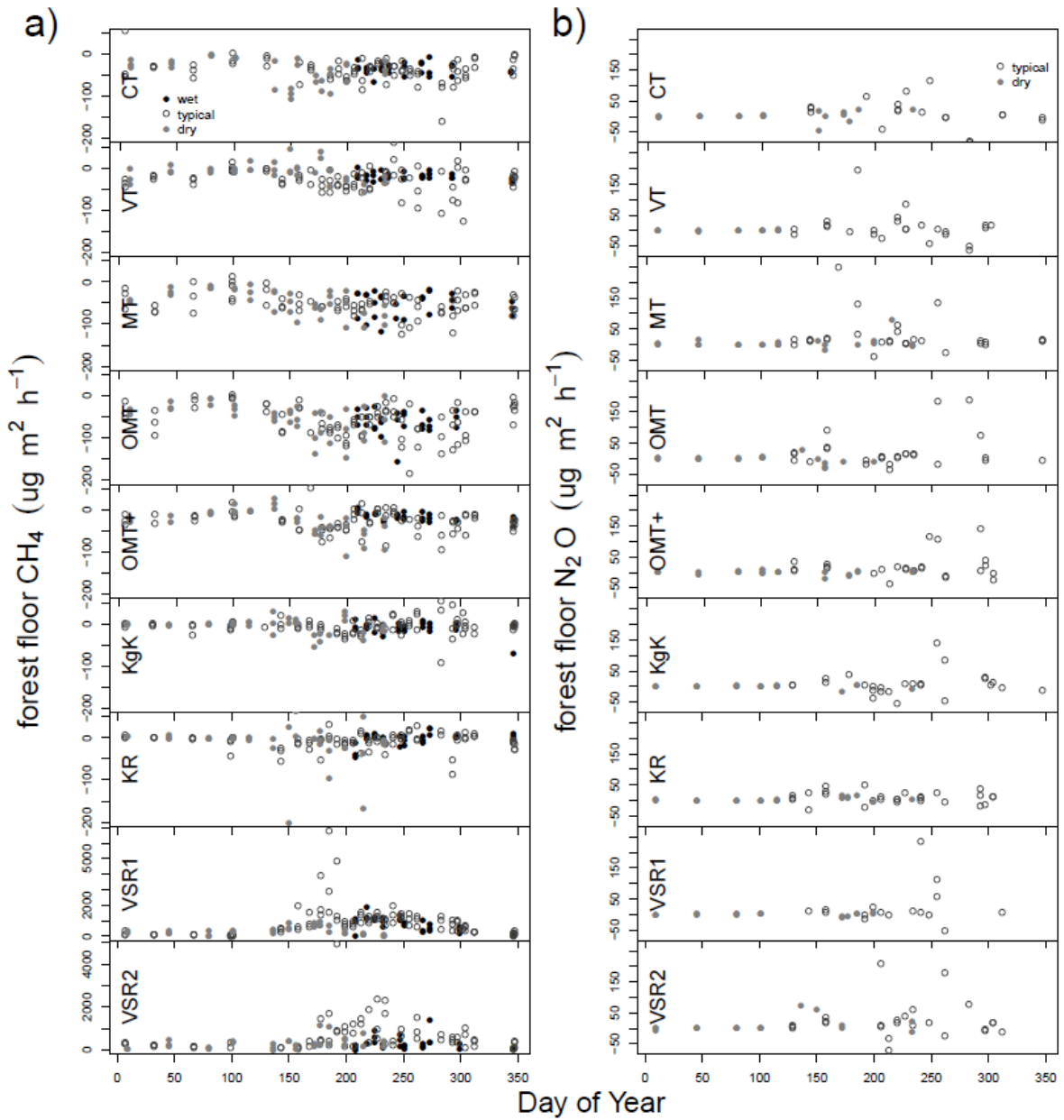


Figure 3. The boxplots of forest floor CH<sub>4</sub> fluxes (μg m<sup>-2</sup> h<sup>-1</sup>) for each forest/mire type (a), and (b) for uplands (CT, VT, MT, OMT), transitions (OMT+, KgK, KR), and mires (VSR1, VSR2) during the whole period. The left-right arrangement of sites mimics the locations on the slope (see Fig. 1).



Supplement Figure 3. The momentary forest floor gas fluxes ( $\mu\text{g m}^{-2} \text{ h}^{-1}$ ) of a)  $\text{CH}_4$  and b)  $\text{N}_2\text{O}$  in forest/mire types (uplands CT, VT, MT, OMT, transitions OMT+, KgK, KR, and mires VSR1, VSR2) as measured during the years with exceptional moisture (wet, typical, and dry). The top-down arrangement of sites mimics the locations on the slope (see Fig. 1).

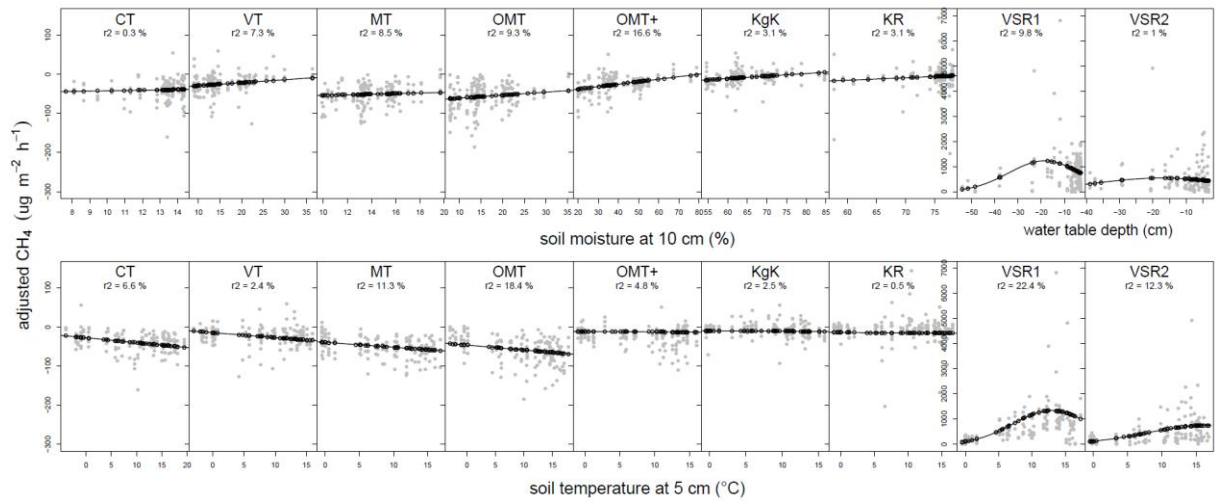


Figure 4. Comparison of sensitivity of forest floor CH<sub>4</sub> fluxes ( $\mu\text{g m}^{-2} \text{h}^{-1}$ ) to environmental factors for nine forest/mire types. In the upper panels is modeled CH<sub>4</sub> flux response to soil moisture at 10 cm (uplands and transitions) or to water table depth cm (mires) for uplands (CT, VT, MT, OMT) Eq. (1), for transitions (OMT+, KgK, KR) Eq. (2), and for mires (VSR1, VSR2) Eq. (3). Water table depth is indicated as negative when it is below the soil surface. In the lower panels, CH<sub>4</sub> flux response (Eq. (1), Eq. (2), Eq. (3)) is modeled to soil temperature at 5 cm of the same forest/mires types and during the same period as in the upper row. The CH<sub>4</sub> flux response for each individual environmental factor is illustrated so that the simulated value for each data point was recalculated by allowing only one factor at a time to vary while the others were set to their mean levels. To the adjusted CH<sub>4</sub> flux responses (black points) the corresponding residual of each data point was added in order to describe the unexplained model variation (gray points). The  $r^2$  (%) is the proportion of explained variance. The left-right arrangement of sites mimics the locations on the slope (see Fig. 1).

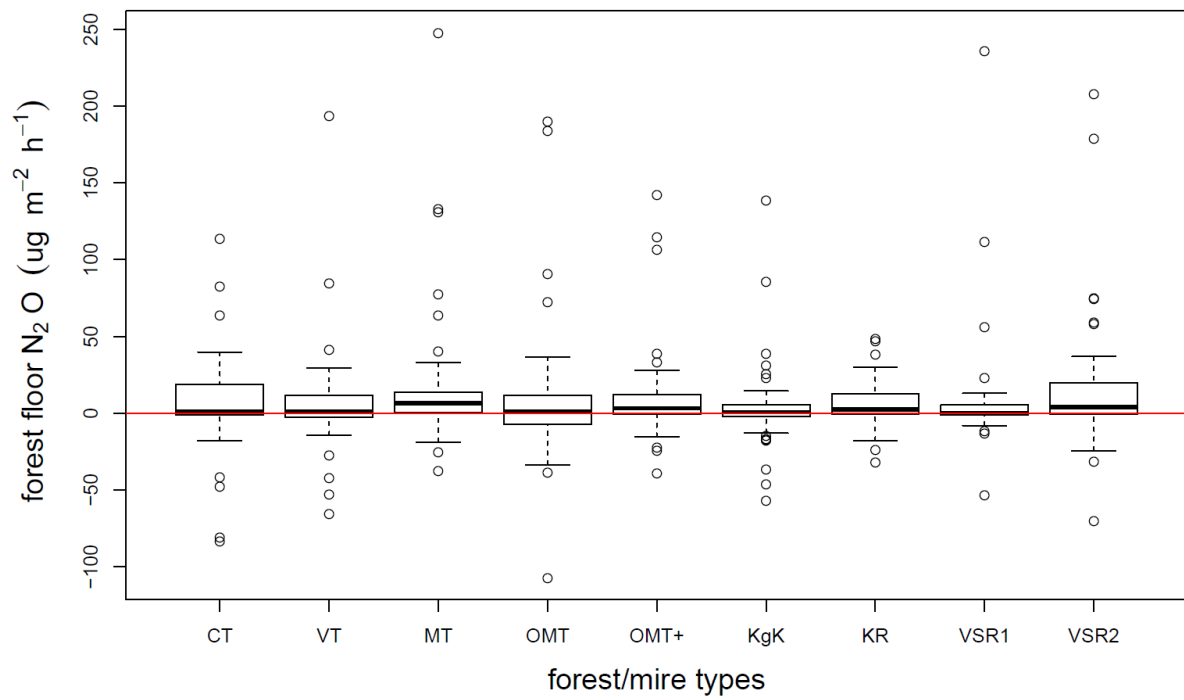


Figure 5. The boxplot of forest floor  $\text{N}_2\text{O}$  fluxes ( $\mu\text{g m}^{-2} \text{h}^{-1}$ ) for each forest/mire type (uplands - CT, VT, MT, OMT; transitions - OMT+, KgK, KR; and mires - VSR1, VSR2) during the period including typical and dry years. The left-right arrangement of sites mimics the locations on the slope (see Fig. 1).

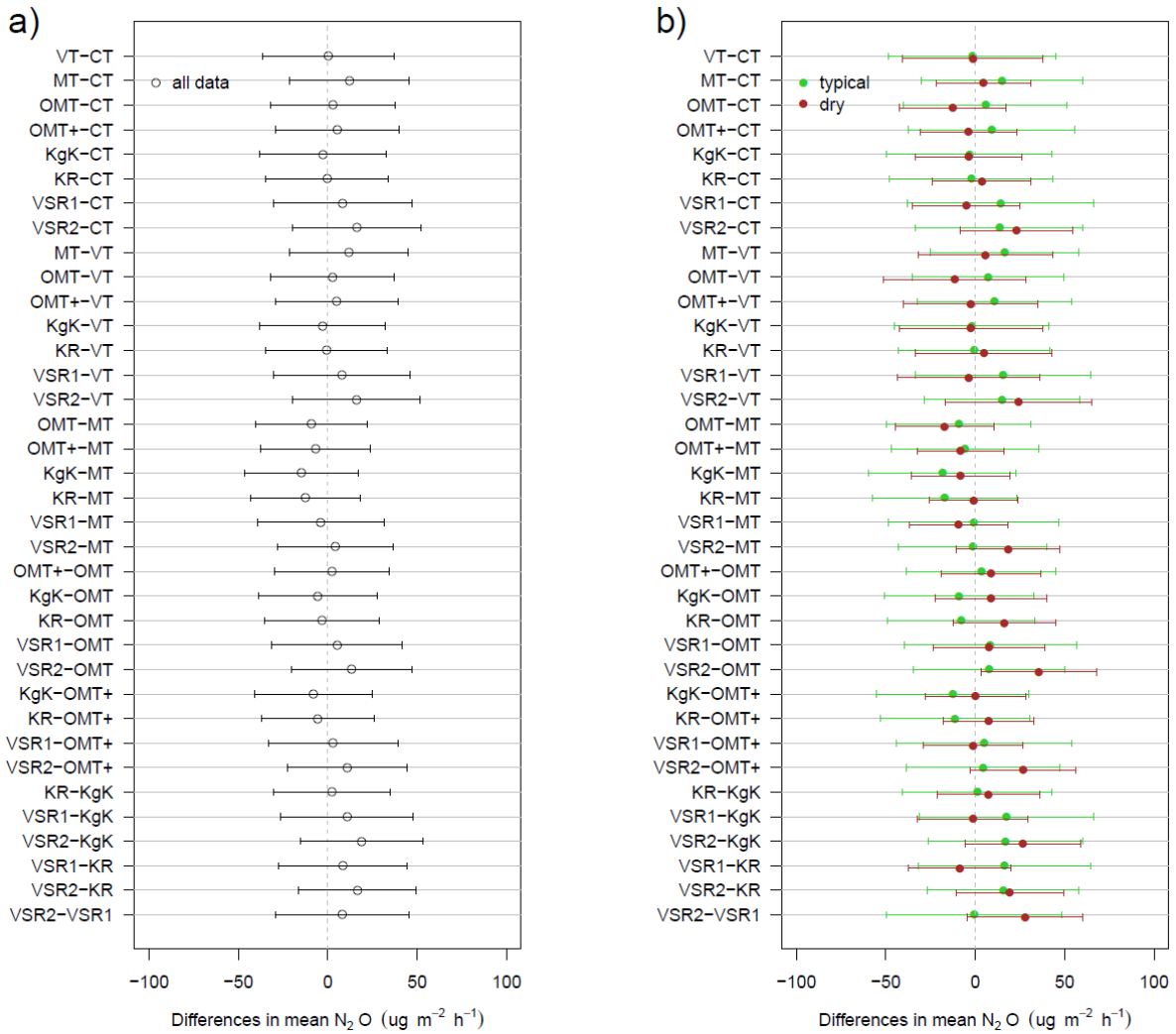


Figure 6. The post-hoc Tukey differences (error bars for 95% confidence intervals) of mean  $N_2O$  ( $\mu g m^{-2} h^{-1}$ ) fluxes from forest floor for the pair-wise comparisons of forest/mire types (uplands - CT, VT, MT, OMT; transitions - OMT+, KgK, KR; and mires - VSR1, VSR2): a) the  $N_2O$  flux differences over the whole period for a typical and dry year, b) the  $N_2O$  flux differences only for snowless seasons and separately for typical and dry years.

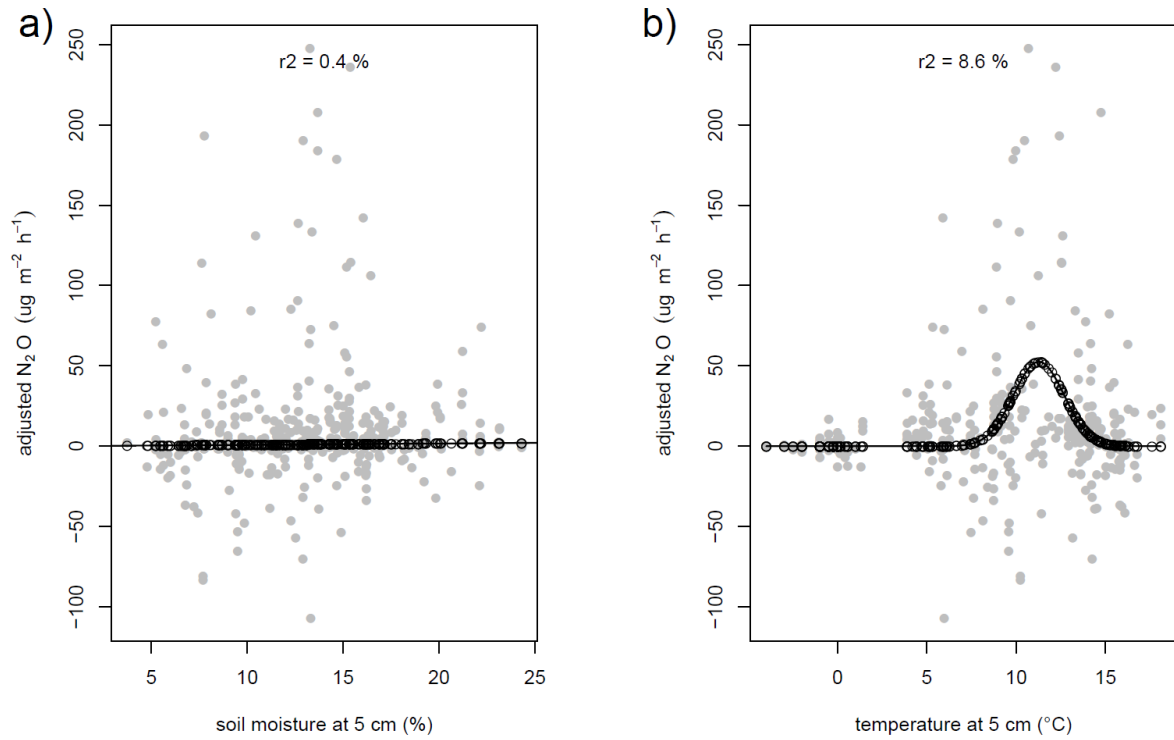


Figure 7. Sensitivity of forest floor  $N_2O$  fluxes ( $\mu g\ m^{-2}\ h^{-1}$ ) of forest/mire types together with environmental factors a)  $N_2O$  flux response to soil moisture at 5 cm, and b)  $N_2O$  flux response to soil temperature at 5 cm during the period including wet, typical, and dry years. The  $N_2O$  flux response form to each individual environmental factor is illustrated so that the simulated value by Eq. (4) for each data point was recalculated by allowing only one factor at a time to vary while the others were set their mean levels. To the adjusted  $N_2O$  flux responses (black points) the corresponding residual of each data point was added in order to describe the unexplained model variation (gray points). The  $r^2$  (%) is the proportion of explained variance.

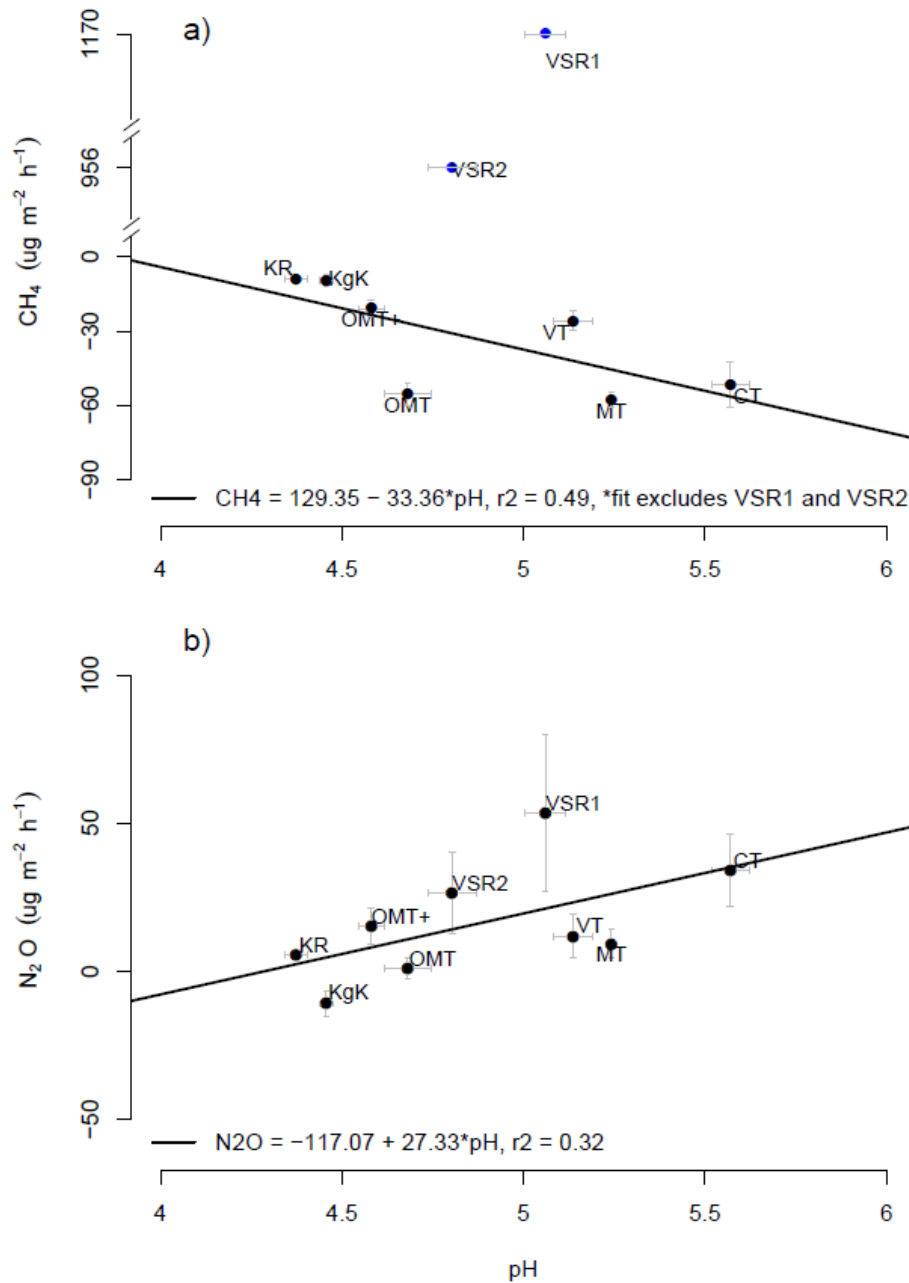
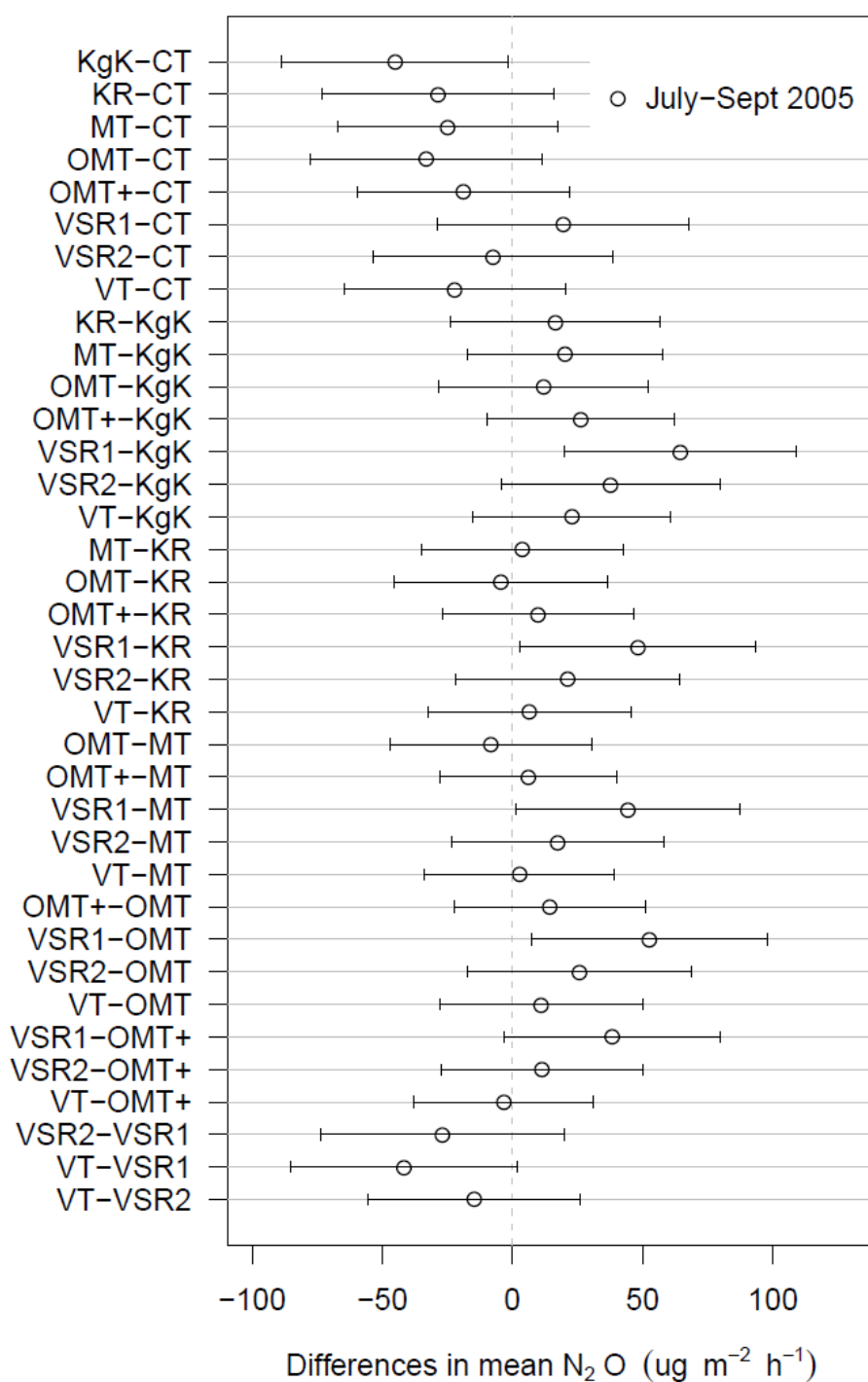


Figure 8. Scatterplot between site specific mean pH and mean flux ( $\text{ugm}^{-2}\text{g}^{-1}$ ) of a) CH<sub>4</sub> or b) N<sub>2</sub>O for the summer with intermediate moisture over the period of the soil water sampling campaign (July-September 2005). The error bars show standard error. The CH<sub>4</sub> error bars for VSR1 and VSR2 are not shown.



1



2

3 Figure 9. The post-hoc Tukey differences (error bars for 95% confidence intervals) of mean  
 4  $N_2O$  ( $\mu g m^{-2} h^{-1}$ ) fluxes from forest floor for the pair-wise comparisons of forest/mire types  
 5 (uplands - CT, VT, MT, OMT; transitions - OMT+, KgK, KR; and mires - VSR1, VSR2)  
 6 over the soil water sampling campaign period (July-September 2005).

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