

CH₄ and N₂O dynamics in the boreal forest-mire ecotone

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Abstract

In spite of advances in greenhouse gas research, the spatio-temporal CH₄ and N₂O dynamics of boreal landscape remain challenging e.g. we need clarification of whether forest-mire transitions are occasional hotspots of landscape CH₄ and N₂O emissions during exceptionally high and low ground water level events.

In our study, we tested the differences and drivers of CH₄ and N₂O dynamics of forest/mire types in field conditions along the soil moisture gradient of the forest-mire ecotone. Soils changed from podzols to histosols and ground water rose downslope from the depth of 10 m in upland sites to 0.1 m in mires. Yearly meteorological conditions changed from being exceptionally wet to typical and exceptionally dry for the local climate. The median fluxes measured with a static chamber technique varied from -51 to 586 $\mu\text{g m}^{-2} \text{h}^{-1}$ for CH₄ and from 0 to 6 $\mu\text{g m}^{-2} \text{h}^{-1}$ for N₂O between forest/mire types throughout the entire wet-dry period.

In spite of the highly dynamic soil water fluctuations in carbon rich soils in forest-mire transitions, there were no large peak emissions in CH₄ and N₂O 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 CH₄ emissions, which were reduced entirely during the exceptional summer drought period. Near zero N₂O fluxes did not differ significantly between the forest/mire types probably due to their low nitrification potential. When upscaling boreal landscapes, pristine forest-mire transitions should be regarded as CH₄ sinks and minor N₂O sources instead of CH₄ and N₂O emission hotspots.

1 **1 Introduction**

2 Soil fertility, soil water content and soil carbon storage of boreal forest varies between well
3 drained mineral soils mainly found in uplands and poorly drained organic soils mainly found
4 in peatlands (Seibert et al. 2007, Weishampel et al. 2009). The CH₄ and N₂O fluxes from
5 mineral and organic soils are impacted by varying soil moisture conditions (Solondz et al.
6 2008, Pihlatie et al. 2004). Typical mineral soil forests are small sinks of CH₄ and small
7 sources or sinks of N₂O (Moosavi and Crill 1997, Pihlatie et al. 2007). Sparsely forested
8 peatlands are typically large or small sources of CH₄ and small sources or sinks of N₂O
9 (Martikainen et al. 1995, Nykänen et al. 1995, D'Angelo and Reddy, 1998). Field CH₄ and
10 N₂O studies of natural boreal forest-mire ecotones are rare (e.g. Ullah et al. 2009, Ullah and
11 Moore 2011) in comparison to those of typical forests or mires. **However, the area of forest-**
12 **mire transitions is relatively large, e.g. in Finland, forested mires with an organic**
13 **horizon < 30 cm cover 1.5 million ha or approximately 7% of the total forest area**
14 **(Finnish statistical yearbook of forestry 2013); and up to date it's not clear whether the**
15 **terrestrial-aquatic interfaces, such as the forest-mire transition, represents a**
16 **biogeochemical “hotspot” of CH₄ and N₂O emissions (McClain et al. 2003).**

17
18 **The “lagg transitional zone” in the forest-mire ecotone receives nutrients from the**
19 **adjacent mineral soil runoff, and is thus more minerotrophic, biologically diverse, and**
20 **productive than open mires or bogs (Howie and Meerveld 2011).** Furthermore, ecotones
21 between forests and mires are ecological switches (Agnew et al. 1993), where the vegetation
22 of forests and mires coincide and soils frequently undergo fluctuations in water level position
23 and chemistry (Hartshorn et al. 2003, Howie and Meerveld 2011), and where the CH₄ and
24 N₂O dynamics of forest-mire transitions may be expected to differ generally and on a year-to-
25 year basis from those of typical forests and mires.

26
27 The CH₄ uptake of forest soils is a result of CH₄ oxidizing aerobic methanotrophs sensitive to
28 water saturation, soil porosity, moisture, temperature, pH, and ammonium (Moosavi and Crill
29 1997, Saari et al. 2004, Jaatinen et al. 2004). Unsaturated upland forest soils oxidize CH₄ at
30 higher rates than more water saturated, acidic, and ammonium rich forested peat soils (Saari
31 et al. 2004). In contrast to the CH₄ sinks of upland forest soils, and drained peatlands, natural
32 mires emit CH₄ to the atmosphere (Bubier et al. 1995, Nykänen et al. 1998, Kettunen et al.

1 1999). CH₄ production in peat soil is a result of methanogenic and methanotrophic active
2 bacteria, whose activity depends on anoxic and oxic conditions below and above the water
3 level, temperature and availability of carbon substrate (Kettunen et al. 1999). Increasing soil
4 wetness increases anoxic conditions necessary for increased methanogenesis (Juottonen et al.
5 2005), and as a result CH₄ emissions increase (Saarnio et al. 1997, Ojanen et al. 2010, Yrjälä
6 et al. 2011). **Methane production potential in peat soils generally increases positively
7 with pH (Juottonen et al. 2005, Ye et al. 2012), whereas CH₄ oxidation of forested
8 peatlands has narrow pH optimum around 5.5 (Saari et al. 2004). Increased pH levels
9 e.g. through the inflow of less acidic mineral soil water, typically containing greater
10 calcium and bicarbonate concentrations than peat water, could increase CH₄ emissions
11 from transitions (Howie and Meerveld 2011).**

12
13 N₂O emissions in well-drained boreal forest soils are controlled by soil moisture, pH,
14 available nitrate, ammonium, oxygen, and carbon concentrations (Regina et al. 1996, Ullah et
15 al. 2008). N₂O production is limited by the amount of nitrogen and is subject to denitrification
16 and nitrification processes (Ambus et al. 2006). In well-drained soils NO₃ limitation, anoxic
17 microsites, and larger soil porosity may also promote N₂O consumption (Frasier et al. 2010).
18 N₂O consumption of soils correlates with dehydrogenase activity, which is affected by
19 oxidation-reduction status and possibly controlled by soil moisture (Włodarczyk et al. 2005).
20 The N₂O consumption by soils is attributed to respiratory reduction (Conrad 1996) caused by
21 denitrifiers and nitrifiers (Rosenkranz et al. 2006). N₂O emissions increase during drier
22 periods through increased ammonification and nitrification (Regina et al. 1996, Nykänen et al.
23 1995, von Arnold et al. 2005). In water saturated minerotrophic peatlands nitrification
24 supplies nitrate (Wrage et al. 2001) for denitrification, which is the main but small N₂O
25 source (Wray et al. 2007, Frasier et al. 2010). In nutrient rich mires, N₂O emissions increase
26 during drier periods through increased ammonification and nitrification (Regina et al. 1996,
27 Nykänen et al. 1995, von Arnold et al. 2005). Nitrification and the supply of nitrate for
28 denitrification increases with higher pH (Regina et al., 1996). However, if nitrate is available,
29 low pH increases N₂O emissions (Weslien et al., 2009). Therefore, if nitrate was present
30 during water level drawdown, the forest-mire transitions could become sources of N₂O.

Our aims were 1) to test whether forest floor CH₄ and N₂O fluxes of the forest-mire transition differ from the typical upland forests and lowland mires of natural boreal landscape and 2) how meteorologically different years, i.e., exceptionally wet (2004), typical (2005), and exceptionally dry (2006), affect the fluxes.

We addressed the question, if in forest-mire transitions increasing wetness promote CH₄ production, and whether dry conditions reduce CH₄ production and increase N₂O emissions. We hypothesized that forest/mire types exhibit distinct levels of CH₄ and N₂O 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 CH₄ and N₂O fluxes. In order to evaluate the underlying factors behind CH₄ and N₂O forest floor fluxes, we measured the fluxes and environmental variables such as soil temperature, soil moisture, water table depth, and soil water pH in 9 sites along the forest-mire ecotone during exceptionally different meteorological conditions. In order to detect statistical significant differences between CH₄ and N₂O fluxes of 9 sites we used two-way analysis of variance; and for better understanding of flux responses to environmental factors we used linear and non-linear 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') (Tūpek et al. 2008). Forest/mire types were classified using the Finnish classification systems (Cajander 1949, Laine et al., 2004) based on soil fertility reflected by the composition and abundance of forest floor vegetation, and by the site location on the slope. The ecotone study sites are situated along a 450 m transect on a hillslope with a relative relief of 15 meters and a 3.3% slope facing NE (Figure 1a). The fertility of the forest/mire sites increase from the poorly fertile sites at the xeric and saturated edges of the ecotone towards the most fertile *Oxalis-Myrtillus* type forest (OMT) in the middle of the hillslope (Figure 1b).

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

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

We measured pH during 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 cm, 10-30 cm) in forest mire transitions and in peatlands. The volume of samples was measured before the oven drying at 70 °C to determine the bulk density. The bulk density of the upper organic layer ranged from 0.24 gcm⁻³ (KR) to 0.48 gcm⁻³ (MT) and was approximately half of the bulk density of the organic layer from 10-30 cm depth (mean of transitions and mires 0.77 gcm⁻³) (Table 1). The C/N ratio was determined once for each plot from the soil organic matter analysed by dry combustion with Leco CNS-1000 (Leco Corp., USA). The C/N ratio was wider in the 0-10 cm profile (mean 37) than in the 10-30 cm profile (mean 27). The

highest N content and lowest C/N ratio along the ecotone was found in forest-mire transitions OMT+ and KgK (Table 1). A more detailed forest/mire type characterization is given by Ľupek et al. (2008).

2.2 Micrometeorological conditions

The micrometeorological measurements along the Vatiharju - Lakkasuo forest-mire ecotone were taken weekly during the summers of 2004 (July-November), 2005 (May-November), 2006 (May-September), and monthly during the winters (December-April). The forest floor soil temperatures ($^{\circ}\text{C}$) 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 (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 6km north - west from the forest-mire ecotone. Missing soil temperature and moisture data of ecotone were gap filled by linear regression between continuous measurements of soil temperature and moisture at SMEARII.

2.3 CH_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 three days interval of the micrometeorological measurements.** If there was packed snow on the ground the gas samples were taken from the top and bottom layers; and the CH_4 ($\mu\text{g m}^{-2} \text{ h}^{-1}$) and N_2O ($\mu\text{g m}^{-2} \text{ h}^{-1}$) fluxes were calculated by the snowpack diffusion method using each gas concentration difference, snow depth, porosity and temperature, and gas diffusion coefficients as in Sommerfeld et al. (1993). Otherwise if there was no snowpack, the samples were taken from 3 opaque, vented, closed, static chambers (\varnothing 315 mm, h 295 mm) placed air tightly on preinstalled collars. On each measuring occasion a sample of ambient gas and four 15 ml samples from each of the three chambers were drawn in syringes at intervals of 5, 10, 15, 20 min from chamber closure, totaling 13 samples for each site. Chamber

temperature was monitored during the sampling. After the sampling event, the gas samples were stored in coolers at +4°C and analyzed within 36 hours in a laboratory with a gas chromatograph. The gas chromatograph (Hewlett-Packard, USA) model number HP-5890A was fitted with a flame ionization detector (FID) for CH₄ and an electron capture detector (ECD) for N₂O 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 CH₄ and N₂O concentration was analyzed. The CH₄ (μg m⁻² h⁻¹) and N₂O (μg m⁻² h⁻¹) fluxes were calculated from the slope of linear regression between the set of 4 gas concentrations and sampling time, time elapsed after the chamber closure, and by applying temperature correction. For the flux calculation we used a MATLAB (The Mathworks Inc.) script developed at the Dept. of Physics, University of Helsinki.

The quantification limit of the gas chromatograph (MQL) was based on 100 subsequently analyzed samples of reference gas of known CH₄ and N₂O concentrations (mean +/- 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 4 CH₄ or N₂O concentrations of reference gas samples (22 μg m⁻² h⁻¹ for CH₄ and 18 μg m⁻² h⁻¹ for N₂O). 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 CH₄ and 49% of N₂O fluxes were discarded.

2.4 Statistical analysis

Two-way analysis of variance (ANOVA) was used to test whether CH₄ and N₂O fluxes of forest/mire types have common means in wet, typical, and dry years. Post-hoc Tukey HSD tests were used to test the pairwise differences between the forest/mire types and years changing from wet to dry. For CH₄ fluxes we ran ANOVA tests twice, first on the whole dataset including nine forest/mire types and then on a subset of data including upland forests and forest-mire transitions, and excluding mires. For testing significant differences between the two groups of data we performed Welch's Two Sample t-test e.g. between the N₂O fluxes from the snow on the ground season (January-April in 2006) and the N₂O 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 CH₄ (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), and c) mires (VSR1, VSR2).

CH₄ 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 CH₄ together and their combinations iteratively by selecting the model combination of variables that were significant.

The CH₄ fluxes for upland forests and transitions included soil moisture at 10 cm (%) (SWC₁₀) and soil temperature at 5 cm (°C) (T₅) as predictors in separate models (Eqs. (1) and (2)):

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

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

where yu_{ij} and yt_{ij} is the CH₄ flux (μg m⁻² h⁻¹) for upland forests or transitions and for a particular i^{th} forest type and the j^{th} observation, β_{CT} through β_{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)), SWC₁₀, and T₅ 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 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 CH₄ fluxes (μg m⁻² h⁻¹) of mires were fitted by using a multiplicative non-linear regression model with a combined response to water table depth and soil temperature at 5 cm Eq. (3):

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

where y_{ij} is the CH_4 flux ($\mu\text{g m}^{-2} \text{h}^{-1}$) for the i^{th} mire (VSR1,VSR2) and for the j^{th} case, WT (cm) is water table depth, T_5 ($^{\circ}\text{C}$) is soil temperature at 5 cm, and a_0 , W_{Topt} , W_{Ttol} , T_{opt} , T_{tol} are parameters (Table 3).

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

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

where z_{ij} is the N_2O flux ($\mu\text{g m}^{-2} \text{h}^{-1}$) for the i^{th} mire (VSR1,VSR2) and for the j^{th} case, SWC_5 (%) is soil moisture at 5 cm, and T_5 ($^{\circ}\text{C}$) is soil temperature at 5 cm, and a_0 , T_{opt} , T_{tol} 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 performed 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°C 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

1 in August, and dropped to 58 mm in September. However, in the warmest summer (2006) the
2 monthly precipitation never reached more than 48 mm. In July 2006, two rainless weeks
3 induced a drought. By drought we mean that the soil water content in the upper soil layer (in
4 mineral soils) was so low that mosses wilted and dried (all along the ecotone). The drought
5 conditions lessened in mid-August and ended in September with increasing rains towards
6 autumn. Late autumn was exceptionally warm and snowless.

8 Monthly median soil temperatures at 5 cm (T_5) ranged from around 5 °C in May, culminated
9 to around 15-16 °C in July and August and subsided again to around 5 °C in October. The
10 non-vegetative season T_5 minimum was close to 0 °C. The warmest T_5 was in upland forest
11 1CT and the coldest was in upper forest-mire transition 5 OMT+. Soil temperature slightly
12 increased from forest-mire transitions towards mires. In spite of the ambient air temperature
13 difference throughout all the months in the 3 years, we detected differences mainly during
14 early and late season in 2004, 2005, and 2006 T_5 (Figure 2a).

15 The median water table (WT) showed the obvious rise from 10 m at the summit of the hill, to
16 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
17 the level (Figure 2b). The seasonal WT rise in 2005 was observed between the July and
18 August medians. During the drought of 2006, the WT values dropped less than 0.1 m for the
19 uppermost forest sites, but dropped heavily by ~1 m in the forest-mire transitions, and more
20 than 0.5 m in the lowermost peatland sites.

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

25 **3.2 CH₄ fluxes**

26 The median fluxes from the forest floor varied from -51 to 586 $\mu\text{g m}^{-2} \text{h}^{-1}$ for CH₄ among
27 individual sites during the entire period (Figure 3a). The small negative CH₄ fluxes associated
28 with prevailing oxidation were mostly observed in uplands and in transitions while mires
29 typically showed large positive higher CH₄ fluxes associated with prevailing production. The
30 CH₄ flux dynamics changed exponentially with increasing levels of the ground water table
31 from small uptake to large emissions (Figure 2, Figure 3). The median CH₄ fluxes of uplands

(CT, VT, MT, OMT), transitions (OMT+, KgK, KR), and mires (VSR1, VSR2) varied from -38, -8, and 392 $\mu\text{g m}^{-2} \text{h}^{-1}$ respectively (Figure 3b). Momentary CH_4 fluxes of uplands and transitions ranged from -342 to 143 $\mu\text{g m}^{-2} \text{h}^{-1}$, whereas in mires the fluxes ranged from -12 to 6808 $\mu\text{g m}^{-2} \text{h}^{-1}$ (Figure 3b). The median CH_4 fluxes for one upland (VT) and all the transitions (OMT+, KgK, KR) were found inside the range of the gas chromatograph detection limits ($\text{MQL}_{\text{CH}_4} = 22 \mu\text{g m}^{-2} \text{h}^{-1}$). In forest-mire transitions the ground water level in August 2005 increased towards the surface and approached the levels typically found in mires (Figure 2b), but the soil water saturation in transitions was not followed by CH_4 emissions such as those found in mires.

A two-way analysis of variance (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 $F(16, 1252) = 5, p < 0.001$. Tukey post-hoc 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 dataset, for the group of uplands with transitions there was no difference between wet, typical, and dry years $F(2, 976) = 1, p = 0.292$ or their interactions $F(12, 976) = 1, p = 0.135$. The mean CH_4 uptake of the upland forests ($-42.9 \mu\text{g m}^{-2} \text{h}^{-1}$) was for the whole period significantly larger than the mean CH_4 uptake of the forest-mire transitions ($-12.8 \mu\text{g m}^{-2} \text{h}^{-1}$) according to Welch's two sample t-test $t(994) = 15.56, p < 0.001$. Tukey post-hoc comparison of the

differences in the mean CH₄ fluxes for 21 pairs of seven upland and transitional forest types was significant for 17 pairs at $p < 0.001$ and ranged from OMT-VT ($M = -35$, 95% CI [-45, -25]) to KR-OMT ($M = 51$, 95% CI [41, 61]). Tukey post-hoc comparisons showed non-significant p values for 4 of the 21 pairs of CH₄ fluxes of transitional and upland forest types (MT-CT 0.056, OMT+-VT 0.965, OMT-MT 0.431, and KR-KgK 0.999).

3.3 Factors controlling CH₄ fluxes

The mean level of CH₄ fluxes of upland and transitional forests differed (Table 2, parameter “group bi”), though the sensitivity response to environmental factors was similar (Figure 4). The largest part of the CH₄ 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 CH₄ 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 CH₄ flux response between dry and water saturated soil differed by $50 \mu\text{g m}^{-2} \text{h}^{-1}$. A stronger gradient than that in the soil moisture was detected by modeling stronger temperature responses of CH₄ fluxes for the uplands and the nearly flat response for the transitions (Figure 4). The model parameter to soil temperature at 5 cm in the uplands was highly significant at $p < 0.001$, in contrast to transitions where the temperature parameter was insignificant $p = 0.629$ (Table 2). In the mires the observed range of water level during wet, typical, and dry years spanned from the surface to a depth of 54 cm and showed a sigmoidal response with lower CH₄ fluxes towards the extreme ends. The optimum water level for CH₄ emissions was 18 cm (se 2.2) below the surface with 16.6 cm tolerance which is deviation of water level up to 60% of CH₄ flux maximum (Figure 4, $p < 0.001$, WT_{opt} and WT_{tol} in Table 3). Optimum near surface peat temperature for the CH₄ emissions was found at 13.9 °C (se 1.4) with 6.4 °C tolerance (Figure 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 N₂O fluxes of forest/mire types ranged from -107 to 248 $\mu\text{g m}^{-2} \text{h}^{-1}$. The median N₂O fluxes were similar for the forest/mire types and ranged only from 0 to 6 $\mu\text{g m}^{-2} \text{h}^{-1}$ (Figure 5). The median N₂O fluxes of all forest/mire types were found inside the range of the method quantification limits ($MQL_{N_2O} =$

18 $\mu\text{g m}^{-2} \text{h}^{-1}$). 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) (Figure 6).

In general N_2O fluxes were low and did not show clear spatial differences in relation to increasing soil moisture from xeric uplands to water saturated mires, but the N_2O fluxes were lower in the dry than in the typical years. 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 pair-wise differences during the whole period and also during the snowless periods of wet or dry years (Figure 6). The significant N_2O flux difference for VSR2-OMT in a dry year ($M = 35$, 95% CI [3, 68], $p = 0.02$) was caused by a small decrease in OMT and increase in VSR2 fluxes.

3.5 Factors controlling N_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, Figure 7). The modeled Gaussian type response showed optimum N_2O production at 11.3 ($^{\circ}\text{C}$) soil temperature at a depth of 5 cm with a very narrow temperature range increasing from 7 $^{\circ}\text{C}$ and subsiding at 14 $^{\circ}\text{C}$.

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 CH₄ fluxes and soil water pH was significant ($r = -0.32$, $p < 0.001$). Mean values of summer 2005 CH₄ of upland forests and forest-mire transition were negatively correlated with mean pH ($\text{CH}_4 = 129.35 - 33.36 \cdot \text{pH}$, $r^2 = 0.49$, Fig. 8a). The ecotone N₂O fluxes were significantly correlated with pH ($r = 0.174$, $p = 0.004$). The mean N₂O values of sites increased with mean pH ($\text{N}_2\text{O} = -117.07 + 27.33 \cdot \text{pH}$, $r^2 = 0.32$, Fig. 8b). However, the post-hoc Tukey differences of mean N₂O fluxes from forest floor for the pair-wise comparisons of forest/mire types were not significant for 31 pairs and mean N₂O flux differences were significant only for 5 pairs (KgK-CT, VSR1-KgK, VSR1-KR, VSR1-MT, VSR1-OMT, Figure 9). We did not find significant correlation between site specific mean CH₄ and N₂O flux and bulk density and/or C/N ratio.

4 Discussion

4.1 CH₄ dynamics

The forest/mire types significantly differed in forest floor CH₄ 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, CH₄ uptake also showed significant differences between the forest types on mineral soil (uplands) and organo-mineral soil (transitions). Our study demonstrated that the CH₄ flux response to soil moisture changes with the relatively small mesoscale levels of a forest-mire ecotone (450 m long transect) (Figure 4). The CH₄ flux sensitivity to soil moisture showed a positive linear response to CH₄ oxidation for the drier soils of transitions and uplands. **Alternatively CH₄ 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 CH₄ emissions during short-term water level fluctuations.

The lack of an increase in CH₄ emissions during increased ground water levels in the transitions in our study could be attributed more to the relatively slow response of CH₄ producing bacteria than to the effectiveness of CH₄ oxidation which was reduced by a reduction in the aerated soil layer. Mäkiranta et al. (2009) showed that in forested peatlands

1 the highest abundance of respiratory microbes could be found in the zone around the average
2 water level. It is also known that the depth of maximum CH₄ production and oxidation is
3 strongly related to 30-day average water level depth with time lag differences between the
4 drier and wetter microsites (Kettunen et al. 1999). The duration of exceptionally increased
5 high water levels was probably too short for CH₄ producing bacteria to relocate and/or adapt
6 to water saturated conditions. **The methane production potential of mire varies in relation**
7 **to methanogen communities, substrate availability, pH, and temperature (Juottonen et**
8 **al. 2005, Juottonen et al. 2008).** Unlike open mires, in drier conditions (similar to our
9 forest-mire margin) decreases in the methanogen community is associated with low CH₄
10 production potential and with low emissions (Yrjälä et al. 2011). In forest-mire margin,
11 also relatively small population of methanotrophic microbes, coupled with *Sphagnum*
12 mosses, and low CH₄ oxidation potential, related to low CH₄ concentrations in moss
13 layer, could indicate low production potential (Larmola et al. 2010). It's known that
14 water level depth is major control of CH₄ oxidation, and that *Sphagnum* species
15 originally not oxidising CH₄ need several days up to a month to activate methanotrophs
16 through a water phase (Larmola et al. 2010, Putkinen et al. 2012).

17
18 Temporally water saturated soil layers of pristine forest-mire transitions had low CH₄
19 emissions possibly due to low pH, imposing physiological restrictions on soil microbial
20 communities. Methanogenic activity in water saturated organic soils can be reduced by high
21 acidity (e.g. Ye et al. 2012). **Activity of methanotrophic microbes is also pH dependent**
22 **with optimum above 5 (Danilova and Dedysh 2013, Saari et al. 2004).** Our forest-mire
23 transitions had mean pH below 5 and demonstrated lower net CH₄ uptake rates in
24 comparison to upland forests on mineral soils (Fig.8) which is in line with Saari et al.
25 (2004). In spite of positive pH and CH₄ correlation found for the group of transitions
26 and uplands together, the net CH₄ sink of upland well-drained mineral soil sites was
27 **primarily determined by high oxygen content.** Small momentary CH₄ emissions
28 (Supplement Fig. 3a) observed in forest-mire transitions also indicated potential for
29 occasionally higher production than oxidation.

30
31 **Beside differences in microsite soil water saturation, pH, and microbial communities,**
32 **also plant communities (e.g. Saarnio et al., 1997, Strom et al. 2003, Riutta et al., 2007,**

Dorodnikov et al. 2011) play important role in explaining net CH₄ emissions. In the forest-mire margin sites (KR and KgK) vascular plants (Fig. 1c) contributed to net forest floor CH₄ emissions (Supplement Fig. 3), if methane production occasionally increased. It's 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 CH₄ from peat to the atmosphere without oxidation in the acrotelm, and increases net CH₄ emissions (Hornibrook et al. 2009, Dorodnikov et al. 2011). 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 CH₄ emissions as observed in relatively dry Scots pine dominated forests (VT – *Vaccinium Vitis idea* type) (Figure 3) with sandy podzol soil and ground water depths around two meters, have been occasionally found in mineral soil forests in other studies. **The occasional mineral soil CH₄ effluxes suggested that plants' deepest roots transport CH₄ via the transpiration stream (Megonigal and Guenther 2008).** Ullah et al. (2009) found that Spruce forest soils produced CH₄ only during the spring thaw season but later under drier summer conditions soils switched to CH₄ consumption. In our study the rare occurrence of small CH₄ 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 CH₄ emissions could be also partly attributed to the random noise in measurements. However, all the data showed a significant reduction of CH₄ uptake with increasing soil moisture at 10 cm, this may be associated with oxidation processes.

The form of dependence of CH₄ 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 CH₄ 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 CH₄ oxidations

1 than promoted such CH₄ emissions as found in nearby permanently saturated mires. Beside
2 the sensitivity of CH₄ fluxes to moisture we also observed sensitivity to soil temperature
3 (Figure 4) possibly also reflecting the role of soil physiochemical properties and/or the
4 activity of methanogens. The linearly increasing CH₄ oxidation rates with temperature in
5 upland forest types could reflect the importance of soil physiochemical properties, whereas
6 the Gaussian form may also reflect a biological driven response in mires.

7
8 In our upland forests the role of soil physiochemical and microbiological drivers may have
9 contributed to the fact that the temperature and moisture explained just 10% of the variation.
10 Although our mean CH₄ data did not show significant correlations with bulk density, the
11 porous organic horizon is known to enable larger diffusion and CH₄ oxidation (Nakamo et al.
12 2004, Ullah and Moore 2011). It was difficult to assess the differences in sensitivity of CH₄
13 oxidation because of poor MQL and low fluxes of CH₄ oxidation. The absolute levels of the
14 temperature effect on CH₄ fluxes in forest-mire transitions caused part of the signal to be
15 mixed with variable sources of sampling errors and gas chromatograph precision errors.
16 Though, in transitions both soil physiochemical and microbiological drivers may be important
17 for CH₄ oxidations, as our forest-mire transitions showed a significant relation to soil moisture
18 but not to temperature. The weak response of CH₄ oxidation to temperature was in contrast to
19 the strong response to moisture and bulk density found in forests growing on mineral soils
20 (Hashimoto et al. 2011). However, Nakamo et al. (2004) reported a clear relation with
21 temperature but not with moisture for boreal birch forest (similar to our KR – Spruce Pine
22 Swamp).

23
24 **In mires, the form of CH₄ sensitivity to temperature and water table depth may be also**
25 **determined by differences in pH, and the composition of microbial and plant functional**
26 **communities (Bubier et al. 1995, Jaatinen et al. 2004, Juottonen et al. 2005, Juottonen et**
27 **al. 2008, Larmola et al. 2010, Riutta et al. 2007, Saarnio et al. 1997, Saari et al. 2004,**
28 **Yrjälä et al. 2011). The CH₄ emissions in VSR1 were larger than in VSR2 (Figure 4).**
29 **Differences in pH could favor methanogen activity in less acid fen (Juottonen et al. 2005,**
30 **Yrjälä et al. 2011, Ye et al. 2012). Different coverage of vascular aerenchymous plants**
31 **and *Sphagnum* mosses between VSR1 and VSR2 could affect site specific CH₄**
32 **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 CH₄ transport (Bubier et al. 1995, Macdonald et al. 1998), whereas in VSR2 *Menyanthes* species was absent. Shallower form of CH₄ sensitivity to water table in a hummock type fen VSR2 than in lawn type of fen VSR1 could result from differences in plant mediated CH₄ emissions (e.g. Riutta et al. 2007, Hornibrook et al. 2009, Dorodnikov et al. 2011) or CH₄ oxidation potential between *Sphagnum* species (Larmola et al. 2010). For example in the study by Saarnio et al. (1997) the CH₄ 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 N₂O dynamics

The momentary N₂O 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 (Figure 5) were in the proximity of values for soils in similar climates (von Arnold et al. 2005a, Von Arnold et al. 2005b, Pihlatie et al. 2007, Matson et al. 2009, Ullah et al. 2009, Ojanen et al. 2010). Forest floor N₂O fluxes did not differ significantly for the nine forest/mire types of the ecotone $p = 0.637$ for the whole period from May 2005 to September 2006 probably due to the low nitrification potential of boreal forest in natural conditions (Regina et al. 1996). 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 N₂O 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 (Arnold et al. 2005a, Arnold et al. 2005b).

Soil incubation studies under various moisture and temperature regimes (Pihlatie et al., 2004, Szukics et al., 2010) imply that our higher forest floor N₂O 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 observed also mean N₂O flux of dry pine forest significantly larger than that of paludified spruce forest (larger CT

than KgK), whereas mean N₂O flux of water saturated mire was larger than four sites (VSR1-KgK, VSR1-KR, VSR1-MT, VSR1-OMT) (Fig. 8, Fig. 9). Therefore during fluctuating soil moisture, we could expect increased N₂O fluxes of 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 N₂O emissions through denitrification (Regina et al., 1996, Ste-Marie and Pare', 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 N₂O fluxes. Highly acid conditions prevent development of nitrifiers, substrate affinity and nitrification, even if ammonium is available (Ste-Marie and Pare', 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 would be present low pH would enhance N₂O emissions due to inhibiting di-nitrogenoxide reductase and increasing N₂O/N₂ 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 N₂O 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 N₂O 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 N₂O 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 N₂O 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

1 mobilized from e.g., fast decomposition of deciduous foliage during the drought related early
2 peak in litterfall or during sudden soil freeze-thaw cycles (Pihlatie et al. 2007). However,
3 during the active growing season these events might be rare in typical boreal conditions where
4 plants are adapted to a rapid uptake of limited rates of soil N mineralization (Hikosaka 2003,
5 Korhonen et al. 2013, Lupi et al. 2013).

6
7 Several studies (Martikainen et al. 1995, Regina et al. 1996) reported that peatlands in a
8 pristine state showed small N₂O emissions, but when drained, nitrification rates were
9 enhanced depending on nutrient status (a large increase for rich sites and no increase for poor
10 sites). The limited increase in N₂O emissions during the summer drought in our mires may be
11 therefore attributed to low nutrient levels, a low supply of nitrate and/or low nitrification
12 potential. Relatively low fertility may also be expected to limit the N₂O emissions during the
13 dry season of our forests and forest-mire transitions as the N₂O emissions are also known to
14 correlate with site fertility e.g., expressed as C/N ratio (Klemedtsson et al 2005, Ojanen et al.
15 2010, Hashimoto et al. 2011).

16
17 The N₂O fluxes of forest/mire types fitted by nonlinear regression models showed positive
18 linear response to soil moisture at a depth of 5 cm and significant Gaussian type response to
19 temperature at depths of 5 cm (Table 4, Figure 7). However, the residuals of the moisture and
20 temperature model were large (Figure 7) and r^2 was only 10%. Luo et al. (2012) demonstrated
21 for temperate forests that N₂O emissions depended nonlinearly on the soil moisture and
22 positively on soil temperature. In our study, the weak linear response of soil moisture to N₂O
23 fluxes could be an artifact of fitting several N₂O processes of different sensitivity to different
24 forest/mire types. For example in well drained uplands the N₂O fluxes may be mainly due to
25 processes of ammonification and nitrification while in mires nitrification in the drier surface
26 layer may be coupled with denitrification in deeper water-saturated layers (Ambus et al. 2006,
27 Regina et al. 1996). The soil moisture and temperature from deeper layers did not
28 significantly explain the N₂O fluxes (results not shown). An active depth of 5 cm
29 corresponding to the top of the organic layer is in agreement with Pihlatie et al. (2007) who
30 demonstrated that N turnover in poor boreal forest soil takes place in the litter layer and that
31 N₂O emissions originate mainly from the top soil. The N₂O production in our study, increased
32 with rising soil temperature of the humus layer from 7 °C typically found after the soil thawed

during spring warming and in autumn during soil cooling. These could be the periods when the nitrification potential increased; in spring probably due to mobilization of nitrogen during freeze-thaw cycles and in autumn probably due to mobilization of nitrogen from the quickly decomposing foliar litterfall (Pihlatie et al. 2007, Pihlatie et al. 2010, Luo et al. 2012).

5 Conclusions

The CH₄ 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 CH₄ oxidation rather than emission with very small sensitivity to wet and dry events. The N₂O fluxes of forest mire types were generally low. Despite small N₂O peaks in spring and autumn, the N₂O 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 CH₄ and N₂O 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 CH₄ and N₂O emissions. **Therefore, when making attempts to up-scale boreal landscape carbon and nitrogen cycles,** the organo-mineral soils of pristine forest-mire transitions should be regarded as CH₄ sinks and minor N₂O sources rather than having the peak emissions on the landscape level.

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3

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20

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

2

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

3

Table 2. Parameter estimates and their standard errors for trend coefficients of CH₄ fluxes (μg m⁻² h⁻¹) of the upland forest types (CT, VT ... OMT (Eq. (1)), and for the forest-mire transitions (OMT+, KgK, and KR (Eq. (2))). Both equations are functions of volumetric soil moisture at 10 cm (%) and soil temperature at a depth of 5 cm (°C).

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

p < 0.001 for all parameters, except ^a p = 0.011, ^b p = 0.629

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

Table 3. Parameter estimates and their standard errors for trend coefficients of CH₄ fluxes (μg m⁻² h⁻¹) of the mires (VSR1, VSR2 (Eq. (3)). The Eq. 3 is a function of water table depth (cm) and soil temperature at a depth of 5 cm (°C).

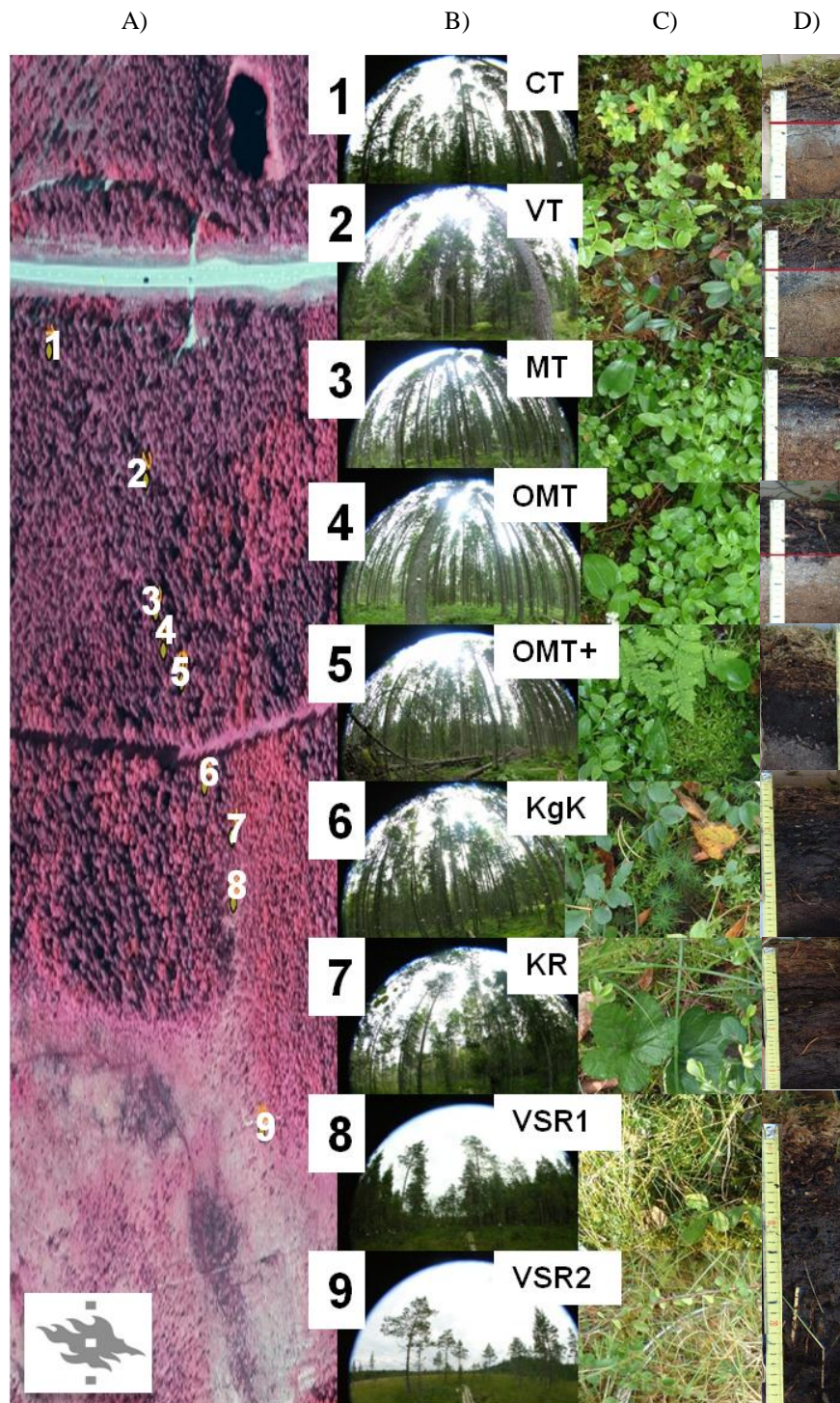
Eq. 3)	a0	a0 SE	T _{opt}	T _{opt} SE	T _{tol}	T _{tol} SE	WT _{opt}	WT _{opt} SE	WT _{tol}	WT _{tol} SE	N	RMSE
mires	1207.1	126.7	13.9	1.4	6.4	1.3	18.0	1.9	16.6	2.1	324	656
VSR1	1570.3	155.1	13.0	0.8	5.8	0.8	18.6	1.6	15.5	1.7	162	424
VSR2	801.3	190.8	16.6 ^a	6.8	8.7 ^b	4.5	17.3 ^c	5.3	20.7 ^d	9.7	162	558

p values < 0.001, except ^a p = 0.016, ^b p = 0.053, ^c p = 0.002, ^d p = 0.035

Table 4. Parameter estimates and their standard errors for forest floor N₂O fluxes ($\mu\text{g m}^{-2} \text{ h}^{-1}$) of all forest/mire types (CT, VT ...VSR2) in one group Eq. (4). The Eq. (4) is function of volumetric soil moisture at 5 cm (%) and soil temperature at a depth of 5 cm (°C).

Eq. 4)	a0	a0 SE	T _{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



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

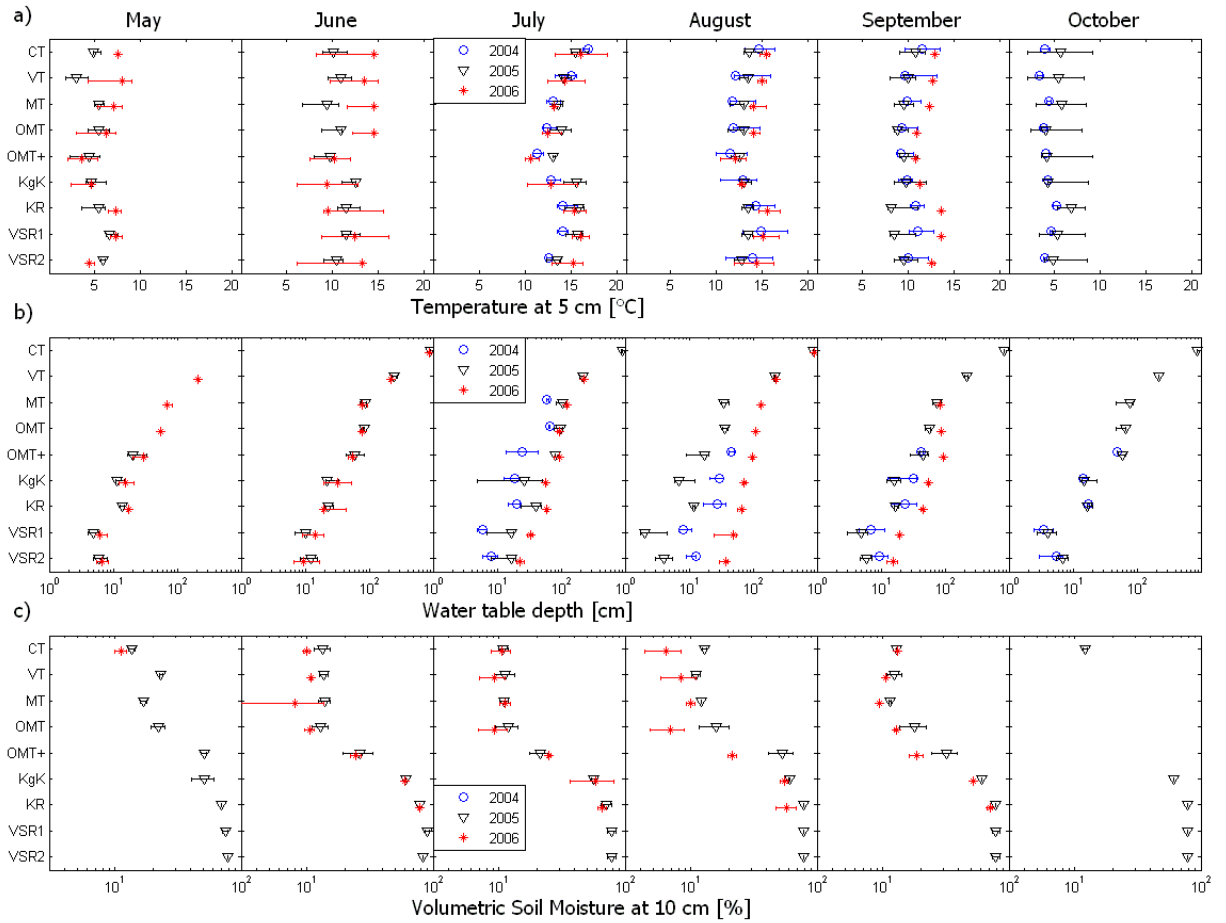


Figure 2. The panel a, b, c shows the monthly medians of environmental variables: a) soil temperature at a depth of 5 cm, b) ground water level, and c) volumetric soil moisture at 10 cm depth observed along the forest/mire ecotone during wet (2004), intermediate (2005), and dry year (2006). The top-down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

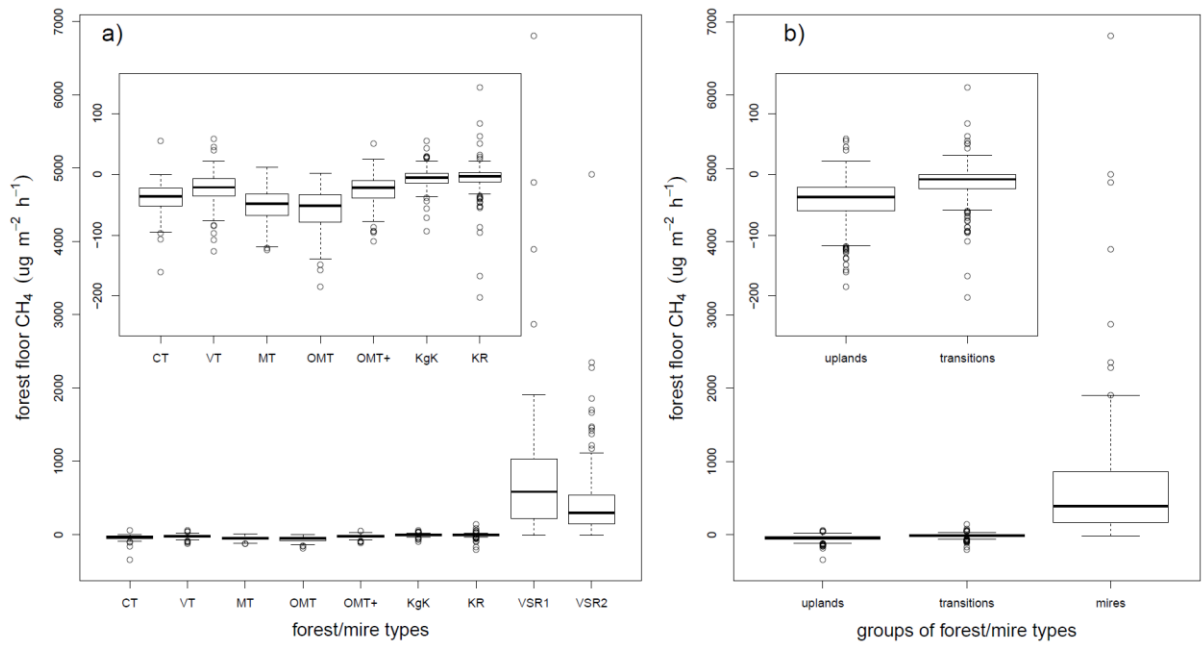
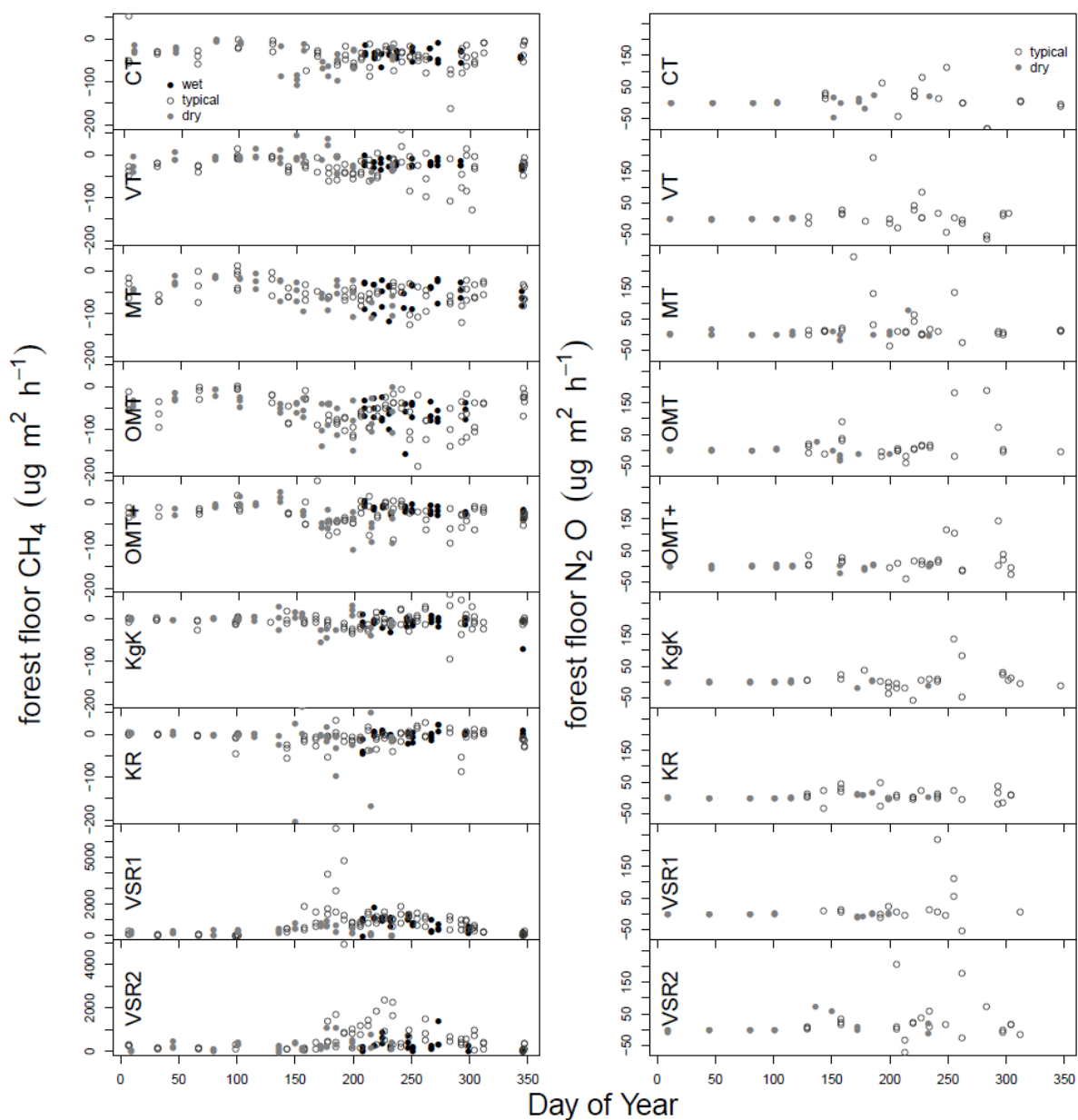


Figure 3. The boxplots of forest floor CH₄ fluxes (μg m⁻² h⁻¹) for each forest/mire type (a), and (b) for uplands (CT, VT, MT, OMT), transitions (OMT+, KgK, KR), and mires (VSR1, VSR2) during the whole period. The left-right arrangement of sites mimics the locations on the slope (see Fig. 1).



Supplement Figure 3. The momentary forest floor gas fluxes ($\mu\text{gm}^{-2} \text{h}^{-1}$) of a) CH₄ and b) N₂O in forest/mire types (uplands CT, VT, MT, OMT, transitions OMT+, KgK, KR, and mires VSR1, VSR2) as measured during the years with exceptional moisture (wet, typical, and dry). The top-down arrangement of sites mimics the locations on the slope (see Fig. 1).

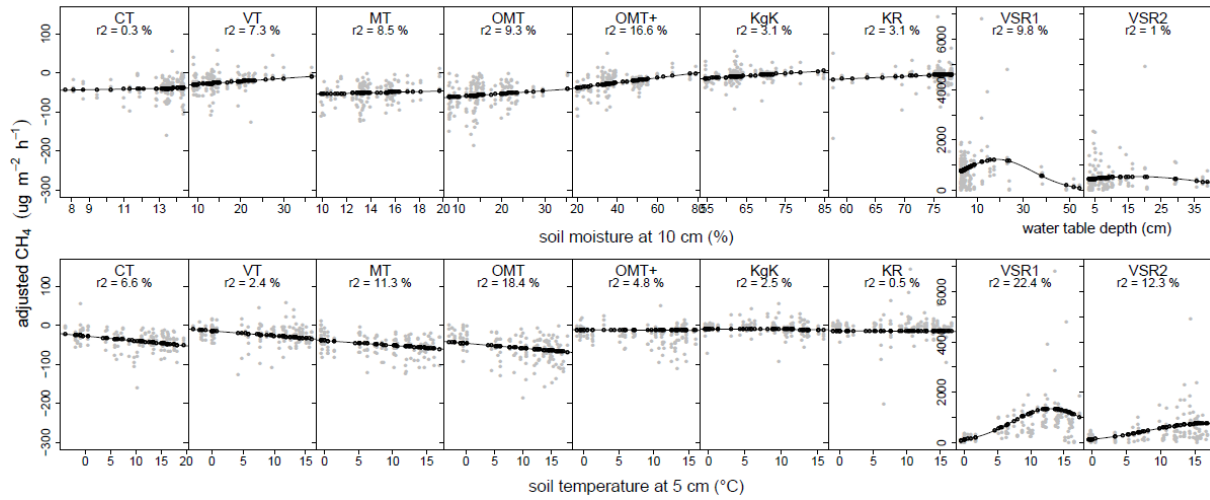


Figure 4. Comparison of sensitivity of forest floor CH_4 fluxes ($\mu\text{g m}^{-2} \text{h}^{-1}$) to environmental factors for nine forest/mire types. In the upper panels is modeled CH_4 flux response to soil moisture at 10 cm (uplands and transitions) or to water table depth cm (mires) for uplands (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 below the soil surface. In the lower panels, CH_4 flux response (Eq. (1), Eq. (2), Eq. (3)) is modeled to soil temperature at 5 cm of the same forest/mires types and during the same period as in the upper row. The CH_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 others were set to their mean levels. 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).

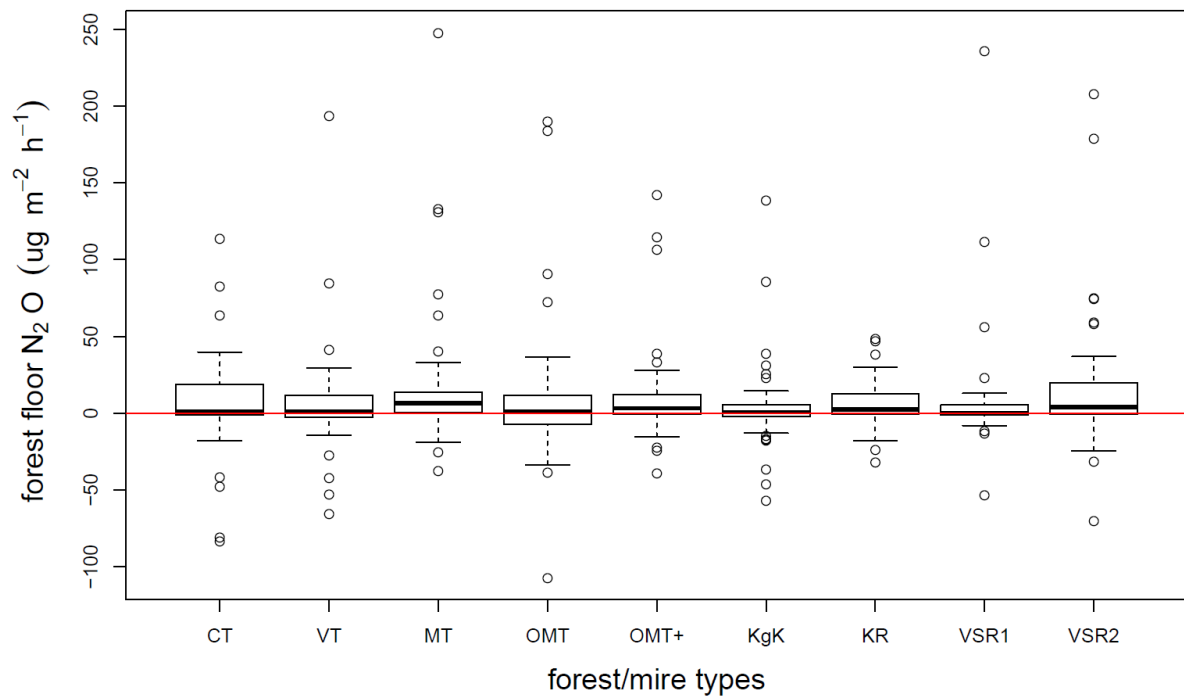


Figure 5. The boxplot of forest floor N_2O fluxes ($\mu\text{g m}^{-2} \text{h}^{-1}$) for each forest/mire type (uplands - CT, VT, MT, OMT; transitions - OMT+, KgK, KR; and mires - VSR1, VSR2) during the period including typical and dry years. The left-right arrangement of sites mimics the locations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

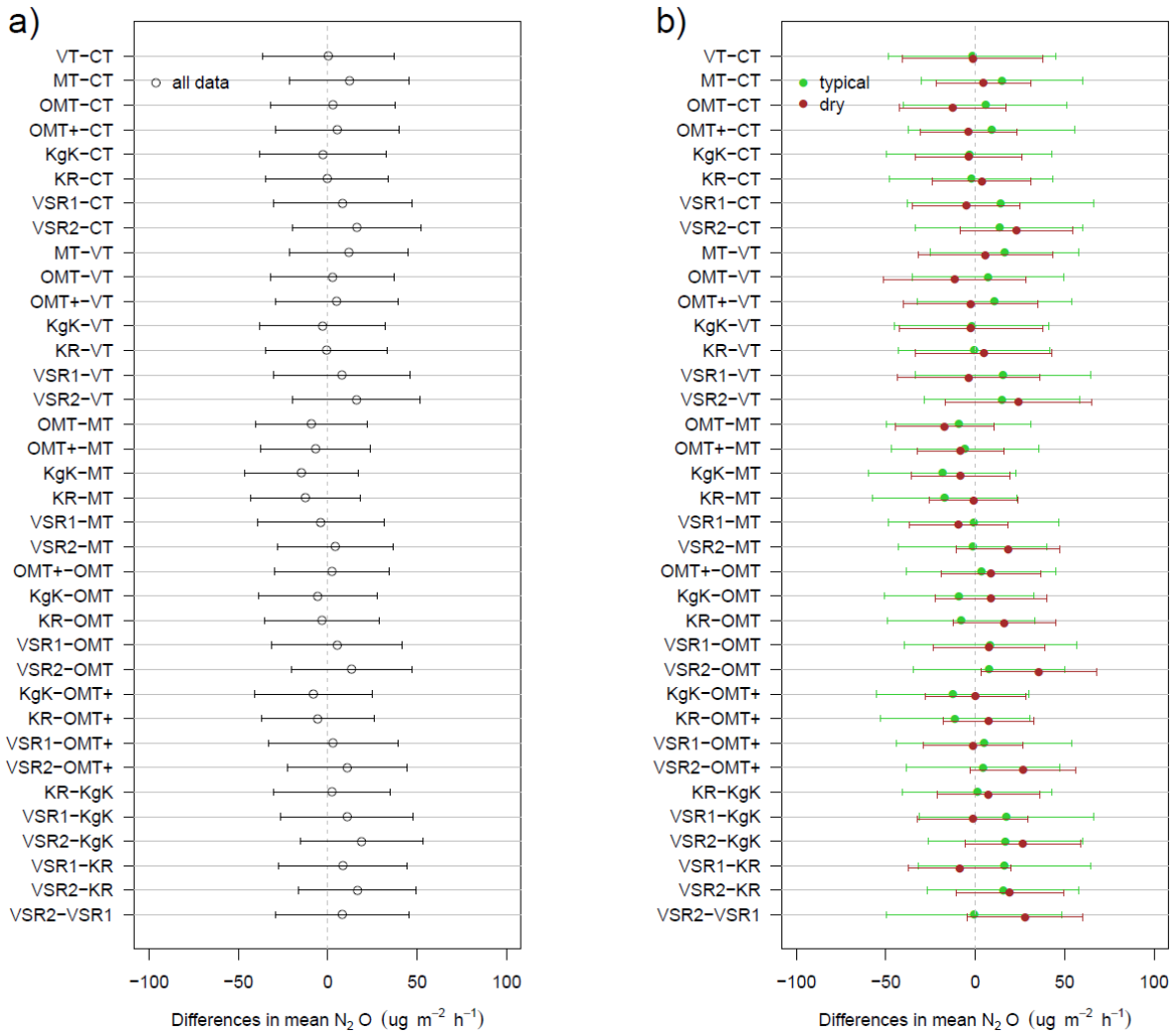


Figure 6. The post-hoc Tukey differences (error bars for 95% confidence intervals) of mean N_2O ($\mu g m^{-2} h^{-1}$) fluxes from forest floor for the pair-wise comparisons of forest/mire types (uplands - CT, VT, MT, OMT; transitions - OMT+, KgK, KR; and mires - VSR1, VSR2): a) the N_2O flux differences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

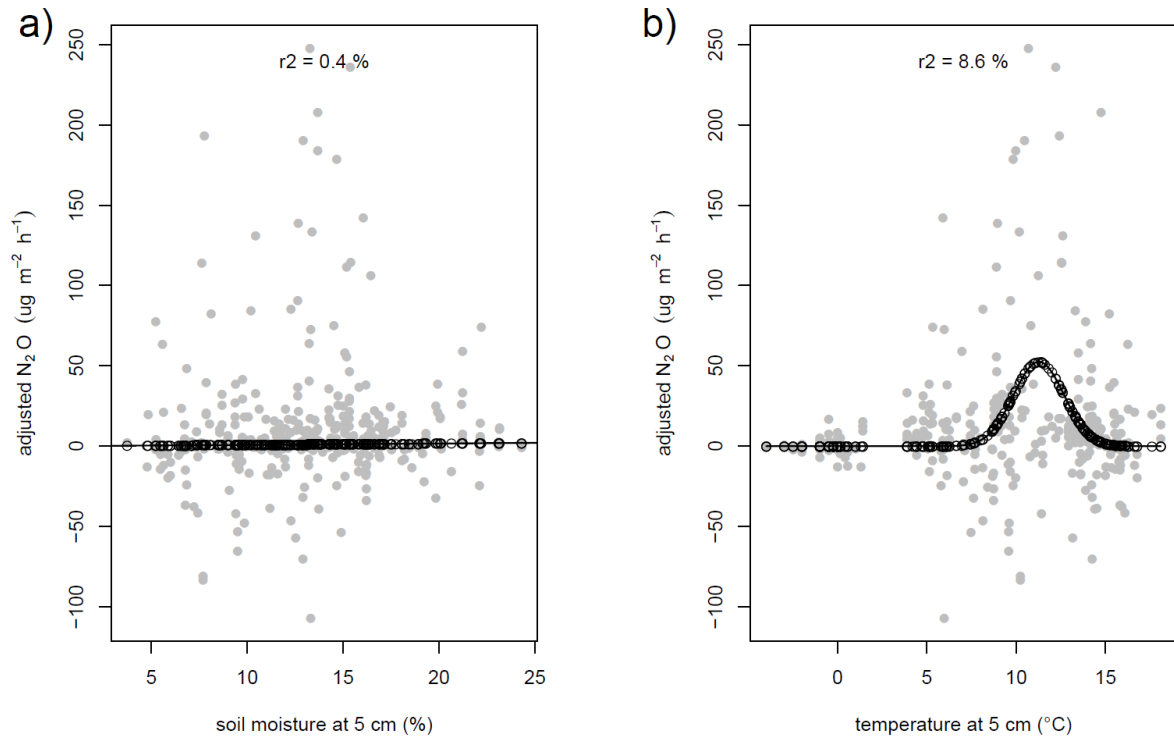


Figure 7. Sensitivity of forest floor N_2O fluxes ($\mu g\ m^{-2}\ h^{-1}$) of forest/mire types together with environmental factors a) N_2O flux response to soil moisture at 5 cm, and b) N_2O flux response to soil temperature at 5 cm during the period including wet, typical, and dry years. The N_2O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

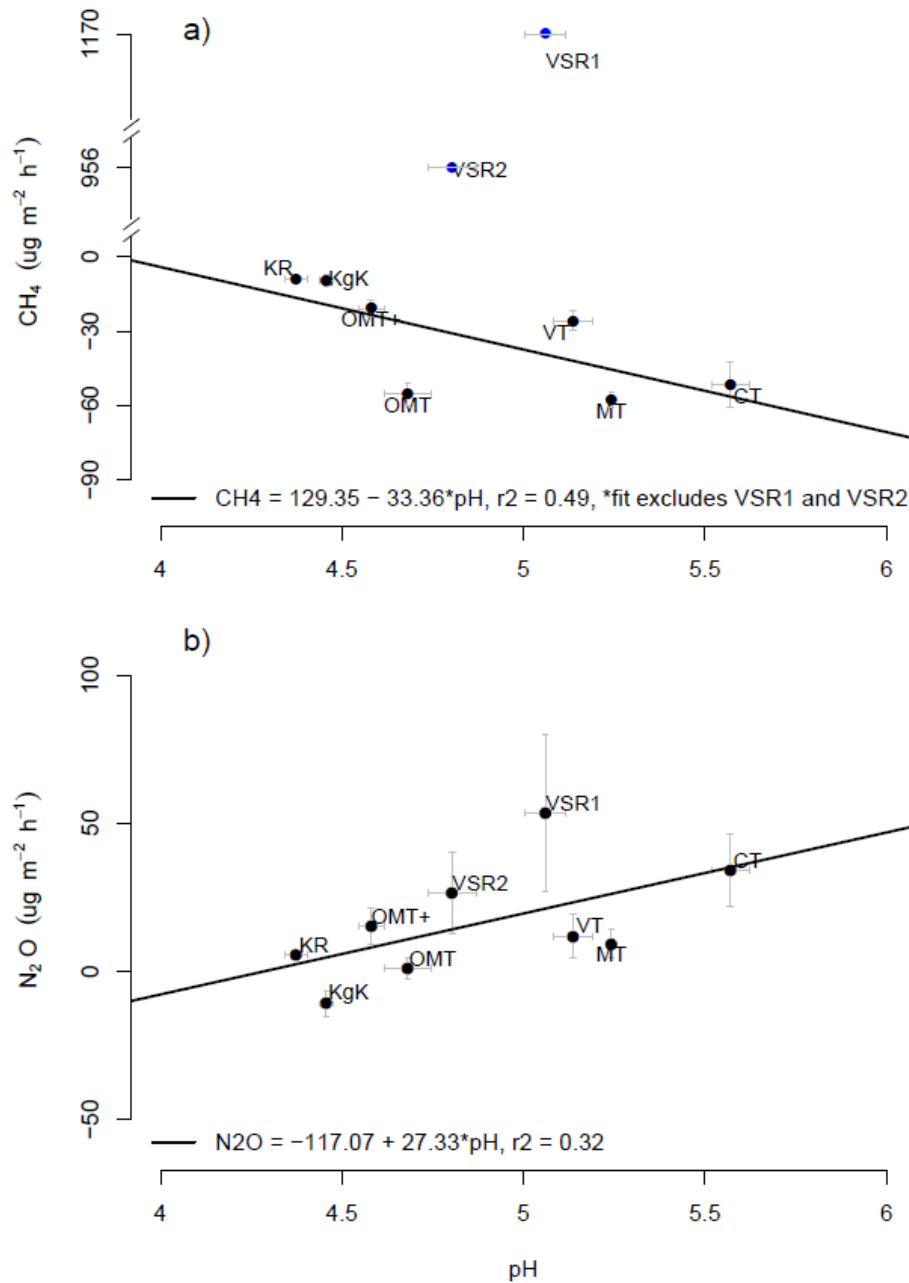
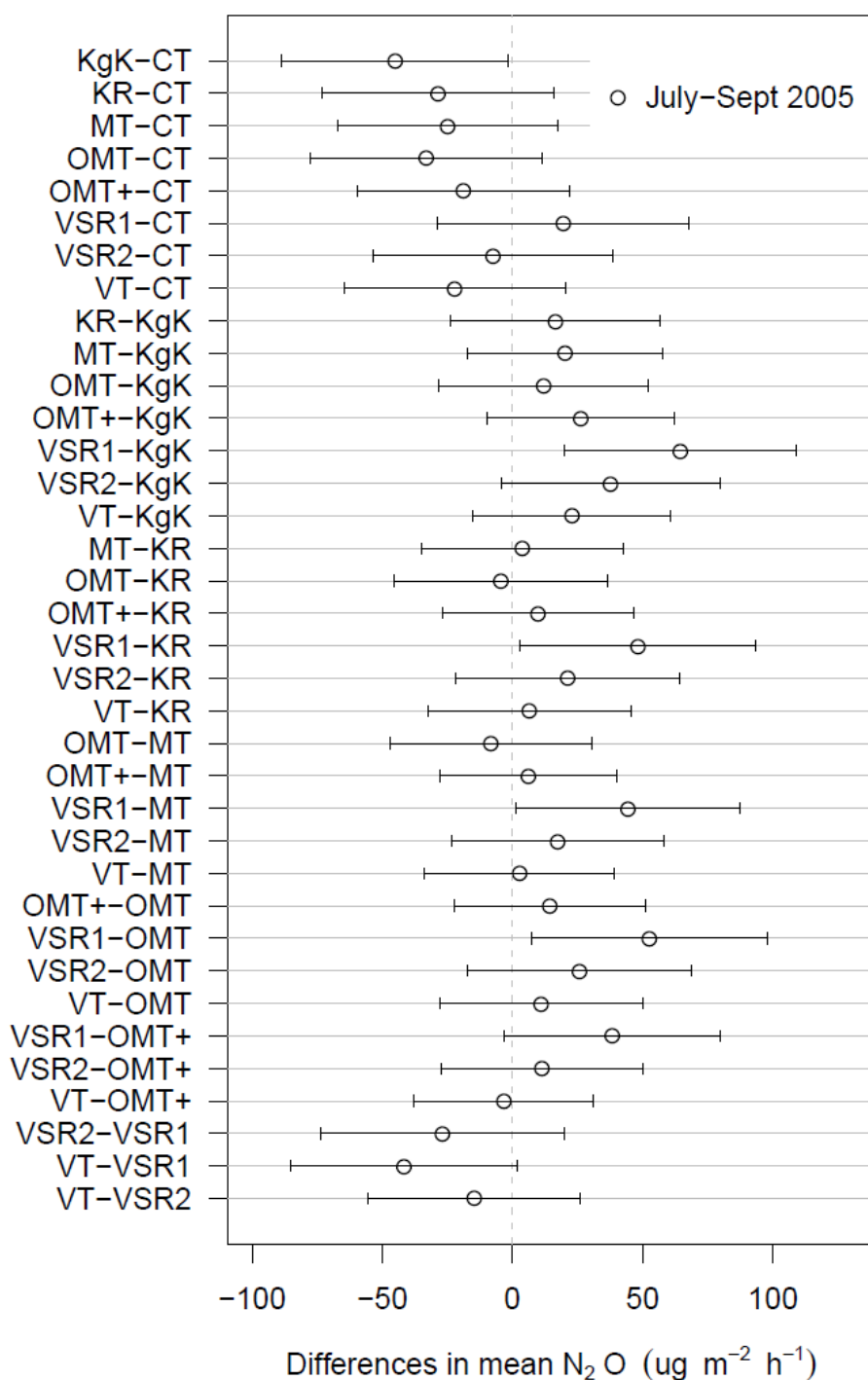


Figure 8. Scatterplot between site specific mean pH and mean flux (ugm⁻²g⁻¹) of a) CH₄ or b) N₂O of summer with intermediate moisture over the period of soil water sampling campaign (July-September 2005). Error bars show standard error. The CH₄ error bars for VSR1 and VSR2 are not shown.

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

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