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CH$_4$ and N$_2$O 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$_2$O 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$_2$O emissions during exceptionally high and low ground water level events.

In our study, we tested the differences and drivers of CH$_4$ and N$_2$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 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$_2$O 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$_2$O 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$_2$O 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$_2$O sources instead of CH$_4$ and N$_2$O 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$_2$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$_4$ and small sources or sinks of N$_2$O (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$_2$O (Martikainen et al., 1995; Nykänen et al., 1995; D'Angelo and Reddy, 1998). Field CH$_4$ and N$_2$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 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$_2$O 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$_2$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$_4$ 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$_2$O 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$_2$O 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$_2$O consumption (Frasier et al., 2010). N$_2$O 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$_2$O consumption by soils is attributed to respiratory reduction (Conrad, 1996) caused by denitrifiers and nitrifiers (Rosenkranz et al., 2006). N$_2$O 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$_2$O source (Wray et al., 2007; Frasier et al., 2010). In nutrient rich mires, N$_2$O 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$_2$O emissions (Weslien et al., 2009). Therefore, if nitrate were present during water level drawdown, the forest–mire transitions could become sources of N$_2$O.

Our aims were (1) to test whether forest floor CH$_4$ and N$_2$O 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$_2$O emissions. We hypothesized that forest/mire types exhibit distinct levels of CH$_4$ and N$_2$O 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$_2$O fluxes. In order to evaluate the underlying factors behind CH$_4$ and N$_2$O 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$_2$O 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 mean	SE	VT mean	SE	MT mean	SE	OMT mean	SE	OMT+ mean	SE	KgK mean	SE	KR mean	SE	VSR1 mean	SE	VSR2 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	
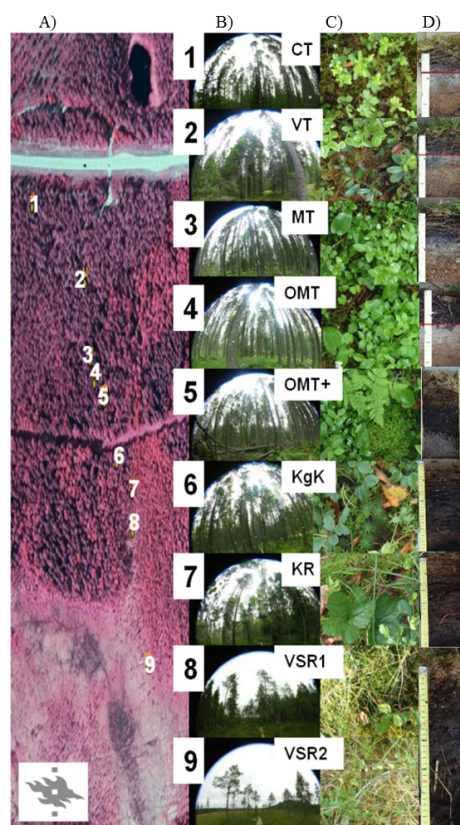
Figure 1. (a) Airborne infrared photograph shows a 450 m long boreal forest–mire ecotone located on the NE slope of the glacial Vatiharju–Lakkasuo esker in Finland (61°47′, 24°19′). **(b)** The fisheye photographs show tree stands of xeric (1), subxeric (2), mesic (3), herb rich (4), paludified (5–7), 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 ($\varnothing$ 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$_2$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 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$_4$ (μg m^{-2} h^{-1}) and N$_2$O (μg 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 ($\varnothing$ 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, 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$_2$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$_4$ and N$_2$O concentra-

tion was analyzed. The CH$_4$ (μg m^{-2} h^{-1}) and N$_2$O (μg 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$_2$O concentrations (mean $\pm$ two SD: 1.837 ± 0.055 and 0.295 ± 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$_2$O concentrations of reference gas samples (22 μg m^{-2} h^{-1} for CH$_4$ and 18 μg m^{-2} h^{-1} for N$_2$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$_4$ and 49 % of N$_2$O fluxes were discarded.

2.4 Statistical analysis

Two-way analysis of variance (ANOVA) was used to test whether CH$_4$ and N$_2$O 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$_2$O fluxes from the snow on the ground season (January–April in 2006) and the N$_2$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$_4$ (μg 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 (μg 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):

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

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

where yu_{ij} and yt_{ij} are the CH$_4$ flux (μg m^{-2} h^{-1}) for upland forests or transitions and for a particular ith forest type and the jth observation, β_{CT} through β_{KR} are the fixed effect coefficients for a particular ith 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 ith forest type, and ε_{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 (μg 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 (μg m^{-2} h^{-1}) for the ith mire (VSR1,VSR2) and for the jth 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$_2$O fluxes (μg 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$_2$O flux (μg m^{-2} h^{-1}) for the ith mire (VSR1,VSR2) and for the jth 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$_2$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$_4$ and N$_2$O 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 ~ 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 586μg 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
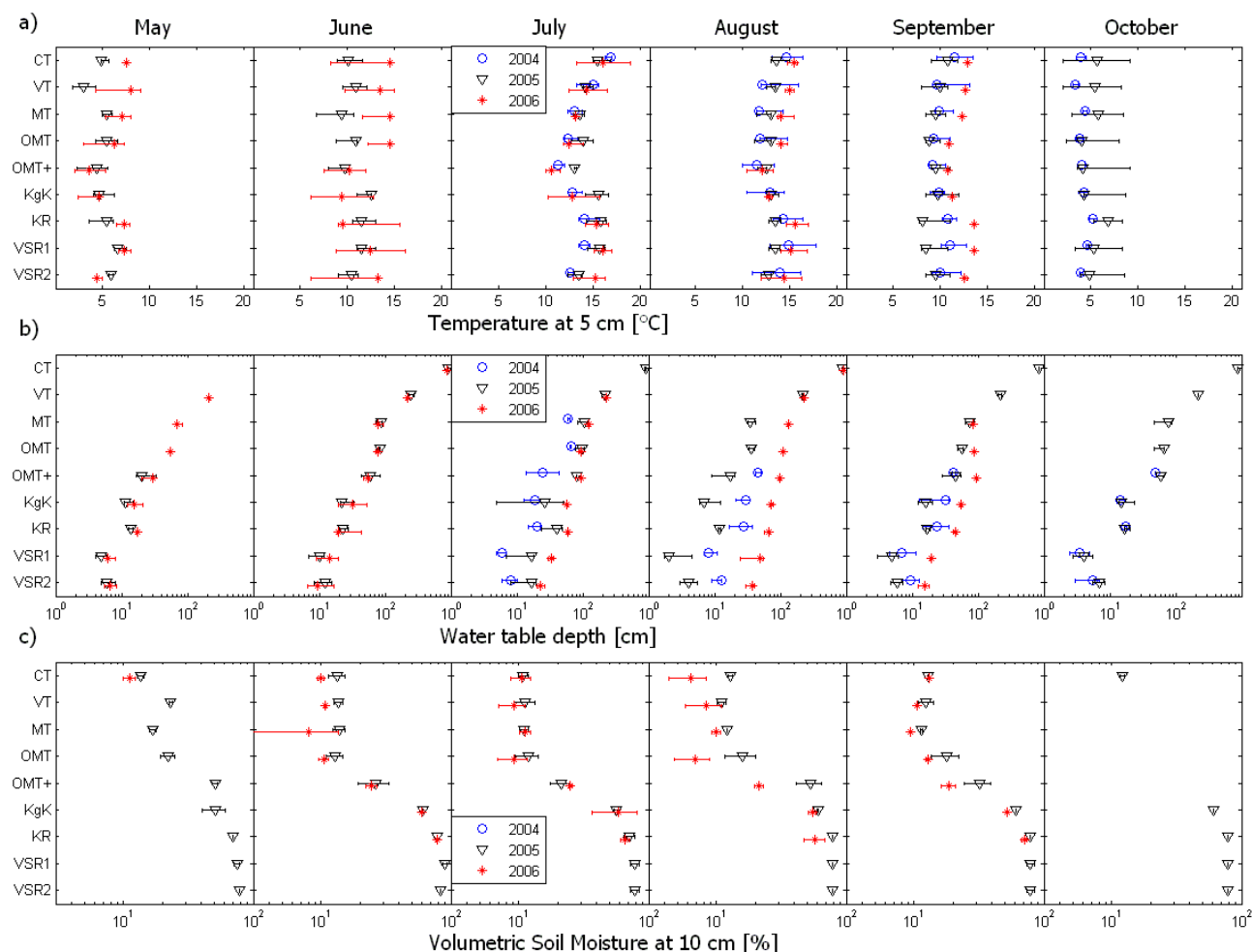
Figure 2. The panels **(a–c)** show the monthly medians of environmental variables: **(a)** soil temperature at a depth of 5 cm, **(b)** ground water level, and **(c)** volumetric soil moisture at 10 cm depth observed along the forest–mire ecotone during wet (2004), intermediate (2005), and dry years (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$_2$O fluxes (μg 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 for-

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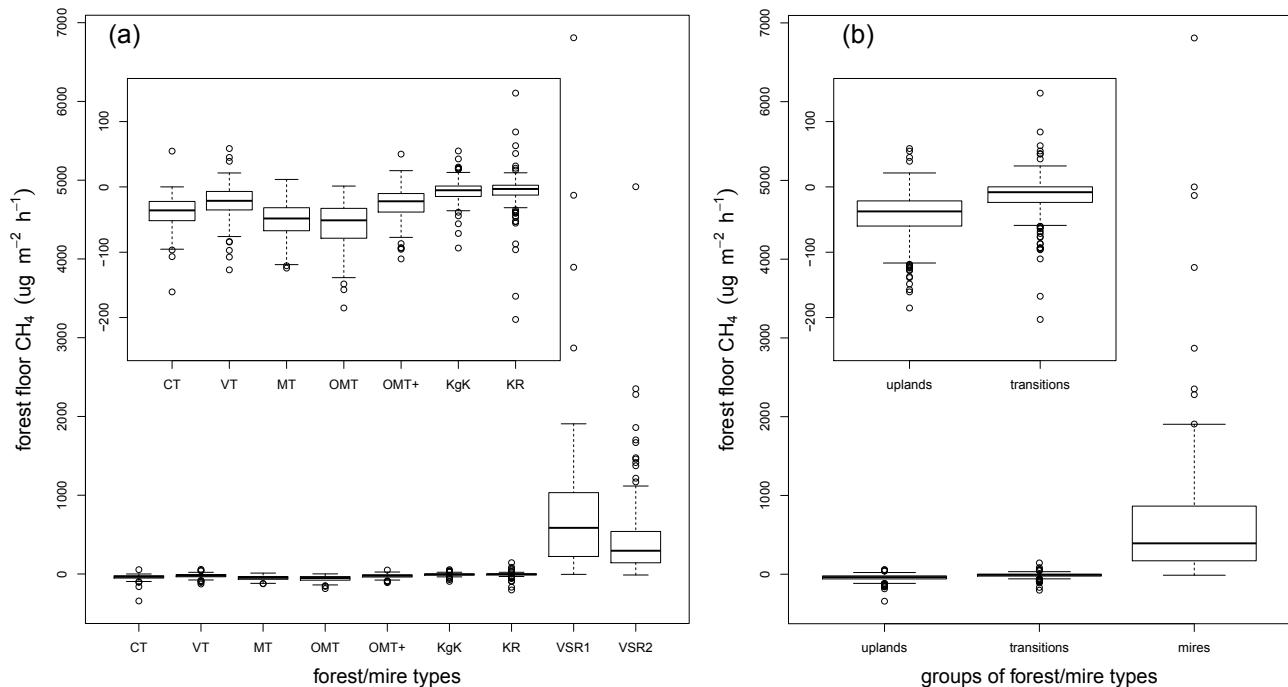
Figure 3. The box plots of forest floor CH_4 fluxes ($\mu g\,m^{-2}\,h^{-1}$) for each forest/mire type (a), and (b) for uplands (CT, VT, MT, OMT), transitions (OMT+, KgK, KR), and mires (VSR1, VSR2) during the whole period. The left–right arrangement of sites mimics the locations on the slope (see Fig.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

3.3 Factors controlling CH₄ 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 toler-

ance 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 N₂O 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
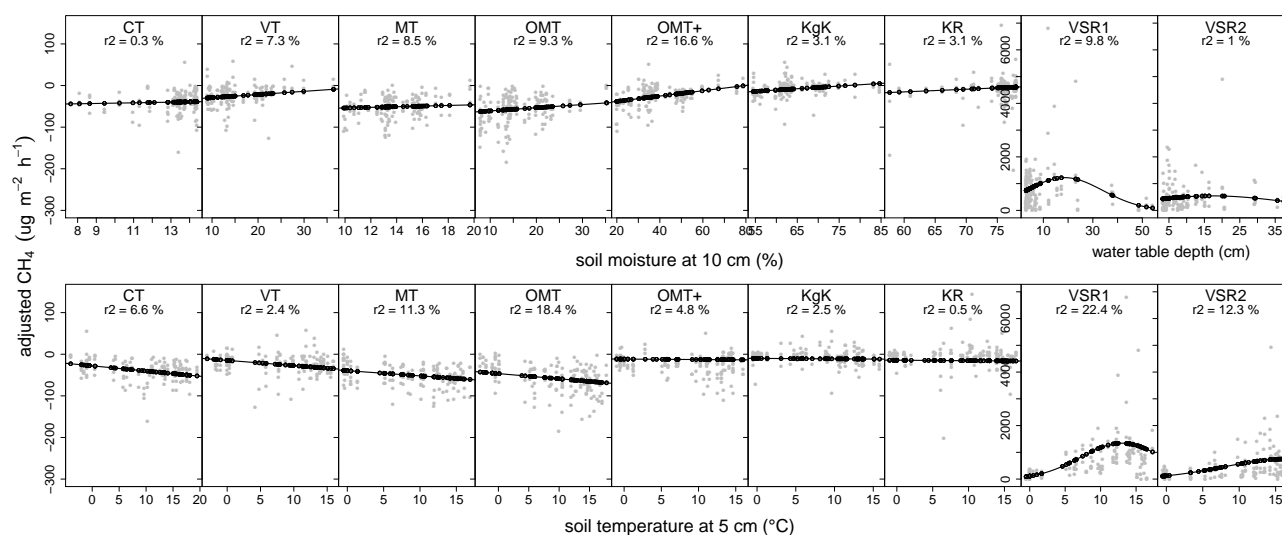
Figure 4. Comparison of sensitivity of forest floor CH_4 fluxes ($\mu g\,m^{-2}\,h^{-1}$) to environmental factors for nine forest/mire types. Modeled in the upper panels is CH_4 flux response to soil moisture at 10 cm (uplands and transitions) or to water table depth (cm) (mires) for uplands (CT, VT, 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).
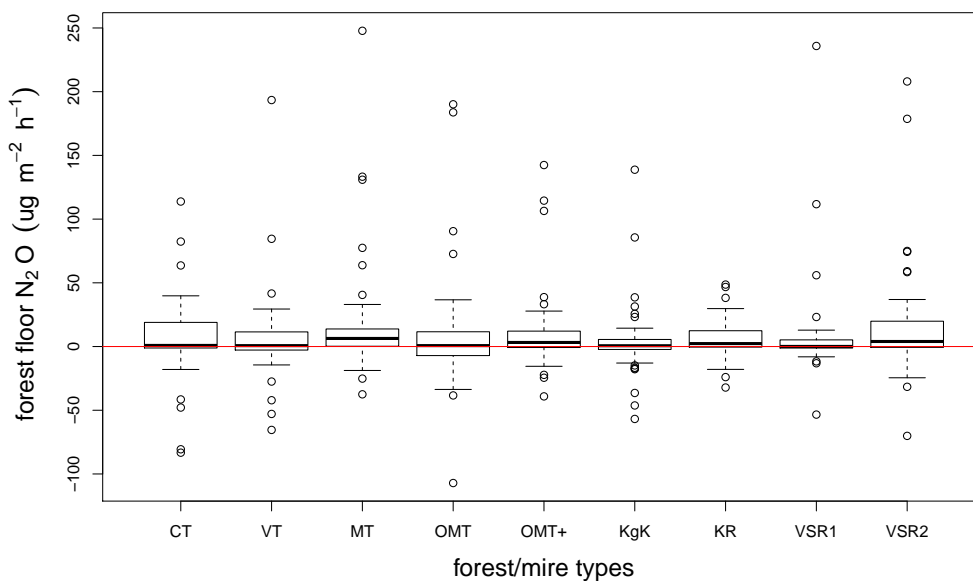

Figure 5. The box plot of forest floor N_2O fluxes ($\mu g\,m^{-2}\,h^{-1}$) for each forest/mire type (uplands – CT, VT, MT, OMT; transitions – OMT+, KgK, KR; and mires – VSR1, VSR2) during the period including typical and dry years. The left–right arrangement of sites mimics the locations on the slope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

est/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
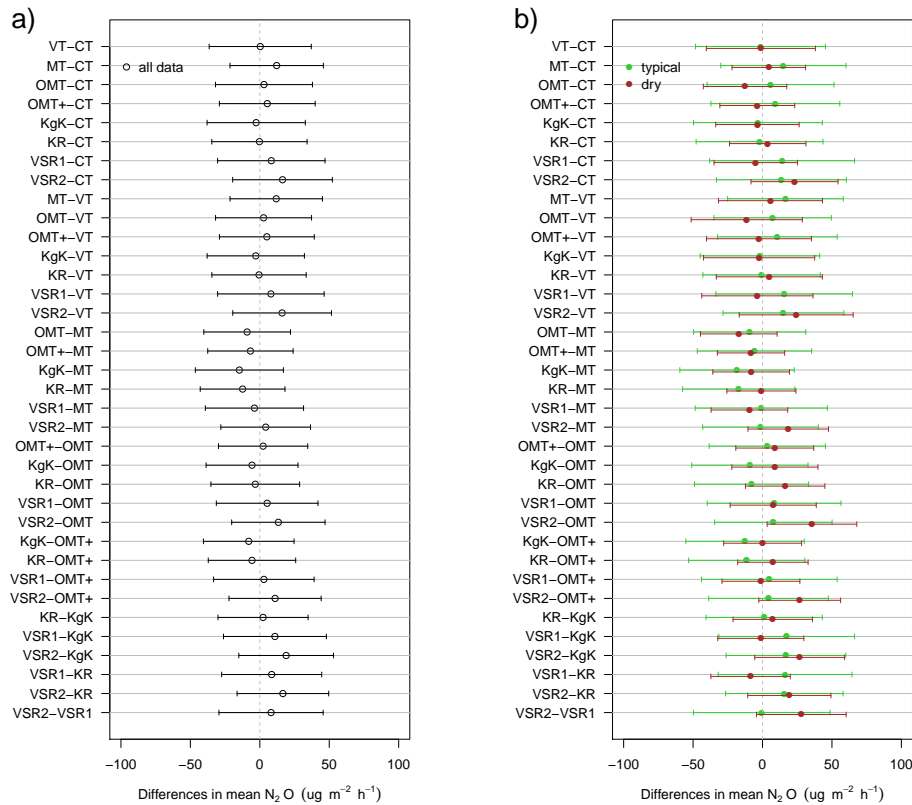
Figure 6. The post hoc Tukey differences (error bars for 95 % confidence intervals) of mean N$_2$O (µg m^{-2} h^{-1}) fluxes from the forest floor for the pairwise comparisons of forest/mire types (uplands – CT, VT, MT, OMT; transitions – OMT+, KgK, KR; and mires – VSR1, VSR2): **(a)** the N$_2$O flux differences over the whole period for a typical and dry year, **(b)** the N$_2$O 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$_2$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, Fig. 7). The modeled Gaussian type response showed optimum N$_2$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$_4$ and N$_2$O flux

The site-specific momentary CH$_4$ and N$_2$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$_2$O 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$_2$O fluxes were significantly correlated with pH ($r = 0.174$, $p = 0.004$). The mean N$_2$O values of sites increased with mean pH (N$_2$O $= -117.07 + 27.33 \times$ pH, $r^2 = 0.32$; Fig. 8b). However, the post hoc Tukey differences of mean N$_2$O fluxes from the forest floor for the pairwise comparisons of forest/mire types were not significant for 31 pairs and mean N$_2$O 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$_2$O 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
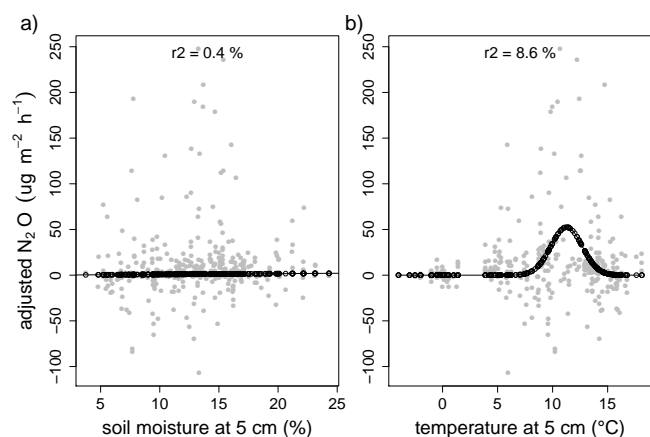
Figure 7. Sensitivity of forest floor N$_2$O fluxes (µg m^{-2} h^{-1}) of forest/mire types together with environmental factors: **(a)** N$_2$O flux response to soil moisture at 5 cm, and **(b)** N$_2$O flux response to soil temperature at 5 cm during the period including wet, typical, and dry years. The N$_2$O 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$_2$O 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.

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
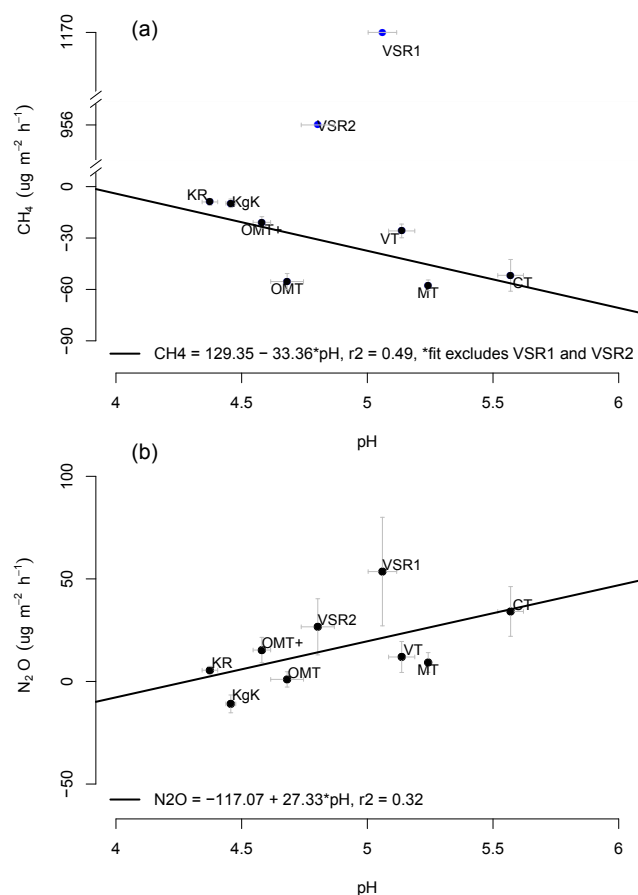

Figure 8. Scatterplot between site-specific mean pH and mean flux (µg m^{-2} h^{-1}) of **(a)** CH$_4$ or **(b)** N$_2$O of summer with intermediate moisture over the period of soil water sampling campaign (July–September 2005). Error bars show standard error. The CH$_4$ error bars for VSR1 and VSR2 are not shown.

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).
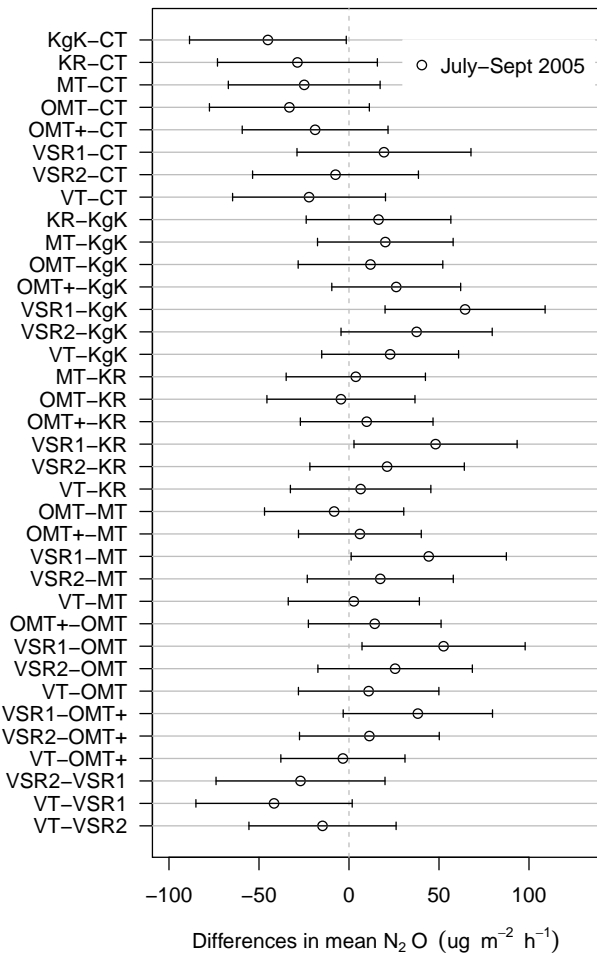
Figure 9. The post hoc Tukey differences (error bars for 95 % confidence intervals) of mean N$_2$O (μgm^{-2}h^{-1}) fluxes from the forest floor for the pairwise comparisons of forest/mire types (uplands – CT, VT, MT, OMT; transitions – OMT+, KgK, KR; and mires – VSR1, VSR2) over the period of the soil 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$_2$O dynamics

The momentary N$_2$O fluxes in the range from −107 to 248 (µg m^{-2} h^{-1}) and median emissions close to 0 (µg 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$_2$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 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$_2$O 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$_2$O 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$_2$O flux of dry pine forest significantly larger than that of paludified spruce forest (larger CT than KgK), whereas mean N$_2$O 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$_2$O 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$_2$O 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$_2$O 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$_2$O 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 nitri-

fication, 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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References

Agnew, A. D. Q., Wilson, J. B., and Sykes, M. T.: A vegetation switch as the cause of a forest/mire ecotone in New Zealand, J. Veget. Sci., 4, 273–278, 1993.

Alm, J., Talanov, A., Saarnio, S., Silvola, J., Ilkkonen, E., Aaltonen, H., Nykänen, H., and Martikainen, P. J.: Reconstruction of carbon balance for microsites in a boreal oligotrophic pine fen, Finland, Oecologia, 110, 423–431, 1997.

Alm, J., Shurpali, N. J., Tuittila, E.-S., Laurila, T., Maljanen, M., Saarnio, S., and Minkkinen, K.: Methods for determining emission factors for the use of peat and peatlands – flux measurements and modelling, Boreal Env. Res., 12, 85–100, 2007.

Ambus, P., Zechmeister-Boltenstern, S., and Butterbach-Bahl, K.: Sources of nitrous oxide emitted from European forest soils, Biogeosciences, 3, 135–145, doi:10.5194/bg-3-135-2006, 2006.

Bubier, J., Moore, T., and Juggins, S.: Predicting methane emissions from bryophyte distribution in northern Canadian peatlands, Ecology, 76, 677–693, 1995.

Cajander, A. K.: Forest types and their significance, Acta Forestalia Fennica, 56, 1–69, 1949.

D'Angelo, E. and Reddy, K.: Regulators of heterotrophic microbial potentials in wetland soils, Soil Biol. Biochem., 31, 815–830, 1999.

Danilova, O. V. and Dedysh, S. N.: Abundance and diversity of methanotrophic *Gammaproteobacteria* in northern wetlands, Microbiology, 83, 67–76, 2014.

Dorodnikov, M., Knorr, K.-H., Kuzyakov, Y., and Wilmking, M.: Plant-mediated CH4 transport and contribution of photosynthates to methanogenesis at a boreal mire: a ^{14}C pulse-labeling study, Biogeosciences, 8, 2365–2375, 2011, http://www.biogeosciences.net/8/2365/2011/.

Frasier, R., Ullah, S., and Moore, T. R.: Nitrous oxide consumption potentials of well-drained forest soils in southern Quebec, Canada, Geomicrobiol. J., 27, 53–60, 2010.

Finnish statistical yearbook of forestry 2013. Finnish Forest Research Institute, Metsäntutkimuslaitos, Finland, http://www.metla.fi/julkaisut/metsatilastollinenvsk/index-en.htm, 2014.

Hari, P. and Kulmala, M.: Station for Measuring Ecosystem–Atmosphere Relations (SMEAR II), Boreal Env. Res., 10, 315–322, 2005.

Hartshorn, A. S., Southard, R. J., and Bledsoe, C. S.: Structure and function of peatland-forest ecotones in southeastern Alaska, Soil Sci. Soc. Am. J., 67, 1572–1581, 2003.

Hashimoto, S., Morishita, T., Sakata, T., Ishizuka, S., Kaneko, S., and Takahashi, M.: Simple models for soil CO$_2$, CH$_4$, and N$_2$O fluxes calibrated using a Bayesian approach and multi-site data, Ecol. Modell., 222, 1283–1292, 2011.

Hikosaka K.: A model of dynamics of leaves and nitrogen in a plant canopy: an integration of canopy photosynthesis, leaf life span, and nitrogen use efficiency, The American Naturalist , 162, 149–164, 2003.

Hornibrook, E. R. C., Bowes, H. L., Culbert, A., and Gallego-Sala, A. V.: Methanotrophy potential versus methane supply by pore water diffusion in peatlands, Biogeosciences, 6, 1491–1504, doi:10.5194/bg-6-1491-2009, 2009.

Howie, S. A. and Tromp-van Meerveld, I.: The essential role of the lagg in raised bog function and restoration: a review, Wetlands, 31, 613–622, 2011.

Huttunen, J., Nykänen, H., Martikainen, P., and Nieminen, M.: Fluxes of nitrous oxide and methane from drained peatlands following forest clear-felling in Southern Finland, Plant Soil, 255, 457–462, 2003.

Jaatinen, K., Knief, C., Dunfield, P. F., Yrjälä, K., and Fritze, H.: Methanotrophic bacteria in boreal forest soil after fire, FEMS Microbiol. Ecol., 50, 195–202, 2004.

Juottonen, H., Galand, P. E., Tuittila, E., Laine, J., Fritze, H., and Yrjälä, K.: Methanogen communities and bacteria along an eco-hydrological gradient in a northern raised bog complex, Environ. Microbiol., 7, 1547–1557, 2005.

Juottonen, H., Tuittila, E., Juutinen, S., Fritze, H., and Yrjälä, K.: Seasonality of rDNA- and rRNA-derived archaeal communities and methanogenic potential in a boreal mire, The ISME J., 2, 1157–1168, 2008.

Kettunen, A., Kaitala, V., Lehtinen, A., Lohila, A., Alm, J., Silvola, J. and Martikainen, P. J.: Methane production and oxidation potentials in relation to water table fluctuations in two boreal mires, Soil Biol. Biochem., 31, 1741–1749, 1999.

Klemedtsson, L., Von Arnold, K., Weslien, P., and Gundersen, P.: Soil CN ratio as a scalar parameter to predict nitrous oxide emissions, Global Change Biol., 11, 1142–1147, 2005.

Korhonen, J. F. J., Pihlatie, M., Pumpanen, J., Aaltonen, H., Hari, P., Levula, J., Kieloaho, A.-J., Nikinmaa, E., Vesala, T., and Ilvesniemi, H.: Nitrogen balance of a boreal Scots pine forest, Biogeosciences, 10, 1083–1095, doi:10.5194/bg-10-1083-2013, 2013.

Laine, J., Komulainen, V.-M., Laiho, R., Minkkinen, K., Rasinmäki, A., Sallantaus, T., Sarkkola, S., Silvan, N., Tolonen, K., Tuittila, E-S., Vasander, H., and Päivänen, J.: Lakkasuo, a guide to mire ecosystems, University of Helsinki Department of Forest Ecology Publications 31, Helsinki, Finland, 123 pp., 2004.

Larmola, T., Tuittila, E.-S., Tiirola, M., Nykäne, H., Martikainen, J.P., Yrjälä, K., Tuomivirta, T., and Fritze, H.: The role of *Sphagnum* mosses in the methane cycling of a boreal mire, Ecology, 91, 2356–2365, 2010.

Luo, G. J., Brüggemann, N., Wolf, B., Gasche, R., Grote, R., and Butterbach-Bahl, K.: Decadal variability of soil CO$_2$, NO, N$_2$O, and CH$_4$ fluxes at the Höglwald Forest, Germany, Biogeosciences, 9, 1741–1763, doi:10.5194/bg-9-1741-2012, 2012.

Lupi, C., Morin, H., Deslauriers, A., Rossi, S., Houle, D.: Role of soil nitrogen for the conifers of the boreal forest: a critical review, International Journal of Plant and Soil Science, 2, 155-189, 2012.

Macdonald, J. A., Fowler, D., Hargreaves, K. J., Skiba, U., Leith, I. D., and Murray, M. B.: Methane emission rates from a north-

ern wetland; response to temperature, water table and transport, Atmos. Environ., 32, 3219–3227, 1998.

Mäkiranta, P., Laiho, R., Fritze, H., Hytönen, J., Laine, J., and Minkkinen, K.: Indirect regulation of heterotrophic peat soil respiration by water level via microbial community structure and temperature sensitivity, Soil Biol. Biochem., 41, 695–703, 2009.

Martikainen, P. J., Nykänen, H., Crill, P., and Silvola, J.: Effect of a lowered water table on nitrous oxide fluxes from northern peatlands, Nature, 366, 51–53, 1993.

Martikainen, P. J., Nykänen, H., Alm, J., and Silvola, J.: Change in fluxes of carbon dioxide, methane and nitrous oxide due to forest drainage of mire sites of different trophy, Plant Soil, 168/169, 571–577, 1995.

Matson, A., Pennock, D., and Bedard-Haughn A.: Methane and nitrous oxide emissions from mature forest stands in the boreal forest, Saskatchewan, Canada, For. Ecol. Manage., 258, 1073–1083, 2009.

McClain, M. E., Boyer, E. W.,Dent, C. L., Gergel, S. E., Grimm, N. B., Groffman, P. M., Hart, S. C., Harvey, J. W., Johnston, C. A., Mayorga, E., McDowell, W. H., and Pinay, G.: Biogeochemical hot spots and hot moments at the interface of terrestrial and aquatic ecosystems, Ecosystems 6, 301–312, 2003.

Megonigal, J. P and Guenther, A. B.: Methane emissions from upland forest soils and vegetation, Tree Physiol., 28, 491–498, 2008.

Moosavi, S. C. and Crill, P. M.: Controls on CH$_4$ and CO$_2$ emissions along two moisture gradients in the canadian boreal zone, J.Geophys.Res., 102, 29261–29277, 1997.

Nakano, T., Tnoue, G., and Fukuda, M.: Methane consumption and soil respiration by a birch forest soil in West Siberia, Tellus B, 56, 223–229, 2004.

Nykänen, H., Alm, J., Lang, K., Silvola, J., and Martikainen, P.: Emissions of CH$_4$, N$_2$O and CO$_2$ from a virgin fen and a fen drained for grassland in Finland, J. Biogeogr., 22, 351–357, 1995.

Nykänen, H., Alm, J., Silvola, J., Tolonen, K., and Martikainen, P. J.: Methane fluxes on boreal peatlands of different fertility and the effect of long-term experimental lowering of the water table on flux rates, Global Biogeochem. Cy., 12, 53–69, 1998.

Ojanen, P., Minkkinen, K., and Alm, J.: Soil–atmosphere CO$_2$, CH$_4$ and N$_2$O fluxes in boreal forestry-drained peatlands, Forest Ecol. Manage., 260, 411–421, 2010.

Paavolainen, L., Fox, M., and Smolander, A.: Nitrification and denitrification in forest soil subjected to sprinkling infiltration, Soil Biol. Biochem., 32, 669–678, 2000.

Pihlatie, M., Syväsalo, E., Simojoki, A., Esala, M., and Regina, K.: Contribution of nitrification and denitrification to N$_2$O production in peat, clay and loamy sand soils under different soil moisture conditions, Nutr. Cy. Agroecosyst., 70, 135–141, 2004.

Pihlatie, M., Pumpanen, J., Rinne, J., Ilvesniemi, H., Simojoki, A., Hari, P., and Vesala, T.: Gas concentration driven fluxes of nitrous oxide and carbon dioxide in boreal forest soil, Tellus B, 59, 458–469, 2007.

Pihlatie, M. K., Kiese, R., Brüggemann, N., Butterbach-Bahl, K., Kieloaho, A.-J., Laurila, T., Lohila, A., Mammarella, I., Minkkinen, K., Penttilä, T., Schönborn, J., and Vesala, T.: Greenhouse gas fluxes in a drained peatland forest during spring frost-thaw event, Biogeosciences, 7, 1715–1727, doi:10.5194/bg-7-1715-2010, 2010.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., and the R Development Core Team: nlme: Linear and Nonlinear Mixed Effects Models, R package version, 3.1, 113, http://cran.r-project.org/web/packages/nlme/nlme.pdf, 2013.

Putkinen, A., Larmola, T., Tuomivirta, T., Siljanen, H.M.P., Bodrossy, L., Tuittila, E.-S., and Fritze, H.: Water dispersal of methanotrophic bacteria maintains functional methane oxidation in Sphagnum mosses, Front. Microbio., 3, 15, doi:10.3389/fmicb.2012.00015, 2012.

R Core Team, R: A language and environment for statistical computing, R Foundation for Statistical Computing, Vienna, Austria, http://www.R-project.org/, 2013.

Regina, K., Nykänen, H., Silvola, J., and Martikainen, P.: Fluxes of nitrous oxide from boreal peatlands as affected by peatland type, water table level and nitrification capacity, Biogeochemistry, 35, 401–418, 1996.

Riutta, T., Laine, J., Aurela, M., Rinne, J., Vesala, T., Laurila, T., Haapanala, S., Pihlatie, M., and Tuittila, E.: Spatial variation in plant community functions regulates carbon gas dynamics in a boreal fen ecosystem, Tellus B, 59, 838–852, 2007.

Rosenkranz, P., Brüggemann, N., Papen, H., Xu, Z., Seufert, G., and Butterbach-Bahl, K.: N$_2$O, NO and CH$_4$ exchange and microbial N turnover over a Mediterranean pine forest soil, Biogeosciences, 3, 121–133, doi:10.5194/bg-3-121-2006, 2006.

Saari, A., Rinnan, R., and Martikainen, P. J.: Methane oxidation in boreal forest soils: Kinetics and sensitivity to pH and ammonium, Soil Biology and Biochemistry, 36, 1037–1046, 2004.

Saarnio, S., Alm, J., Silvola, J., Lohila, A., Nykanen, H., and Martikainen, P.: Seasonal variation in CH$_4$ emissions and production and oxidation potentials at microsites on an oligotrophic pine fen, Oecologia, 110, 414–422, 1997.

Seibert, J., Stendahl, J., and Sørensen, R.: Topographical influences on soil properties in boreal forests, Geoderma, 141, 139–148, 2007.

Solondz, D. S., Petrone, R. M., and Devito, K. J.: Forest floor carbon dioxide fluxes within an upland-peatland complex in the Western Boreal Plain, Canada, Ecohydrology, 1, 361–376, 2008.

Sommerfeld, R. A., Mosier, A. R., and Musselman, R. C.: CO$_2$, CH$_4$ and N$_2$O flux through a Wyoming snowpack and implications for global budgets, Nature, 361, 140–142, 1993.

Starr, M. R.: Variation in the quality of tension lysimeter soil water samples from a Finnish forest soil. Soil Sci., 140, 453–461, 1985.

Ste-Marie, C. and Pareé, D.: Soil, pH and N availability effects on net nitrification in the forest floors of a range of boreal forest stands, Soil Biol. Biochem., 31, 1579–1589, 1999.

Strom, L., Ekberg, A., Mastepanov, M., and Christensen, T. R.: The effect of vascular plants on carbon turnover and methane emissions from a tundra wetland, Global Change Biol., 9, 1185–1192, doi:10.1046/j.1365-2486.2003.00655.x., 2003.

Szukics, U., Abell, G.C., Hödl, V., Mitter, B., Sessitsch, A., Hackl, E., and Zechmeister-Boltenstern, S.: Nitrifiers and denitrifiers respond rapidly to changed moisture and increasing temperature in a pristine forest soil, FEMS Microbiol. Ecol., 72, 395–406, 2010.

Ťupek, B., Minkkinen, K., Kolari, P., Starr, M., Chan, T., Alm, J., Vesala, T., Laine, J., and Nikinmaa, E.: Forest floor versus ecosystem CO$_2$ exchange along boreal ecotone between upland forest and lowland mire, Tellus B, 60, 153–166, 2008.

Ullah, S. and Moore, T. R.: Soil drainage and vegetation controls of nitrogen transformation rates in forest soils, southern Quebec, J. Geophys. Res., 114, 01014, doi:10.1029/2008JG000824, 2009.

Ullah, S. and Moore, T. R.: Biogeochemical controls on methane, nitrous oxide, and carbon dioxide fluxes from deciduous forest soils in eastern Canada, J. Geophys. Res., Biogeosciences, 116, G03010, doi:10.1029/2010JG001525, 2011.

Ullah, S., Frasier, R., King, L., Picotte-Anderson, N., and Moore, T. R.: Potential fluxes of N$_2$O and CH$_4$ from three forests type soils in eastern Canada, Soil Biol. Biochem., 40, 986–994, 2008.

Ullah, S., Frasier, R., Pelletier, L., and Moore, T. R.: Greenhouse gas fluxes from boreal forest soils during the snow-free period in Quebec, Canada, Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere, 39, 666-680, 2009.

Von Arnold, K., Ivarsson, M., Öqvist, M., Majdi, H., Björk, R.G., Weslien P., and Klemedtsson, L.: Can distribution of trees explain variation in nitrous oxide fluxes?, Scand. J. Forest. Res., 20, 481–489, 2005a.

Von Arnold, K., Weslien, P., Nilsson, M., Svensson, B., and Klemedtsson, L.: Fluxes of CO$_2$, CH$_4$ and N$_2$O from drained coniferous forests on organic soils, Forest Ecol. Manage., 210, 239–254, 2005b.

Weishampel, P., Kolka, R., and King, J. Y.: Carbon pools and productivity in a 1 km^2 heterogeneous forest and peatland mosaic in Minnesota, USA, Forest Ecol. Manage., 257, 747–754, 2009.

Weslien, P., Kasimir Klemedtsson, Å., Börjesson, G., and Klemedtsson, L.: Strong pH influence on N$_2$O and CH$_4$ fluxes from forested organic soils, Europ. J. Soil Sci., 60, 311–320, 2009.

Włodarczyk, T., Szarlip, P., and Brzezińska, M.: Nitrous oxide consumption and dehydrogenase activity in Calcaric Regosols, Polish J. Soil Sci., 2, 97–110, 2005.

Wrage, N., Velthof, G. L., van Beusichem, M. L., and Oenema, O.: Role of nitrifier denitrification in the production of nitrous oxide, Soil Biol. Biochem., 33, 1723–1732, 2001.

Wray, H. E. and Bayley, S. E.: Denitrification rates in marsh fringes and fens in two boreal peatlands in Alberta, Canada, Wetlands, 27, 1036–1045, 2007.

Ye, R. Z., Jin, Q. S., Bohannan, B., Keller, J. K., McAllister, S. A., and Bridgham, S. D.: pH controls over anaerobic carbon mineralization, the efficiency of methane production, and methanogenic pathways in peatlands across an ombrotrophic-minerotrophic gradient, Soil Biol. Biochem., 54, 36–47, 2012.

Yrjälä, K., Tuomivirta, T., Juottonen, H., Putkinen, A., Lappi, K., Tuittila, E., Penttilä, T., Minkkinen, K., Laine, J., Peltoniemi, K., and Fritze, H.: CH$_4$ production and oxidation processes in a boreal fen ecosystem after long-term water table drawdown, Glob. Change Biol., 17, 1311–1320, 2011.