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# $CH_4$ and $N_2O$ dynamics in the boreal forest–mire ecotone

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**Abstract.** In spite of advances in greenhouse gas research, the spatiotemporal $CH_4$ and $N_2O$ dynamics of boreal landscapes remain challenging, e.g., we need clarification of whether forest–mire transitions are occasional hotspots of landscape $CH_4$ and $N_2O$ emissions during exceptionally high and low ground water level events.

In our study, we tested the differences and drivers of $CH_4$ and $N_2O$ 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 a 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 $\mu g\,m^{-2}\,h^{-1}$ for $CH_4$ and from 0 to 6 $\mu g\,m^{-2}\,h^{-1}$ for $N_2O$ between forest and 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 $CH_4$ and $N_2O$ fluxes and the flux rates changed minimally between years. Methane uptake was significantly lower in poorly drained transitions than in the well-drained uplands. Water-saturated mires showed large $CH_4$ emissions, which were reduced entirely during the exceptional summer drought period. Near-zero $N_2O$ fluxes did not differ significantly between the forest and mire types probably due to their low nitrification potential. When upscaling boreal landscapes, pristine forest–mire transitions should be regarded as $CH_4$ sinks and minor $N_2O$ sources instead of $CH_4$ and $N_2O$ emission hotspots.

## 1 Introduction

Soil fertility, soil water content, and soil carbon storage of boreal forests 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 $CH_4$ and $N_2O$ 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 $CH_4$ and small sources or sinks of $N_2O$ (Moosavi and Crill, 1997; Pihlatie et al., 2007). Sparsely forested peatlands are typically large or small sources of $CH_4$ and small sources or sinks of $N_2O$ (Martikainen et al., 1995; Nykänen et al., 1995; D'Angelo and Reddy, 1998). Field $CH_4$ and $N_2O$ 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 mires. However, the area of forest–mire transitions is relatively large, e.g., in Finland, forested mires with an organic horizon $< 30$ cm cover 1.5 million hectare or approximately 7 % of the total forest area (Finnish statistical yearbook of forestry, 2013), and at the present time it is not clear whether the terrestrial–aquatic interfaces, such as the forest–mire transition, represents a biogeochemical hotspot of $CH_4$ and $N_2O$ emissions (McClain et al., 2003).

The lagg transitional zone in the forest–mire ecotone receives nutrients from the adjacent mineral soil runoff, and is thus 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 $CH_4$

and $N_2O$ 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 $CH_4$ uptake of forest soils is a result of $CH_4$ 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 $CH_4$ at higher rates than more water-saturated, acidic, and ammonium rich forested peat soils (Saari et al., 2004). In contrast to the $CH_4$ sinks of upland forest soils, and drained peatlands, natural mires emit $CH_4$ to the atmosphere (Bubier et al., 1995; Nykänen et al., 1998; Kettunen et al., 1999). $CH_4$ 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 wetness increases anoxic conditions necessary for increased methanogenesis (Juottonen et al., 2005), and as a result $CH_4$ emissions increase (Saarnio et al., 1997; Ojanen et al., 2010; Yrjälä et al., 2011). Methane production potential in peat soils generally increases positively with pH (Juottonen et al., 2005; Ye et al., 2012), whereas $CH_4$ oxidation of forested peatlands has a narrow pH optimum around 5.5 (Saari et al., 2004). Increased pH levels, e.g., through the inflow of less acidic mineral soil water, typically containing greater calcium and bicarbonate concentrations than peat water (Howie and Meerveld, 2011), could increase $CH_4$ emissions from transitions.

$N_2O$ emissions in well-drained boreal forest soils are controlled by soil moisture, pH, available nitrate, ammonium, oxygen, and carbon concentrations (Regina et al., 1996; Ullah et al., 2008). $N_2O$ production is limited by the amount of nitrogen and is subject to denitrification and nitrification processes (Ambus et al., 2006). In well-drained soils $NO_3$ limitation, anoxic microsites, and larger soil porosity may also promote $N_2O$ consumption (Frasier et al., 2010). $N_2O$ consumption of soils correlates with dehydrogenase activity, which is affected by oxidation-reduction status and possibly controlled by soil moisture (Wlodarczyk et al., 2005). The $N_2O$ consumption by soils is attributed to respiratory reduction (Conrad, 1996) caused by denitrifiers and nitrifiers (Rosenkranz et al., 2006). $N_2O$ emissions increase during drier periods through increased ammonification and nitrification (Regina et al., 1996; Nykänen et al., 1995; Von Arnold et al., 2005). In water-saturated minerotrophic peatlands nitrification supplies nitrate (Wrage et al., 2001) for denitrification, which is the main but small $N_2O$ source (Wray et al., 2007; Frasier et al., 2010). In nutrient rich mires, $N_2O$ emissions increase during drier periods through increased ammonification and nitrification (Regina et al., 1996; Nykänen et al., 1995; Von Arnold et al., 2005). Nitrification and the supply of nitrate for denitrification increases with higher pH (Regina et al., 1996). However, if nitrate is available, low pH increases $N_2O$ emissions (Weslien et al., 2009). Therefore, if nitrate were present during water level drawdown, the forest–mire transitions could become sources of $N_2O$.

Our aims were (1) to test whether forest floor $CH_4$ and $N_2O$ fluxes of the forest–mire transition differ from the typical upland forests and lowland mires of natural boreal landscapes and (2) how meteorologically different years, i.e., exceptionally wet (2004), typical (2005), and exceptionally dry (2006), affect the fluxes.

We addressed the question of whether increasing wetness in forest–mire transitions promotes $CH_4$ production, and whether dry conditions reduce $CH_4$ production and increase $N_2O$ emissions. We hypothesized that forest/mire types exhibit distinct levels of $CH_4$ and $N_2O$ fluxes due to the changing soil structure from Podzols to Histosols and due to increasing soil water content from xeric to saturated. We expected that the occasionally saturated organo-mineral soils of forest–mire transitions are variable sources of $CH_4$ and $N_2O$ fluxes. In order to evaluate the underlying factors behind $CH_4$ and $N_2O$ forest floor fluxes, we measured the fluxes and environmental variables, such as soil temperature, soil moisture, water table depth, and soil water pH, in nine sites along the forest–mire ecotone during exceptionally different meteorological conditions. In order to detect statistically significant differences between $CH_4$ and $N_2O$ fluxes of nine sites we used two-way analysis of variance, and for better understanding of flux responses to environmental factors we used linear and nonlinear regression models, and residual sensitivity analysis.

## 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′) (Ťupek 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 m and a 3.3 % slope facing NE (Fig. 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 (Fig. 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-idaea* type) on the shoulder, and mesic and herb rich Norway spruce dominated types on the back slope and footslope (MT – *Vaccinium myrtillus*

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

| | 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 density 10–30 cm | | | | | | | | | 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 | |

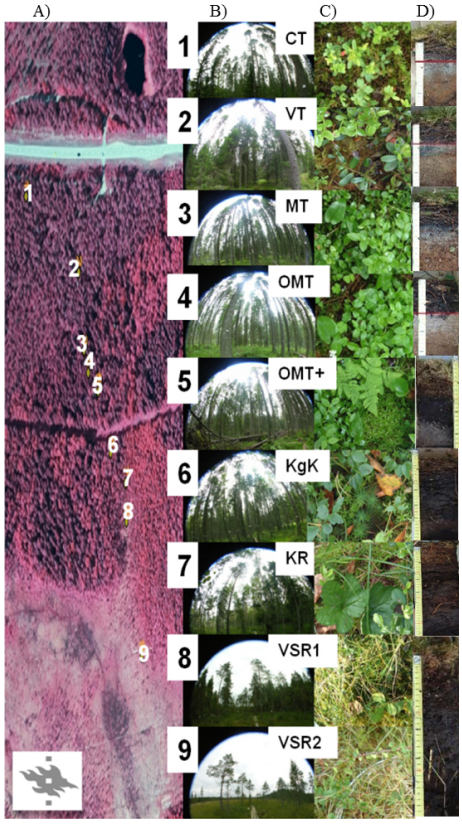


**Figure 1. (a)** Airborne infrared photograph shows a 450 m long boreal forest–mire ecotone located on the NE slope of the glacial Vatiharju–Lakkasuo esker in Finland (61°47′, 24°19′). **(b)** The fish-eye photographs show tree stands of xeric (1), subxeric (2), mesic (3), herb rich (4), paludified (5–7), and saturated (8–9) forest/mire types. **(c)** Photographs show ground vegetation and **(d)** soil profiles of nine forest/mire types. Upland forests: 1 CT – *Calluna*, 2 VT – *Vaccinium vitis-idaea*, 3 MT – *Vaccinium myrtillus*, 4 OMT – *Oxalis-Myrtillus*; forest–mire transition types: 5 OMT+ – *Oxalis-Myrtillus* paludified, 6 KgK – *Myrtillus* spruce forest paludified, 7 KR – spruce pine swamp; sparsely forested wet mire types: 8 VSR1 and 9 VSR2 – tall sedge pine fen.

type, OMT – *Oxalis-Myrtillus* type). The toe slope 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) (Fig. 1b). The forest floor vegetation is composed of site-specific mosses and vascular plants (Fig. 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 (Fig. 1d).

We measured pH during summer campaign 2005 from soil water data collected on all sites by suction cup lysimeters. Three lysimeters were installed in 10 cm and one in 30 cm depth below the soil surface in each site. 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 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 mires were less acid than transitions with pH 5.1 and 4.8 (VSR1 and VSR2, respectively) (Table 1). Collected soil water from 30 cm depth showed generally higher pH than soil water pH at 10 cm depth. 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, 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 g $cm^{-3}$ (KR) to 0.48 g $cm^{-3}$ (MT) and was approximately half of the bulk density of the organic layer from 10 to 30 cm depth (mean of transitions and mires 0.77 g $cm^{-3}$) (Table 1). The C / N ratio was determined once for each plot from the soil organic matter analyzed 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 as well as the 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 Ťupek 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 ($T_5$, $T_{15}$, and $T_{30}$) 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 (soil water content – $SWC_5$, $SWC_{10}$, and $SWC_{30}$) 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 (∅ 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 6 km 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 $CH_4$ and $N_2O$ 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 within 3-days interval of the micrometeorological measurements. If there was packed snow on the ground, the gas samples would be taken from the top and bottom layers; and the $CH_4$ ($\mu g\,m^{-2}\,h^{-1}$) and $N_2O$ ($\mu g\,m^{-2}\,h^{-1}$) 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 would be taken from three opaque, vented, closed, static chambers (∅ 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, and 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 h 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 $CH_4$ and an electron capture detector (ECD) for $N_2O$ 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 $CH_4$ and $N_2O$ concentration was analyzed. The $CH_4$ ($\mu g\,m^{-2}\,h^{-1}$) and $N_2O$ ($\mu g\,m^{-2}\,h^{-1}$) fluxes were calculated from the slope of linear regression between the set of four 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 method quantification limit (MQL) of the gas chromatograph was based on 100 subsequently analyzed samples of reference gas of known $CH_4$ and $N_2O$ concentrations (mean ± 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 four $CH_4$ or $N_2O$ concentrations of reference gas samples (22 $\mu g\,m^{-2}\,h^{-1}$ for $CH_4$ and 18 $\mu g\,m^{-2}\,h^{-1}$ for $N_2O$). 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 $CH_4$ and 49 % of $N_2O$ fluxes were discarded.

### 2.4 Statistical analysis

Two-way analysis of variance (ANOVA) was used to test whether $CH_4$ and $N_2O$ fluxes of forest/mire types have common means in wet, typical, and dry years. Post hoc Tukey HSD (honest significant difference) tests were used to test the pairwise differences between the forest and mire types and years changing from wet to dry. For $CH_4$ fluxes we ran ANOVA tests twice, first on the whole data set 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 $N_2O$ fluxes from the snow on the ground season (January–April in 2006) and the $N_2O$ 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 $CH_4$ ($\mu g\,m^{-2}\,h^{-1}$) and the gap filled half-hourly environmental variables in separate models for: (a) the upland forests on mineral soils (CT, VT, MT, OMT), and (b) forest–mire transitions on organo-mineral soils and (OMT+, KgK, and KR) (c) mires (VSR1, VSR2).

$CH_4$ fluxes ($\mu g\,m^{-2}\,h^{-1}$) 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 $CH_4$ together and their combinations iteratively by selecting the model combination of variables that were significant.

The $CH_4$ fluxes for upland forests and transitions included soil moisture at 10 cm (%) ($SWC_{10}$) and soil temperature at 5 cm (°C) ($T_5$) as predictors in separate models (Eqs. 1 and 2):

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

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

where $yu_{ij}$ and $yt_{ij}$ are the $CH_4$ flux ($\mu g\,m^{-2}\,h^{-1}$) for upland forests or transitions and for a particular $i$th forest type and the $j$th observation, $\beta_{CT}$ through $\beta_{KR}$ are the fixed effect coefficients for a particular $i$th forest type (CT, VT, MT, OMT Eq. 1, or OMT+, KgK, and KR Eq. 2), $SWC_{10}$, 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, $b_{CT}$ through $b_{KR}$ are intercepts for the random effect for a particular $i$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 $CH_4$ fluxes ($\mu g\,m^{-2}\,h^{-1}$) of mires were fitted by using a multiplicative nonlinear regression model with a combined response to water table depth and soil temperature at 5 cm Eq. (1):

$$y_{ij} = a_0 e^{\left(-0.5\left(\frac{WT-WTopt}{WTtol}\right)^2\right)} e^{\left(-0.5\left(\frac{T5-Topt}{Ttol}\right)^2\right)} + \varepsilon_{ij}, \quad (3)$$

where $y_{ij}$ is the $CH_4$ flux ($\mu g\,m^{-2}\,h^{-1}$) for the $i$th mire (VSR1,VSR2) and for the $j$th case, WT (cm) is water table depth, $T5$ (°C) is soil temperature at 5 cm, and $a_0$, WTopt, WTtol, Topt, and Ttol are parameters (Table 3).

The $N_2O$ fluxes ($\mu g\,m^{-2}\,h^{-1}$) of all forest/mire types were fitted by using one multiplicative nonlinear regression model with a combined response to soil moisture and soil temperature at 5 cm Eq. (4):

$$z_{ij} = a_0 SWC_5 e^{\left(-0.5\left(\frac{T5-Topt}{Ttol}\right)^2\right)} + \varepsilon_{ij}, \quad (4)$$

where $z_{ij}$ is the $N_2O$ flux ($\mu g\,m^{-2}\,h^{-1}$) for the $i$th mire (VSR1,VSR2) and for the $j$th case, $SWC_5$ (%) is soil moisture at 5 cm, and T5 (°C) is soil temperature at 5 cm, and $a_0$, Topt, and Ttol are parameters (Table 4).

To illustrate the sensitivity of $CH_4$ and $N_2O$ 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 $CH_4$ and $N_2O$ fluxes and pH, and soil properties we preformed the Pearson's correlation tests. The statistical analyses were performed in MATLAB R2012a (The Mathworks Inc.) and in R (R Core Team 2013) software environments.

## 3 Results

### 3.1 Micrometeorological conditions

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

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

The median water table (WT) showed the obvious rise from 10 m at the summit of the hill, to 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 the level (Fig. 2b). The seasonal WT rise in 2005 was observed between the July and 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 $\sim$ 1 m in the forest–mire transitions, and more than 0.5 m in the lowermost peatland sites.

Volumetric 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 (Fig. 2c). The largest drought reduction of SWC was in August 2006 on the well-drained sandy Podzols at the summit of the hill, and also on the poorly drained Histic Podzols on the toe slope.

### 3.2 $CH_4$ fluxes

The median fluxes from the forest floor varied from $-51$ to 586 $\mu g\,m^{-2}\,h^{-1}$ for $CH_4$ among individual sites during the entire period (Fig. 3a). The small negative $CH_4$ fluxes associated with prevailing oxidation were mostly observed

**Table 2.** Parameter estimates and their standard errors for trend coefficients of $CH_4$ fluxes ($\mu g\,m^{-2}\,h^{-1}$) of the upland forest types (CT, VT, MT, and 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 | $\beta i1$ | $\beta i1$ SE | $\beta i2$ | $\beta i2$ SE | $N$ | RMSE |
|---|---|---|---|---|---|---|---|---|---|
| CT | −39.345 | −43.632 | 9.102 | 0.762[a] | 0.299 | −1.249 | 0.223 | 137 | 35.2 |
| VT | −26.213 | | | | | | | 143 | 25.1 |
| MT | −50.984 | | | | | | | 139 | 25.2 |
| OMT | −57.985 | | | | | | | 144 | 32.1 |
| Eq. (2) | | | | | | | | | |
| OMT+ | −49.898 | −50.248 | 7.507 | 0.638 | 0.105 | −0.109[b] | 0.226 | 139 | 22.3 |
| KgK | −48.216 | | | | | | | 146 | 17.9 |
| KR | −52.630 | | | | | | | 149 | 31.5 |
| Eq. (2) soil temperature excluded from fitting | | | | | | | | | |
| OMT+ | −51.799 | −52.466 | 6.341 | 0.660 | 0.099 | | | 139 | 22.3 |
| KgK | −50.404 | | | | | | | 146 | 17.9 |
| KR | −55.196 | | | | | | | 149 | 31.5 |

$p < 0.001$ for all parameters, except [a] $p = 0.011$, [b] $p = 0.629$. $\beta i1$ – soil moisture at 10 cm, $\beta i2$ – soil temperature at 5 cm.

**Table 3.** Parameter estimates and their standard errors for trend coefficients of $CH_4$ fluxes ($\mu g\,m^{-2}\,h^{-1}$) of the mires (VSR1, VSR2, Eq. 3). Equation (3) is a function of water table depth (cm) and soil temperature at a depth of 5 cm (°C).

| Eq. (3) | $a0$ | $a0$ SE | $T_{opt}$ | $T_{opt}$ SE | $T_{tol}$ | $T_{tol}$ SE | $WT_{opt}$ | $WT_{opt}$ SE | $WT_{tol}$ | $WT_{tol}$ 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[a] | 6.8 | 8.7[b] | 4.5 | −17.3[c] | 5.3 | 20.7[d] | 9.7 | 162 | 558 |

$p$ values $< 0.001$, except [a] $p = 0.016$, [b] $p = 0.053$, [c] $p = 0.002$, [d] $p = 0.035$.

in uplands and in transitions, while mires typically showed large positive $CH_4$ fluxes associated with prevailing production. The $CH_4$ flux dynamics changed exponentially with increasing levels of the ground water table from small uptake to large emissions (Figs. 2, 3). The median $CH_4$ fluxes of uplands (CT, VT, MT, OMT), transitions (OMT+, KgK, KR), and mires (VSR1, VSR2) varied from −38, −48, and 392 $\mu g\,m^{-2}\,h^{-1}$, respectively (Fig. 3b). Momentary $CH_4$ fluxes of uplands and transitions ranged from −342 to 143 $\mu g\,m^{-2}\,h^{-1}$, whereas in mires the fluxes ranged from −12 to 6808 $\mu g\,m^{-2}\,h^{-1}$ (Fig. 3b). The median $CH_4$ fluxes for one upland (VT) and all the transitions (OMT+, KgK, KR) were found inside the range of the gas chromatograph detection limits ($MQL_{CH_4} = 22\ \mu g\,m^{-2}\,h^{-1}$). In forest–mire transitions the ground water level in August 2005 increased towards the surface and approached the levels typically found in mires (Fig. 2b), but the soil water saturation in transitions was not followed by $CH_4$ emissions such as those found in mires.

ANOVA showed that forest floor $CH_4$ 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 $CH_4$ fluxes of forest/mire types and wet, typical, and dry years F(16, 1252) = 5, $p < 0.001$. The post hoc Tukey comparison of the nine forest/mire types indicated that the mires had significantly higher $CH_4$ fluxes than the forests. 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 $CH_4$ 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 $CH_4$ fluxes of mires were highly reduced. The comparison of mean $CH_4$ 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 forest types (transitions, uplands) were not significant when analyzed together with the $CH_4$ fluxes of mires, but became significantly different F(6, 976) = 71, $p < 0.001$, when ANOVA was run without mires. Though unlike the nine forest/mire type data set, for the

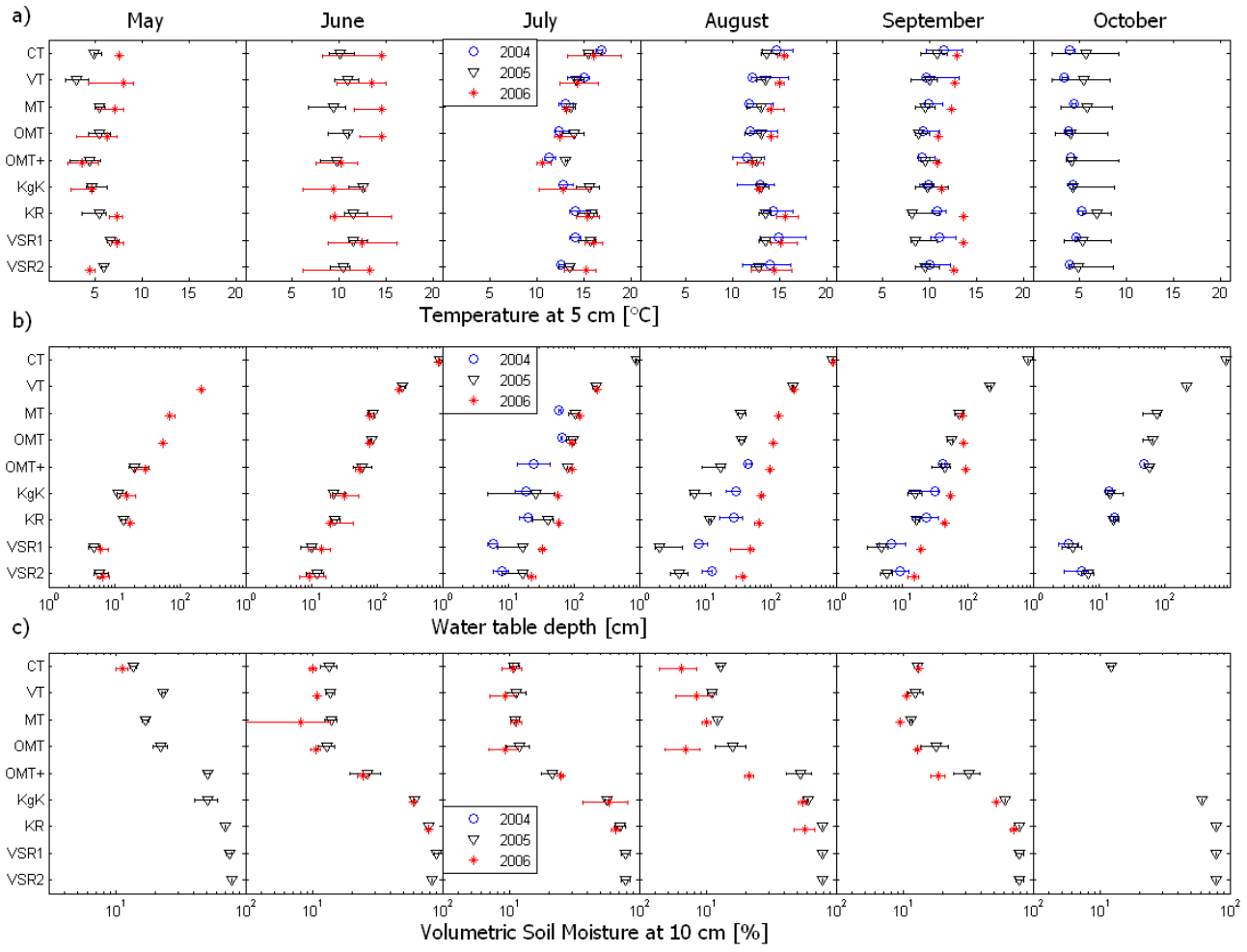


**Figure 2.** The panels **(a–c)** show the monthly medians of environmental variables: **(a)** soil temperature at a depth of 5 cm, **(b)** ground water level, and **(c)** volumetric soil moisture at 10 cm depth observed along the forest–mire ecotone during wet (2004), intermediate (2005), and dry years (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.

**Table 4.** Parameter estimates and their standard errors for forest floor $N_2O$ fluxes ($\mu g\,m^{-2}\,h^{-1}$) of all forest/mire types (CT–VSR2) in one group Eq. (4). 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 | $T_{opt}$ | $T_{opt}$ SE | $T_{tol}$ | $T_{tol}$ 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.

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 $CH_4$ uptake of the upland forests ($-42.9\,\mu g\,m^{-2}\,h^{-1}$) was for the whole period significantly larger than the mean $CH_4$ uptake of the forest–mire transitions ($-12.8\,\mu g\,m^{-2}\,h^{-1}$) according to Welch's two sample $t$ test $t(994) = 15.56$, $p < 0.001$. The post hoc Tukey comparison of the differences in the mean $CH_4$ 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]). The post hoc Tukey comparisons showed non-significant $p$ values for 4 of the 21 pairs of $CH_4$ fluxes of transitional and upland forest types (MT–CT 0.056, OMT+–VT 0.965, OMT–MT 0.431, and KR–KgK 0.999).

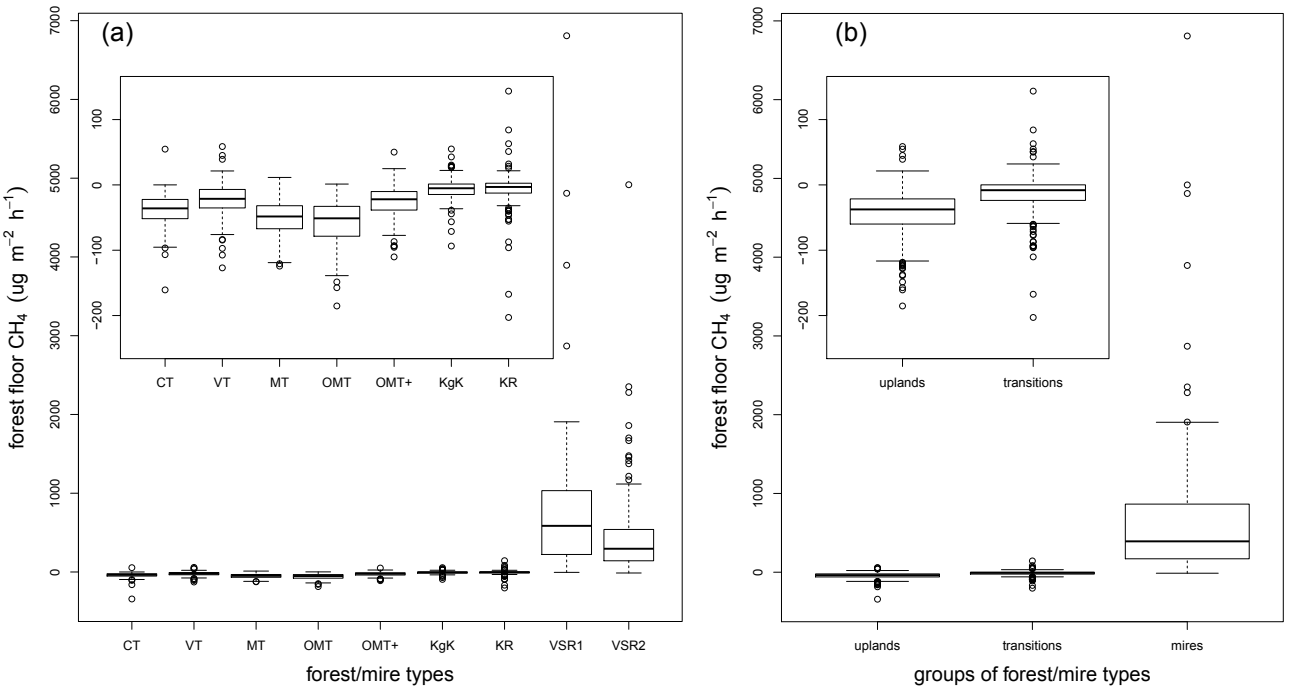


**Figure 3.** The box plots of forest floor $CH_4$ fluxes ($\mu g\,m^{-2}\,h^{-1}$) for each forest/mire type (a), and (b) for uplands (CT, VT, MT, OMT), transitions (OMT+, KgK, KR), and mires (VSR1, VSR2) during the whole period. The left–right arrangement of sites mimics the locations on the slope (see Fig. 1).

### 3.3 Factors controlling $CH_4$ fluxes

The mean level of $CH_4$ fluxes of upland and transitional forests differed (Table 2, parameter group bi), though the sensitivity response to environmental factors was similar (Fig. 4). The largest part of the $CH_4$ 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 $CH_4$ flux response for the upland and transitional forest sites 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 $CH_4$ flux response between dry and water-saturated soil differed by $50\,\mu g\,m^{-2}\,h^{-1}$. A stronger gradient than that in the soil moisture was detected by modeling stronger temperature responses of $CH_4$ fluxes for the uplands and the nearly flat response for the transitions (Fig. 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 $CH_4$ fluxes towards the extreme ends. The optimum water level for $CH_4$ emissions was 18 cm below the surface with 16.6 cm tolerance which is deviation of water level up to 60 % of $CH_4$ flux maximum (Fig. 4; $p < 0.001$, $WT_{opt}$ and $WT_{tol}$ in Table 3). Optimum near-surface peat temperature for the $CH_4$ emissions was found at 13.9 °C with 6.4 °C tolerance (Fig. 4; $p < 0.001$, $T_{opt}$ and $T_{tol}$ in Table 3).

### 3.4 $N_2O$ fluxes

During the typical and dry years the momentary forest floor $N_2O$ fluxes of forest/mire types ranged from −107 to $248\,\mu g\,m^{-2}\,h^{-1}$. The median $N_2O$ fluxes were similar for the forest/mire types and ranged only from 0 to $6\,\mu g\,m^2\,h^{-1}$ (Fig. 5). The median $N_2O$ fluxes of all forest/mire types were found inside the range of the method quantification limits ($MQL_{N_2O} = 18\,\mu g\,m^{-2}\,h^{-1}$). The $N_2O$ fluxes of the snow on the ground period were significantly lower than the $N_2O$ fluxes of the snowless period according to Welch's two sample $t$ test $t(297) = 5.094$, $p < 0.001$. Forest floor $N_2O$ 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 $N_2O$ fluxes were significantly different in typical and dry snowless seasons $F(1, 284) = 6.157$, $p < 0.014$. $N_2O$ 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) (Fig. 6).

In general $N_2O$ fluxes were low and did not show clear spatial differences in relation to increasing soil moisture from

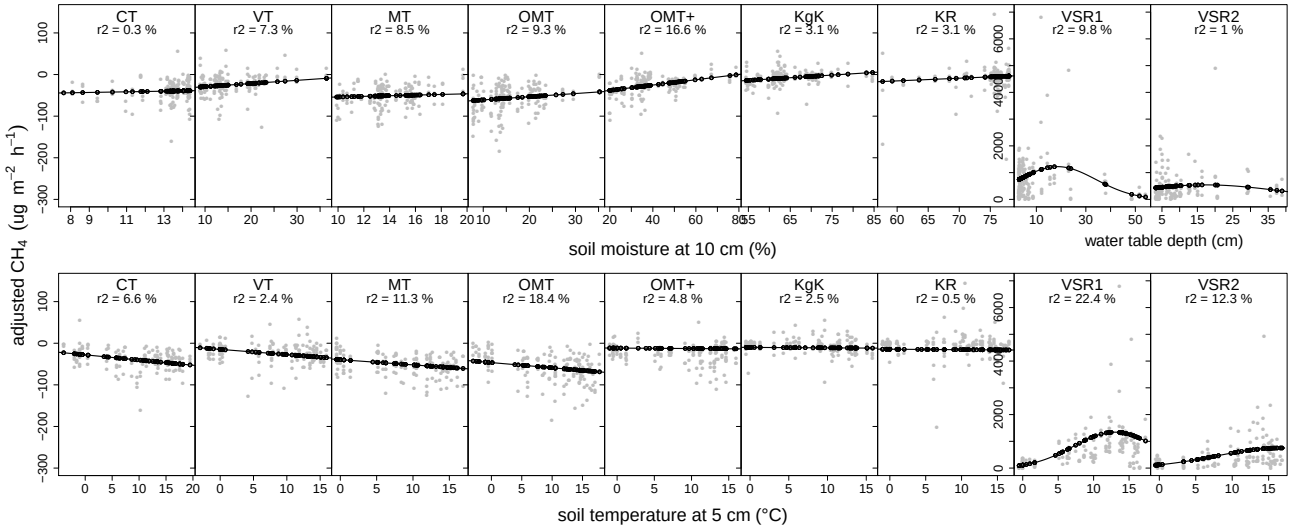


**Figure 4.** Comparison of sensitivity of forest floor $CH_4$ fluxes ($\mu g\,m^{-2}\,h^{-1}$) to environmental factors for nine forest/mire types. Modeled in the upper panels is $CH_4$ flux response to soil moisture at 10 cm (uplands and transitions) or to water table depth (cm) (mires) for uplands (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 above the soil surface. In the lower panels, $CH_4$ flux response (Eqs. 1–3) is modeled to soil temperature at 5 cm of the same forest/mires types and during the same period as in the upper panel. The $CH_4$ 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 other was set to its mean level. To the adjusted $CH_4$ 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).

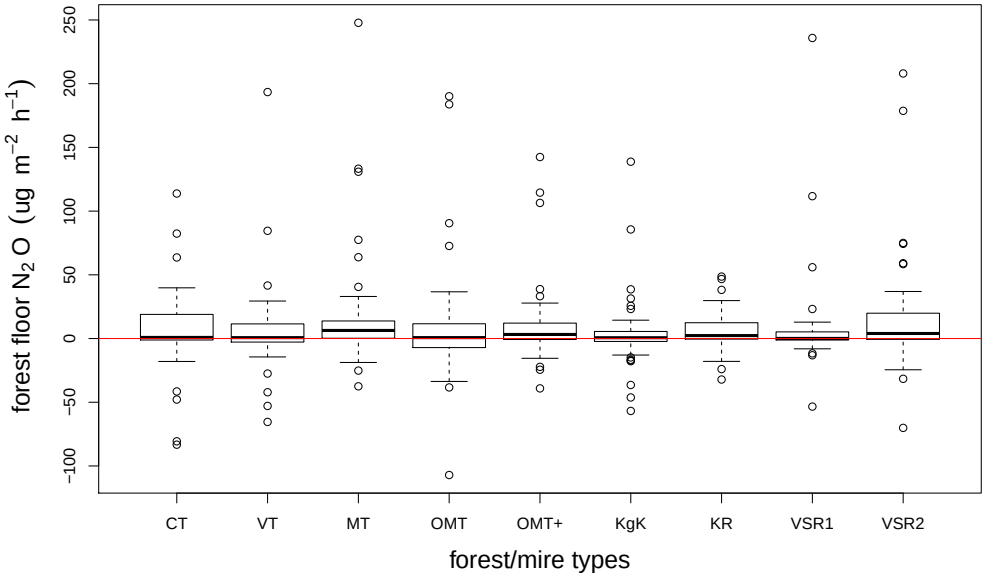


**Figure 5.** The box plot of forest floor $N_2O$ fluxes ($\mu g\,m^{-2}\,h^{-1}$) for each forest/mire type (uplands – CT, VT, MT, OMT; transitions – OMT+, KgK, KR; and mires – VSR1, VSR2) during the period including typical and dry years. The left–right arrangement of sites mimics the locations on the slope (see Fig. 1).

xeric uplands to water-saturated mires, but the $N_2O$ fluxes were lower in the dry than in the typical year. The post hoc Tukey tests of means and 95 % confidence limits of $N_2O$ fluxes for all pairs (except one) showed insignificant forest/mire type pairwise differences during the whole period and also during the snowless periods of wet or dry years (Fig. 6). The significant $N_2O$ flux difference for VSR2–OMT

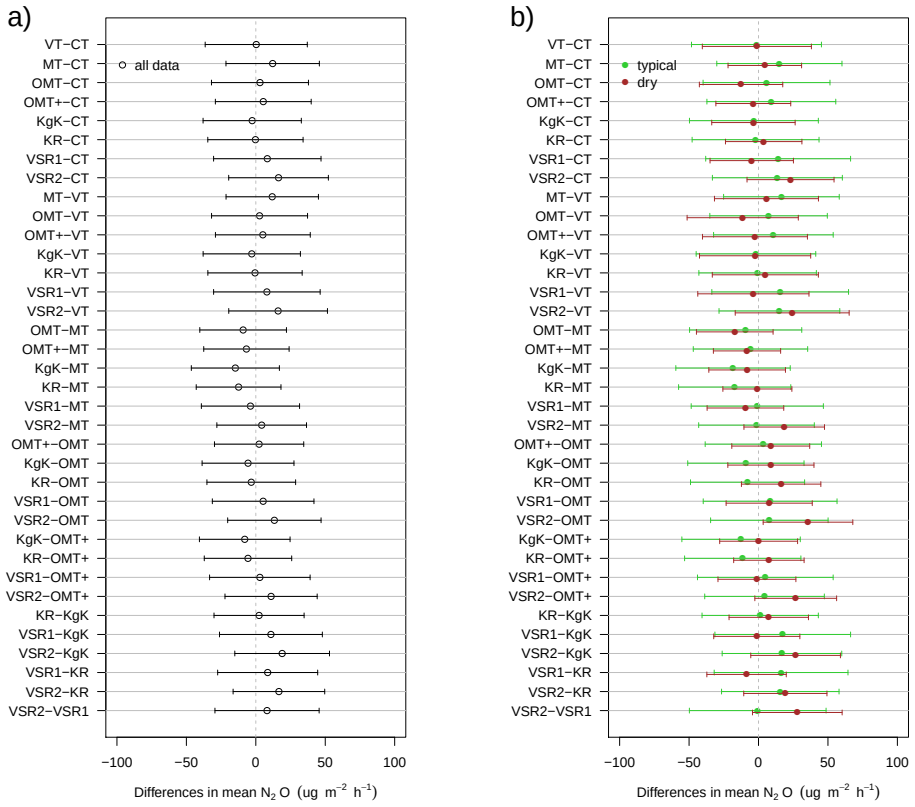


**Figure 6.** The post hoc Tukey differences (error bars for 95 % confidence intervals) of mean $N_2O$ ($\mu g\,m^{-2}\,h^{-1}$) fluxes from the forest floor for the pairwise comparisons of forest/mire types (uplands – CT, VT, MT, OMT; transitions – OMT+, KgK, KR; and mires – VSR1, VSR2): **(a)** the $N_2O$ 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.

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 $N_2O$ 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, Fig. 7). The modeled Gaussian type response showed optimum $N_2O$ 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 $CH_4$ and $N_2O$ flux

The site-specific momentary $CH_4$ and $N_2O$ 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 $N_2O$ and pH at 10 cm). Neither was any correlation found between pH and momentary $CH_4$ on the ecotone level. However, when mires were excluded, Pearson correlation between momentary $CH_4$ fluxes and soil water pH was significant ($r = -0.32$, $p < 0.001$). Mean values of summer 2005 $CH_4$ of upland forests and forest–mire transition were negatively correlated with mean pH ($CH_4 = 129.35–33.36 \times$ pH, $r^2 = 0.49$; Fig. 8a). The ecotone $N_2O$ fluxes were significantly correlated with pH ($r = 0.174$, $p = 0.004$). The mean $N_2O$ values of sites increased with mean pH ($N_2O = -117.07 + 27.33 \times$ pH, $r^2 = 0.32$; Fig. 8b). However, the post hoc Tukey differences of mean $N_2O$ fluxes from the forest floor for the pairwise comparisons of forest/mire types were not significant for 31 pairs and mean $N_2O$ flux differences were significant only for 5 pairs (KgK–CT, VSR1–KgK, VSR1–KR, VSR1–MT, VSR1–OMT, Fig. 9). We did not find significant correlation between site-specific mean $CH_4$ and $N_2O$ flux and bulk density and/or C / N ratio.

## 4 Discussion

### 4.1 $CH_4$ dynamics

The forest/mire types significantly differed in forest floor $CH_4$ fluxes and between wet, typical, and dry years. As expected, the largest difference was found between emissions of mires and the small uptake of other forest types. However, $CH_4$ uptake also showed significant differences between the

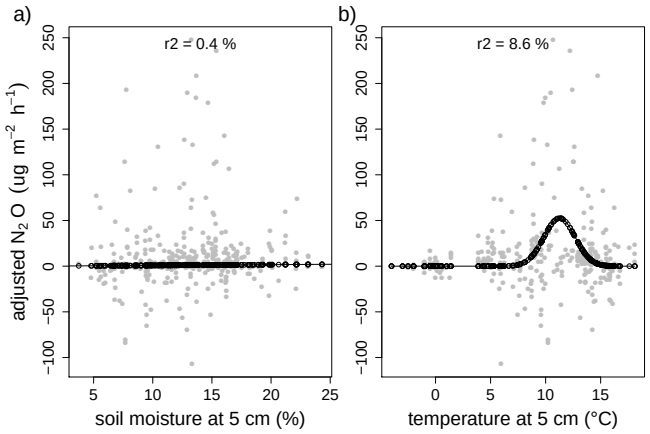


**Figure 7.** Sensitivity of forest floor $N_2O$ fluxes ($\mu g\,m^{-2}\,h^{-1}$) of forest/mire types together with environmental factors: **(a)** $N_2O$ flux response to soil moisture at 5 cm, and **(b)** $N_2O$ flux response to soil temperature at 5 cm during the period including wet, typical, and 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 other was set to its mean level. 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.

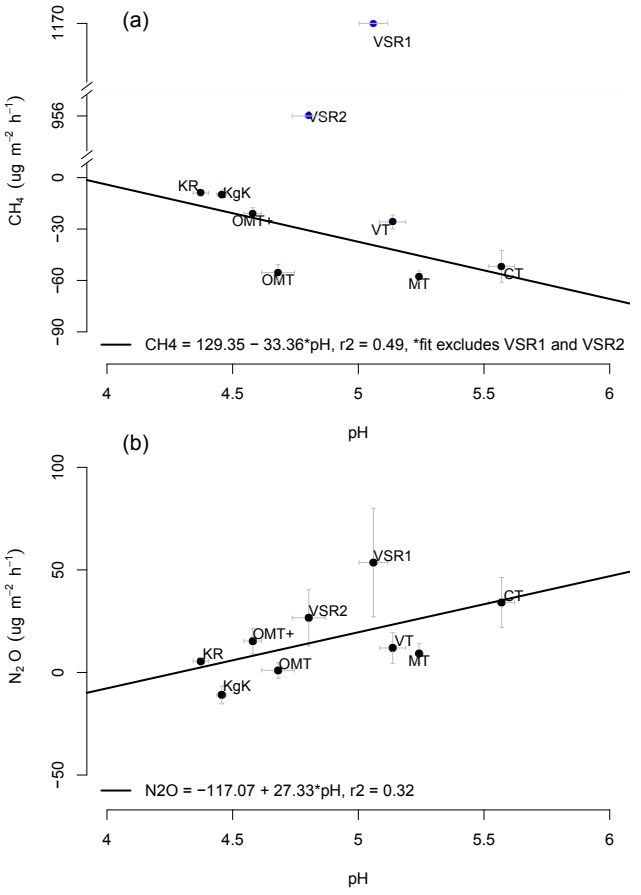


**Figure 8.** Scatterplot between site-specific mean pH and mean flux ($\mu g m^{-2}\,h^{-1}$) of **(a)** $CH_4$ or **(b)** $N_2O$ of summer with intermediate moisture over the period of soil water sampling campaign (July–September 2005). Error bars show standard error. The $CH_4$ error bars for VSR1 and VSR2 are not shown.

forest types on mineral soil (uplands) and organo-mineral soil (transitions). Our study demonstrated that the $CH_4$ flux response to soil moisture changes with the relatively small mesoscale levels of a forest–mire ecotone (450 m long transect) (Fig. 4). The $CH_4$ flux sensitivity to soil moisture showed a positive linear response to $CH_4$ oxidation for the drier soils of transitions and uplands. Alternatively, $CH_4$ emission in mires showed a Gaussian form response to water level depth with a reduction of the optimum under saturated or dry peat conditions (Fig. 4). 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 $CH_4$ emissions during short-term water level fluctuations.

The lack of an increase in $CH_4$ emissions during increased ground water levels in the transitions in our study could be attributed more to the relatively slow response of $CH_4$ producing bacteria than to the effectiveness of $CH_4$ 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 $CH_4$ 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 $CH_4$ producing bacteria to relocate and/or adapt to water-saturated conditions. The methane production potential of mire varies in relation to methanogen communities, substrate availability, pH, and temperature (Juottonen et al., 2005, Juottonen et al., 2008). Unlike open mires, in drier conditions (similar to our forest–mire margin) decreases in the methanogen community are associated with low $CH_4$ production potential and with low emissions (Yrjälä et al., 2011). In the forest–mire margin, a relatively small population of methanotrophic microbes coupled with *Sphagnum* mosses and low $CH_4$ oxidation potential, related to low $CH_4$ concentrations in moss layer, could indicate low production potential (Larmola et al., 2010). It is known that water level depth is a major control of $CH_4$ oxidation, and that *Sphagnum* species originally not oxidising $CH_4$ need from several days to a month to activate methanotrophs through a water phase (Larmola et al., 2010; Putkinen et al., 2012).

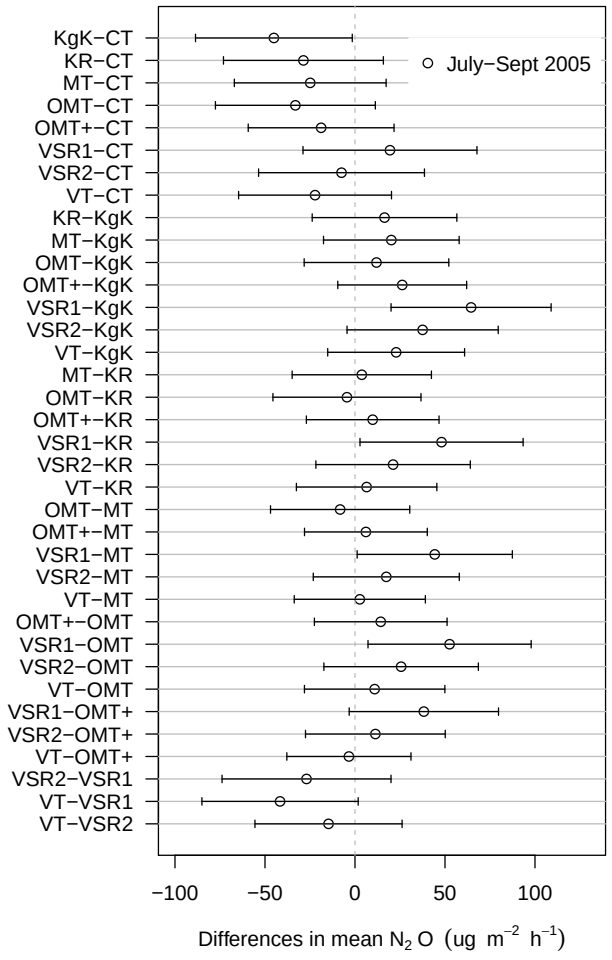


**Figure 9.** The post hoc Tukey differences (error bars for 95 % confidence intervals) of mean $N_2O$ ($\mu g m^{-2} h^{-1}$) fluxes from the forest floor for the pairwise comparisons of forest/mire types (uplands – CT, VT, MT, OMT; transitions – OMT+, KgK, KR; and mires – VSR1, VSR2) over the period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

Temporally water-saturated soil layers of pristine forest–mire transitions had low $CH_4$ emissions possibly due to low pH, 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). Activity of methanotrophic microbes is also pH dependent with optimum above 5 (Danilova and Dedysh, 2013; Saari et al., 2004). Our forest–mire transitions had mean pH below 5 and demonstrated lower net $CH_4$ uptake rates in comparison to upland forests on mineral soils (Fig. 8), which is in line with Saari et al. (2004). In spite of positive pH and $CH_4$ correlation found for the group of transitions and uplands together, the net $CH_4$ sink of upland well-drained mineral soil sites was primarily determined by high oxygen content. Small momentary $CH_4$ emissions (Supplement Fig. S3a) observed in forest–mire transitions also indicated potential for occasionally higher production than oxidation.

Beside differences in microsite soil water saturation, pH, and microbial communities, also plant communities (e.g., Saarnio et al., 1997; Strom et al., 2003; Riutta et al., 2007; Dorodnikov et al., 2011) play an important role in explaining net $CH_4$ emissions. In the forest–mire margin sites (KR and KgK) vascular plants (Fig. 1c) contributed to net forest floor $CH_4$ emissions (Fig. S3), if methane production occasionally increased. It is known that transport of recently photosynthesized carbon downwards to plant roots feeds microbial methane production (Alm et al., 1997; Strom et al., 2003; Dorodnikov et al., 2011). Aerenchyma of vascular plants transports most of produced $CH_4$ from peat to the atmosphere without oxidation in the acrotelm, and increases net $CH_4$ emissions (Hornibrook et al., 2009, Dorodnikov et al., 2011). A smaller amount of produced methane that is transported by pore water diffusion is efficiently oxidized by methanotrophs in the aerobic layer of peat and *Sphagnum* mosses (Hornibrook et al., 2009; Larmola et al., 2010).

Small $CH_4$ emissions as observed in relatively dry Scots pine dominated forests (VT – *Vaccinium vitis-idaea* type) (Fig. 3) with sandy Podzols soil and ground water depths around 2 m, have been occasionally found in mineral soil forests in other studies. The occasional mineral soil $CH_4$ effluxes suggested that plants' deepest roots transport $CH_4$ via the transpiration stream (Megonigal and Guenther 2008). Ullah et al., (2009) found that Spruce forest soils produced $CH_4$ only during the spring thaw season but later under drier summer conditions soils switched to $CH_4$ consumption. In our study the rare occurrence of small $CH_4$ emissions from forest soils differed between forest types and cannot only be attributed to increased soil moisture levels of microsites or transport from deep ground water sources. Small $CH_4$ emissions could be also partly attributed to the random noise in measurements. However, all the data showed a significant reduction of $CH_4$ uptake with increasing soil moisture at 10 cm, this may be associated with oxidation processes.

The form of dependence of $CH_4$ flux on soil moisture is better known from soil incubation studies (Pihlatie et al., 2004; Ullah et al., 2007) than from field studies, as field soil moisture ranges may be narrow (e.g., Nakamo et al., 2004). In order to describe the sensitivity of $CH_4$ uptake to moisture in the field we need a large amount of data covering a wide range of soil conditions (e.g., Hashimoto et al., 2011). In our study soil moisture varied between xeric and saturated conditions both spatially along the ecotone and temporally between years. Temporal soil water saturation in transitional forest–mire sites rather reduced $CH_4$ oxidations than promoted such $CH_4$ emissions as found in nearby permanently saturated mires. Beside the sensitivity of $CH_4$ fluxes to moisture we also observed sensitivity to soil temperature (Fig. 4) possibly also reflecting the role of soil physiochemical properties and/or the activity of methanogens. The linearly increasing $CH_4$ oxidation rates with temperature in up-

land forest types could reflect the importance of soil physiochemical properties, whereas the Gaussian form may also reflect a biological driven response in mires.

In our upland forests the role of soil physiochemical and microbiological drivers may have contributed to the fact that the temperature and moisture explained just 10 % of the variation. Although our mean $CH_4$ data did not show significant correlations with bulk density, the porous organic horizon is known to enable larger diffusion and $CH_4$ oxidation (Nakamo et al., 2004; Ullah and Moore 2011). It was difficult to assess the differences in sensitivity of $CH_4$ oxidation because of poor MQL and low fluxes of $CH_4$ oxidation. The absolute levels of the temperature effect on $CH_4$ fluxes in forest–mire transitions caused part of the signal to be mixed with variable sources of sampling errors and gas chromatograph precision errors. Though, in transitions both soil physiochemical and microbiological drivers may be important for $CH_4$ oxidations, as our forest–mire transitions showed a significant relation to soil moisture but not to temperature. The weak response of $CH_4$ oxidation to temperature was in contrast to the strong response to moisture and bulk density found in forests growing on mineral soils (Hashimoto et al., 2011). However, Nakamo et al. (2004) reported a clear relation with temperature but not with moisture for boreal birch forest (similar to our KR – spruce pine swamp).

In mires, the form of $CH_4$ sensitivity to temperature and water table depth may be also determined by differences in pH, and the composition of microbial and plant functional communities (Bubier et al., 1995; Jaatinen et al., 2004; Juottonen et al., 2005, 2008; Larmola et al., 2010; Riutta et al., 2007; Saarnio et al., 1997; Saari et al., 2004; Yrjälä et al., 2011). The $CH_4$ emissions in VSR1 were larger than in VSR2 (Fig. 4). Differences in pH could favor methanogen activity in less acid fen (Jouttonen et al., 2005; Yrjälä et al., 2011; Ye et al., 2012). Different coverage of vascular aerenchymous plants and *Sphagnum* mosses between VSR1 and VSR2 could affect site-specific $CH_4$ production and oxidation potentials. For example in VSR1 the water level was closer to the surface, and the lawn microsites had abundance of *Menyanthes* species (Fig. 1c), which are known to mediate higher $CH_4$ transport (Bubier et al., 1995; Macdonald et al., 1998), whereas in VSR2 *Menyanthes* species was absent. Shallower form of $CH_4$ sensitivity to water table in a hummock type fen VSR2 than in lawn type of fen VSR1 could resulted from differences in plant mediated $CH_4$ emissions (e.g., Riutta et al., 2007; Hornibrook et al., 2009; Dorodnikov et al., 2011) or $CH_4$ oxidation potential between *Sphagnum* species (Larmola et al., 2010). For example in the study by Saarnio et al. (1997) the $CH_4$ flux response to water level would be exponential if it accounted only for emissions from hummock and *Carex* lawn microsites, but the response was Gaussian for flark, hummock, *Eriophorum* lawn and *Carex* lawn microsites taken together.

### 4.2 $N_2O$ dynamics

The momentary $N_2O$ fluxes in the range from $-107$ to 248 ($\mu g\,m^{-2}\,h^{-1}$) and median emissions close to 0 ($\mu g\,m^{-2}\,h^{-1}$) for forest/mire types (Fig. 5) were in the proximity of values for soils in similar climates (Von Arnold et al., 2005a, b, Pihlatie et al., 2007; Matson et al., 2009; Ullah et al., 2009; Ojanen et al., 2010). Forest floor $N_2O$ 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 forests in natural conditions (Regina et al., 1996). In contrast to our results, Ullah and Moore (2009, 2011) found that soil drainage and dominant tree species strongly control net nitrification rates, and that $N_2O$ emissions from poorly drained soils can be three times larger than those from well-drained soils due to slower denitrification than nitrification activity. Statistically significant differences were also found between drained and undrained forests growing on organic soils and between evergreens and deciduous plants (Von Arnold et al., 2005a, b).

Soil incubation studies under various moisture and temperature regimes (Pihlatie et al., 2004; Szukics et al., 2010) imply that our higher forest floor $N_2O$ emissions during typical summer 2005 than during dry summer 2006 (Supplement Fig. 3b) were probably induced by stimulated N turnover through the soil wetting and drying cycle under favorable temperature. During conditions with intermediate moisture (July–September 2005) we also observed mean $N_2O$ flux of dry pine forest significantly larger than that of paludified spruce forest (larger CT than KgK), whereas mean $N_2O$ flux of water-saturated mire was larger than four sites (VSR1–KgK, VSR1–KR, VSR1–MT, VSR1–OMT) (Figs. 8, 9). Therefore, during fluctuating soil moisture, we could expect increased $N_2O$ fluxes of a normally xeric (CT) and water-saturated (VSR1) site due to stimulated nitrification (CT in rewetting phase, and VSR1 in drying phase). During July–September 2005, CT and VSR1 sites were also least acid along the ecotone which could favor nitrification and consequently $N_2O$ emissions through denitrification (Regina et al., 1996; Ste-Marie and Pareé, 1999; Paavolainen et al., 2000). These studies reported that the increase of pH by rewetting could initiate nitrification. In contrast to less acid CT and VSR1, the more acid forest–mire transitions with the widest range of water level fluctuations ranked into a group of sites with lower $N_2O$ fluxes. Highly acid conditions prevent development of nitrifiers, substrate affinity, and nitrification, even if ammonium is available (Ste-Marie and Pareé, 1999; Paavolainen et al., 2000). The fact that net nitrification of acid sensitive nitrifiers positively increases with forest floor pH, whereas acidification reduces it, suggests that nitrifiers in our sites were acid sensitive and not acid tolerant. The lack of nitrate renders denitrification potential to be negligible. Although, if nitrate were present, low pH would enhance $N_2O$ emissions due to inhibiting di-nitrogenoxide reductase

and increasing $N_2O$ / $N_2$ ratio of denitrification (e.g., Weslien et al., 2009).

In pristine mires nitrification positively depended on pH and negatively on water level (Regina et al., 1996) in supply of nitrate for denitrification, as the main source of $N_2O$ emissions (Regina et al., 1996; Nykänen et al., 1995; Wray et al., 2007). Thus, during drying–rewetting periods as in July–September 2005, our sites could initiate short-term significant differences, but for the whole measurement period the lack of a statistically significant difference in $N_2O$ fluxes was probably due to low nitrification potential. Generally, low pH and high C / N ratios of our forest floors suggest conditions of low nitrification potential. Thus, the lack of a statistically significant difference in $N_2O$ fluxes was probably due to low nitrification potential. Other reasons could be the low field sampling frequency and relatively high noise in the data (MQL compared to low fluxes). Measuring three microsites per site could lead to missing some peak $N_2O$ emission events due to a large microscale spatial variation (Von Arnold et al., 2005a). With our weekly or bi-weekly sampling frequency we could not identify larger microsite specific peak events possibly occurring after N was mobilized from, e.g., fast decomposition of deciduous foliage during the drought related early peak in litterfall or during sudden soil freeze–thaw cycles (Pihlatie et al., 2007). However, during the active growing season these events might be rare in typical boreal conditions where plants are adapted to a rapid uptake of limited rates of soil N mineralization (Hikosaka, 2003; Korhonen et al., 2013; Lupi et al., 2013).

Several studies (Martikainen et al., 1995; Regina et al., 1996) reported that peatlands in a pristine state showed small $N_2O$ emissions, but when drained, nitrification rates were enhanced depending on nutrient status (a large increase for rich sites and no increase for poor sites). The limited increase in $N_2O$ emissions during the 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 $N_2O$ emissions during the dry season of our forests and forest–mire transitions as the $N_2O$ emissions are also known to correlate with site fertility, e.g., expressed as C / N ratio (Klemedtsson et al., 2005; Ojanen et al., 2010; Hashimoto et al., 2011).

The $N_2O$ 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, Fig. 7). However, the residuals of the moisture and temperature model were large (Fig. 7) and $r^2$ was only 10 %. Luo et al. (2012) demonstrated for temperate forests that $N_2O$ emissions depended nonlinearly on the soil moisture and positively on soil temperature. In our study, the weak linear response of soil moisture to $N_2O$ fluxes could be an artifact of fitting several $N_2O$ processes of different sensitivity to different forest/mire types. For example in well-drained uplands the $N_2O$ 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 $N_2O$ 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 $N_2O$ emissions originate mainly from the top soil. The $N_2O$ 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, 2010; Luo et al., 2012).

## 5 Conclusions

The $CH_4$ 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 $CH_4$ oxidation rather than emission with very small sensitivity to wet and dry events. The $N_2O$ fluxes of forest mire types were generally low. Despite small $N_2O$ peaks in spring and autumn, the $N_2O$ 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. In spite of the potential of pristine forest–mire transitions to represent biogeochemical hotspots in the landscape, the $CH_4$ and $N_2O$ flux levels in the transitions changed minimally during extremely large range of weather conditions. Our pristine forest–mire transitions did not act as biogeochemical hotspots for $CH_4$ and $N_2O$ emissions. Therefore, when making attempts to upscale boreal landscape carbon and nitrogen cycles, the organo-mineral soils of pristine forest–mire transitions should be regarded as $CH_4$ sinks and minor $N_2O$ sources rather than having the peak emissions on the landscape level.

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