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CH_4 and N_2O dynamics in the boreal forest–mire ecotone

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Abstract

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

In our study, we tested the differences and drivers of CH_4 and N_2O dynamics of forest/mire types in field conditions along the soil moisture gradient of the forest–mire ecotone. Soils changed from podzols to histosols and ground water rose downslope from 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 $\mu g\, m^{-2}\, h^{-1}$ for CH_4 and from 0 to 6 $\mu g\, m^{-2}\, h^{-1}$ for N_2O between forest/mire types throughout the entire wet-dry period.

In spite of the highly dynamic soil water fluctuations in carbon rich soils in forest–mire transitions, there were no large peak emissions in CH_4 and N_2O fluxes and the flux rates changed minimally between years. Methane oxidations were significantly lower in poorly drained transitions than in the well-drained uplands. Water saturated mires showed large CH_4 emissions, which were reduced entirely during the exceptional summer drought period. Near zero N_2O fluxes did not differ significantly between the forest/mire types probably due to their low nitrification potential. When up scaling boreal landscapes, pristine forest–mire transitions should be categorized as CH_4 oxidation types and background N_2O emission types instead of CH_4 and N_2O emission hotspots.

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1 Introduction

Soil fertility, soil water content and soil carbon storage of boreal forest varies between well drained mineral soils mainly found in uplands and poorly drained organic soils mainly found in peatlands (Seibert et al., 2007; Weishampel et al., 2009). The CH_4 and N_2O fluxes from mineral and organic soils are impacted by varying soil moisture conditions (Solondz et al., 2008; Pihlatie et al., 2004). Typical mineral soil forests are small sinks of CH_4 and small sources or sinks of N_2O (Moosavi and Crill, 1997; Pihlatie et al., 2007). Sparsely forested peatlands are typically large or small sources of CH_4 and small sources or sinks of N_2O (Martikainen et al., 1995; Nykänen et al., 1995; D'Angelo and Reddy, 1998). Field CH_4 and N_2O studies of natural boreal forest–mire ecotones are rare (e.g. Ullah et al., 2009; Ullah and Moore, 2011) in comparison to those of typical forests or peatlands. However, the forest–mire ecotone "the lagg transitional zone" collects nutrients from the adjacent mineral soil runoff and is often more minerotrophic, biologically diverse, and productive than open mires or bogs (Howie and Meerveld, 2011). Furthermore, ecotones between forests and mires are ecological switches (Agnew et al., 1993), where the vegetation of forests and mires coincide and soils frequently undergo fluctuations in water level position and chemistry (Hartshorn et al., 2003; Howie and Meerveld, 2011), and where the CH_4 and N_2O dynamics of forest–mire transitions may be expected to differ generally and on a year-to-year basis from those of typical forests and mires.

The CH_4 uptake of forest soils is a result of CH_4 oxidizing aerobic methanotrophs sensitive to water saturation, soil porosity, moisture, temperature, pH, and ammonium (Moosavi and Crill, 1997; Saari et al., 2004; Jaatinen et al., 2004). Unsaturated upland forest soils oxidize CH_4 at higher rates than more water saturated, acidic, and ammonium richer 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 moisture increases anoxic conditions favorable for increased methanogenesis (Juottonen et al., 2005), and as a result increases CH_4 emissions (Saarnio et al., 1997; Ojanen et al., 2010; Yrjälä et al., 2011).

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

Our aims were (1) to test whether forest floor CH_4 and N_2O fluxes of the forest–mire transition differ from the typical upland forests and lowland mires of natural boreal 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 promotes CH_4 production, and whether dry conditions reduce CH_4 production and increase N_2O emissions. We hypothesized that forest/mire types exhibit distinct levels of CH_4 and N_2O fluxes due to the changing soil structure from podzols to histosols and due to increasing soil water content from xeric to saturate. We expected that the occasionally saturated organo–mineral soils of forest–mire transitions are variable sources of CH_4 and N_2O fluxes.

2 Material and methods

2.1 Study site characteristics

The Vatiharju–Lakkasuo ecotone of nine forest and mire study sites forms a gradient in vegetation communities, soil moisture and nutrient conditions in Central Finland (61°47′, 24°19′) (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 Idea* Type) on the shoulder, and mesic and herbrich 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) (Fig. 1b). The forest floor vegetation is composed of site-specific mosses and vascular plants (Fig. 1c).

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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). 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 (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 (Ø 30 mm) installed at each site. Precipitation was measured by an automated bucket system at a station for monitoring forest – atmosphere relations, SMEARII (Hari and Kulmala, 2005), located 6 km north-west from the forest–mire ecotone. Missing soil temperature and moisture data of ecotone were gap filled by linear regression between continuous measurements of soil temperature and moisture at SMEARII.

2.3 CH_4 and N_2O fluxes

The field gas sampling was conducted weekly in the 2004 and 2005 seasons, biweekly during the 2006 season, and monthly during the winters. The gas sampling was done the same day ± one day as the micrometeorological measurements. If there was packed snow on the ground the gas samples were taken from the top and bottom layers; and the CH_4 (µg m^{-2} h^{-1}) and N_2O (µg m^{-2} h^{-1}) fluxes were calculated by the snowpack diffusion method using each gas concentration difference, snow depth,

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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 (ø 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 h in a laboratory with a gas chromatograph. The gas chromatograph (Hewlett–Packard, USA) was fitted with a flame ionization detector (FID) for CH_4 and an electron capture detector (ECD) for N_2O detection. The gas chromatograph was also equipped with a moisture trap. Prior to analysis of field samples and after each set of 13 samples a reference gas sample of known CH_4 and N_2O concentration was analyzed. The CH_4 (µg m^{-2} h^{-1}) and N_2O (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 gas chromatograph (MQL) was based on 100 subsequently analyzed samples of reference gas of known CH_4 and N_2O 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 CH_4 or N_2O concentrations of reference gas samples (22 µg m^{-2} h^{-1} for CH_4 and 18 µg m^{-2} h^{-1} for N_2O). In order to minimize the random error related to gas sampling in the field, fluxes were verified using the ambient field air sample analyzed before each sequence of chamber samples adopting similar criteria as used in Alm et al. (2007). Due to gas sampling disturbances in the field and poor gas chromatograph accuracy 17 % of CH_4 and 49 % of N_2O fluxes were discarded.

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2.4 Statistical analysis

Two-way analysis of variance (ANOVA) was used to test whether CH_4 and N_2O fluxes of forest/mire types have common means in wet, typical, and dry years. Post-hoc Tukey HSD tests were used to test the pairwise differences between the forest/mire types and years changing from wet to dry. For CH_4 fluxes we ran ANOVA tests twice, first on the whole dataset including nine forest/mire types and then on a subset of data including upland forests and forest–mire transitions, and excluding mires. For testing significant differences between the two groups of data we performed Welch's Two Sample *t* test e.g. between the N_2O fluxes from the snow on the ground season (January–April in 2006) and the N_2O fluxes from the snowless seasons (May–November in 2005 and May–September in 2006).

In addition to ANOVA, we tested the dependence between the measured CH_4 ($\mu g\,m^{-2}\,h^{-1}$) and the gap filled half-hourly environmental variables in separate models for: (a) the upland forests on mineral soils (VT, VT, MT, OMT) and (b) forest–mire transitions on organo–mineral soils and (OMT+, KgK, and KR), and (c) mires (VSR1, VSR2).

CH_4 fluxes ($\mu g\,m^{-2}\,h^{-1}$) of uplands and transitions were fitted by two linear mixed-effects regression models with a random effect for forest types (Pinheiro et al., 2013). For both groups of forest types, we evaluated the effect of all our environmental variables on CH_4 together and their combinations iteratively by selecting the model combination of variables, which 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.

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1 and 2):

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

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

where yu_{ij} and yt_{ij} is the CH_4 flux ($\mu g\,m^{-2}\,h^{-1}$) for upland forests or transitions and for a particular ith forest type and the jth case, 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 1).

The CH_4 fluxes ($\mu g\,m^{-2}\,h^{-1}$) 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):

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

where y_{ij} is the CH_4 flux ($\mu g\,m^{-2}\,h^{-1}$) 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, Ttol are parameters (Table 2).

The N_2O fluxes ($\mu g\,m^{-2}\,h^{-1}$) 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):

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

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where z_{ij} is the N_2O flux ($\mu g\,m^{-2}\,h^{-1}$) 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, Ttol are parameters (Table 3).

To illustrate the sensitivity of CH_4 and N_2O flux response to environmental factors we performed the 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. 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 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 1CT and the coldest was in upper forest–mire transition 5 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 soil water content (SWC) in 10 cm depth ranged from a dry value of around 10 % in the mineral soils to a water-saturated value of around 80 % in swamp and mires (Fig. 2c). The largest drought reduction of SWC was in August 2006 on the well-drained sandy podzol at the summit of the hill, and also on the poorly drained histic podzol on the toe slope.

3.2 CH_4 fluxes

The median fluxes from forest floor varied from −51 to 586 $\mu g\, m^{-2}\, h^{-1}$ for CH_4 among individual forest/mire types (CT, VT, MT, OMT, OMT+, KgK, KR, VSR1, VSR2) during the entire period (Fig. 3a). The small negative CH_4 fluxes associated with prevailing oxidation were mostly observed in uplands and in transitions while mires typically showed large positive higher CH_4 fluxes associated with prevailing production. The CH_4 dynamics changed exponentially with increasing levels of the ground water table from small consumptions to large productions (Figs. 2 and 3). The median CH_4 fluxes of uplands (CT, VT, MT, OMT), transitions (OMT+, KgK, KR), and mires (VSR1, VSR2) varied from −38, −8, 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

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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 transitional types 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.

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 mires (VSR1, VSR2) gave significantly higher CH_4 fluxes than the other forest types. Differences in means (M) and 95 % confidence limits (CI) ranged from minimum VSR2-KgK ($M = 481$, 95 % CI [352, 610]) to maximum VSR1-OMT ($M = 793$, 95 % CI [668, 918]) at $p < 0.001$. Also the 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 other forest types (transitions, uplands) were not significant when analyzed together with the CH_4 fluxes of mires. The CH_4 fluxes for the seven transitional and upland forest types were significantly different $F(6, 976) = 71$, $p < 0.001$ when ANOVA was run without mires. Though unlike the nine forest/mire type dataset, for the group of uplands with transitions there was no difference between wet, typical, and dry years $F(2, 976) = 1$, $p = 0.292$ or their interactions $F(12, 976) = 1$, $p = 0.135$. The mean CH_4 oxidation of the upland forests ($-42.9\,\mu g\,m^{-2}\,h^{-1}$) was for the whole period significantly larger than the mean CH_4 oxidation of the forest–mire transitions ($-12.8\,\mu g\,m^{-2}\,h^{-1}$) according to Welch's two sample t test $t(994) = 15.56$, $p < 0.001$. Tukey post-hoc comparison of the differences in the mean CH_4 fluxes for 21 pairs of

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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 CH_4 fluxes of transitional and upland forest types (MT-CT 0.056, OMT+-VT 0.965, OMT-MT 0.431, and KR-KgK 0.999).

3.3 Factors controlling CH_4 fluxes

The mean level of CH_4 fluxes of upland and transitional forests differed (Table 1), though the sensitivity response to environmental factors was similar (Fig. 4). The largest part of the CH_4 fluxes remained unexplained with our models, like the proportion of explained variance was for uplands (10 %), transitions (15 %) and slight increase for mires (22 %). The modeled CH_4 flux response for the upland and transitional forest types to soil moisture at 10 cm was nearly flat, although the soil moisture parameter was significant ($p = 0.011$, Table 1). 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 fluxes 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 1). 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 and the optimum was around 18 cm below the surface (Fig. 4, $p < 0.001$, Table 2). A significant sigmoidal type of response was also observed in mires along the temperature range with an optimum near surface peat temperature for the CH_4 emissions found at around 14 (°C) (Fig. 4, $p < 0.001$, Table 2).

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3.4 N_2O fluxes

During the typical and dry years the momentary forest floor N_2O fluxes of forest/mire types ranged from -107 to $248\,\mu g\,m^{-2}\,h^{-1}$. The median N_2O fluxes were similar for the forest/mire types and ranged only from 0 to $6\,\mu g\,m^2\,h^{-1}$ (Fig. 5). The median N_2O fluxes of all forest/mire types were found inside the range of the method quantification limits ($MQL_{N_2O} = 18\,\mu g\,m^{-2}\,h^{-1}$). The N_2O fluxes of the snow on the ground period were significantly lower than the N_2O fluxes of the snowless period according to Welch's two sample *t* test $t(297) = 5.094$, $p < 0.001$. Forest floor N_2O fluxes did not differ significantly for the nine forest/mire types of the ecotone for the snowless periods $F(8, 284) = 0.708$, $p = 0.684$. Though, the momentarily N_2O fluxes were significantly different in typical and dry snowless seasons $F(1, 284) = 6.157$, $p < 0.014$. N_2O fluxes were during dry snowless seasons lower 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 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 (Fig. 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 3, Fig. 7). The modeled Gaussian type response showed optimum N_2O produc-

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tion 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.

4 Discussion

4.1 CH_4 dynamics

The forest/mire types significantly differ 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 oxidation of other forest types. However, CH_4 oxidation also showed significant differences between the 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 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. Whereas CH_4 emission in mires showed a Gaussian form response with a reduction of the optimum under saturated or drier surface peat conditions. We complemented a few studies on forest–mire gradients (e.g. Moosavi and Crill, 1997; Ullah et al., 2009; Ullah and Moore, 2011) and lowered the likelihood of forest–mire transitions being biogeochemical hotspots of CH_4 emissions during short-term water level fluctuations.

The lack of an increase in CH_4 emissions during increased ground water levels in the transitions in our study could be attributed more to the relatively slow response of CH_4 producing bacteria than to the effectiveness of CH_4 oxidation which was reduced by a reduction in the aerated soil layer. Mäkiranta et al. (2009) showed that in forested peatlands the highest abundance of respiratory microbes could be found in the zone around the average water level. It is also known that the depth of maximum CH_4 production and oxidation is strongly related to 30 day average water level depth with time lag differences between the drier and wetter microsites (Kettunen et al., 1999). The duration of exceptionally increased high water levels was probably too short for CH_4 producing bacteria to relocate and/or adapt to water saturated conditions.

Small CH_4 emissions as observed in relatively dry Scots pine dominated forests (VT – *Vaccinium Vitis idea* type) (Fig. 3) with sandy podzol soil and ground water depths around two meters, have been occasionally found in mineral soil forests in other studies. This implies that plants' deepest roots play a role in CH_4 transport 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 CH_4 flux–soil moisture sensitivity 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 positively increasing CH_4 oxidation rates with temperature in upland forest types could reflect the importance of soil physiochemical properties e.g. bulk density, whereas the Gaussian form may also reflect a biological driven response in mires.

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In our upland forests the role of soil physiochemical and microbiological drivers may have contributed to the fact that the temperature and moisture significantly explained just 10 % of the variation.

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 temperature and moisture CH_4 sensitivity may be also determined by differences in the composition of microbial (Saari et al., 2004; Jaatinen et al., 2004) and plant functional communities (Bubier et al., 1995; Riutta et al., 2007; Saarnio et al., 1997). 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 flurk, hummock, *Eriophorum* lawn and *Carex* lawn microsites taken together. The CH_4 emissions in VSR1 – Tall Sedge Pine Fen were larger than in VSR2 – Tall Sedge Pine Fen (Fig. 4). In VSR1 the water level was closer to the surface, and the lawn microsites had a greater abundance of *Menyanthes* species, which are known to mediate higher CH_4 transport (Bubier et al., 1995; Macdonald et al., 1998).

4.2 N_2O dynamics

The momentary N_2O fluxes in the range from −107 to 248 (µg m^{-2} h^{-1}) and with 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_2O fluxes did not differ significantly for the nine forest/mire types of the ecotone $p = 0.637$ for the whole period from May 2005 to September 2006 probably due to the low nitrification potential of boreal forest in natural conditions (Regina et al., 1996). Low N_2O fluxes of different natural forests or wetlands sometime do not show statistically significant difference (Matson et al., 2009; Ullah et al., 2009) e.g. due to the skewedness of data around zero with few seasonal peak events. However, statistically significant difference may be found between drained and undrained forests growing on organic soils and between evergreens and deciduous plants (Arnold et al., 2005a, b). Our drainage class of forest/mire types ranged from well drained to poorly drained, and our forest stands changed from pine and spruce dominated (uplands) to pine-spruce-birch mixed forests (transitions). Ullah and Moore (2009, 2011) found that soil drainage and dominant tree species strongly control net nitrification rates, and that N_2O emissions from poorly drained soils can be three times larger than those from well drained soils due to slower denitrification than nitrification activity. Also in pristine peatlands nitrification, which supplies nitrate for denitrification, is the main source of N_2O emissions (Regina et al., 1996; Nykänen et al., 1995; Wray et al., 2007). 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

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peak in litterfall or during sudden soil freeze–thaw cycles (Pihlatie et al., 2007). However, 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 and N_2O emissions increased 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 at 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 3, Fig. 7). Although, the residuals of the moisture and temperature model were large (Fig. 7) and R^2 was only 10 %. Luo et al. (2012) demonstrated for temperate forests that N_2O emissions depended nonlinearly on the soil moisture and positively on soil temperature. In our study, the weak linear response of soil moisture to N_2O fluxes could be an artifact of fitting several N_2O processes of different sensitivity to different forest/mire types. For example in well drained uplands the N_2O fluxes may be mainly due to processes of ammonification and nitrification while in mires nitrification in the drier surface layer may be coupled with denitrification in deeper water-saturated layers (Ambus et al., 2006; Regina et al., 1996). The soil moisture and temperature from deeper layers did not significantly explain the N_2O fluxes (results not shown). An active depth of 5 cm corresponding to the top of the organic layer is in agreement with Pihlatie et al. (2007) who demonstrated that N turnover in poor boreal forest soil takes place in the litter layer and that N_2O emissions originate mainly from the top soil. The N_2O production in our study, increased with rising soil temperature of the humus layer from 7 (°C) typically found after the soil thawed during spring warming and in autumn during soil cooling. These could be the periods when the nitrification potential increased; in spring probably due to mobilization of nitrogen during freeze–thaw cycles and in autumn probably due to mobilization of nitrogen from the fast 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. Our pristine forest–mire transitions did not act as biogeochemical hotspots for CH_4 and N_2O emissions. The organo–mineral soils of pristine forest–mire transitions should be categorized as CH_4 oxidation types and background N_2O emission types rather than landscape peak emission types.

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Table 1. 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 ... 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 2. 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. 1). 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	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]$p = 0.035$.

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Table 3. Parameter estimates and their standard errors for forest floor N_2O fluxes ($\mu g\,m^{-2}\,h^{-1}$) 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.

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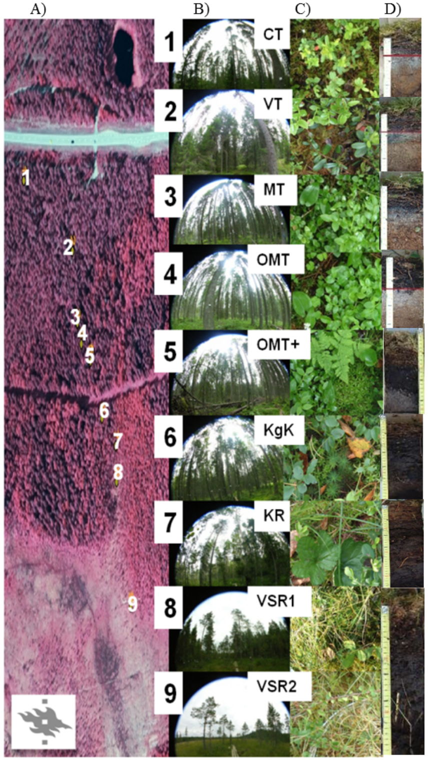

Figure 1. (A) Airborne infrared photograph shows a 450 m long boreal forest–mire ecotone located on the NE slope of the glacial Vatiharju–Lakkasuo esker in Finland (61°47′, 24°19′). **(B)** The fisheye photographs show tree stands of upland xeric, subxeric, mesic and herb-rich forest types. **(C)** Photographs show ground vegetation and **(D)** soil profiles of 9 forest/mire types. *Upland forests: 1 CT – *Calluna,* 2 VT –*Vaccinium Vitis Idea,* 3 MT – *Vaccinium Myrtilus*, 4 OMT – *Oxalis-Myrtillus*); paludified 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.

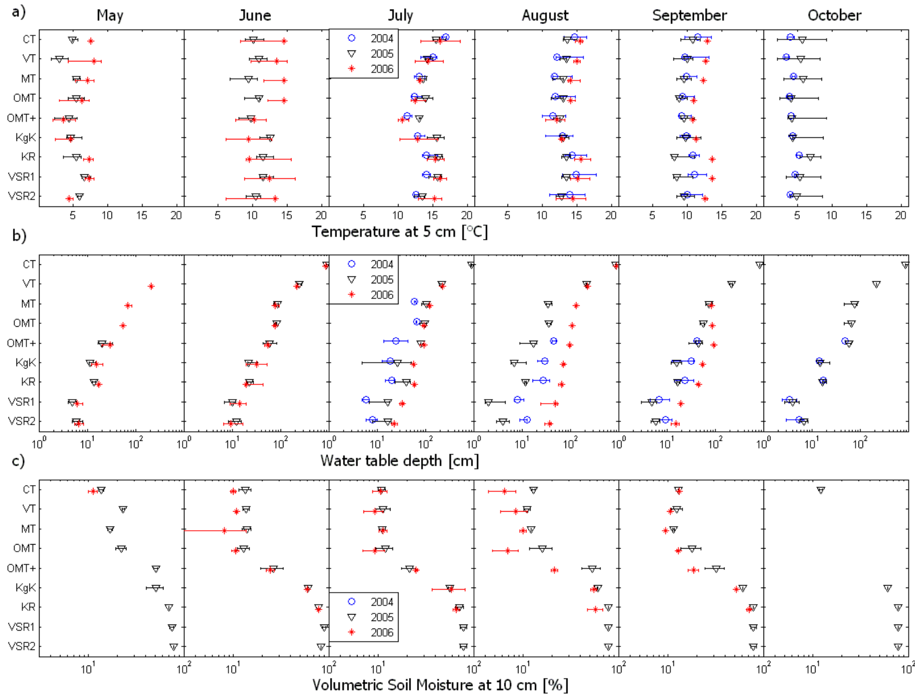

Figure 2. (a–c) show the monthly medians of environmental variables: **(a)** soil temperature at a depth of 5 cm, **(b)** ground water level, and **(c)** volumetric soil moisture at 10 cm depth observed along the forest/mire ecotone during wet (2004), intermediate (2005), and dry year (2006). The top–down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

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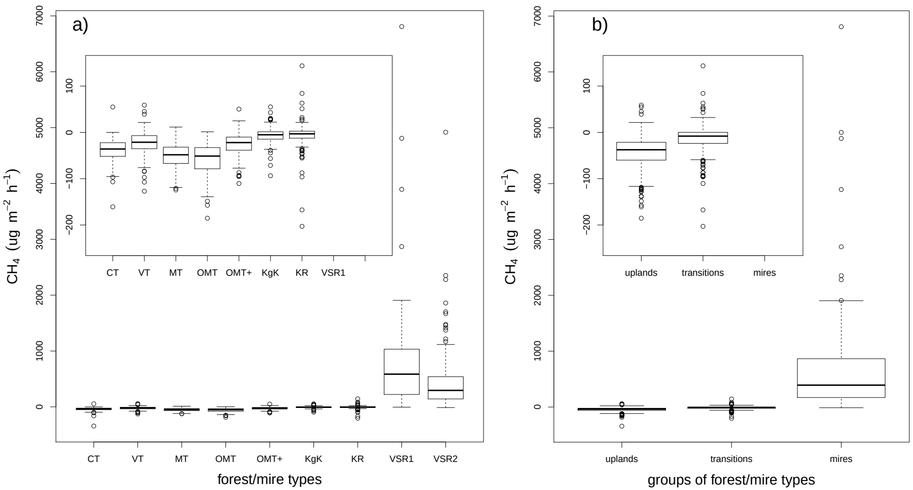

Figure 3. The boxplots of measured forest floor CH_4 fluxes (µg m^{-2} h^{-1}) in forest/mire types **(a)**, and **(b)** in uplands (CT, VT, MT, OMT), transitions (OMT+, KgK, KR), and mires (VSR1, VSR2) during the whole period. The left–right arrangement of sites mimics the locations on the slope (see Fig. 1).

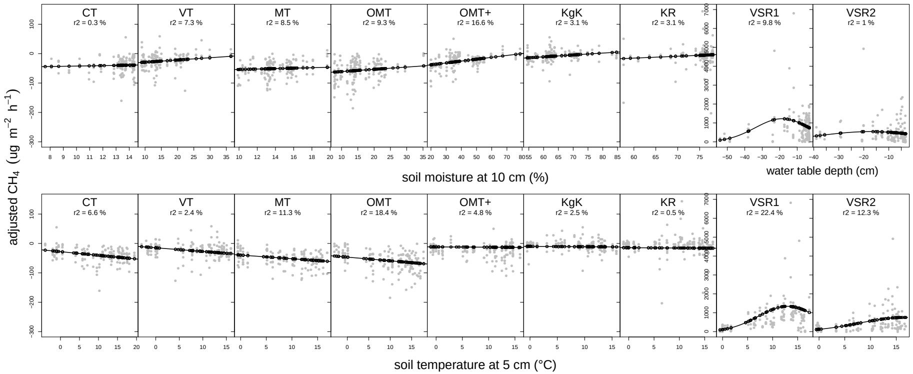

Figure 4. Comparison of sensitivity of forest floor CH_4 fluxes ($\mu g\,m^{-2}\,h^{-1}$) to environmental factors for nine forest/mire types. In the upper panels is modeled CH_4 flux response to soil moisture at 10 cm (uplands and transitions) or to water table depth cm (mires) for uplands (CT, VT,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

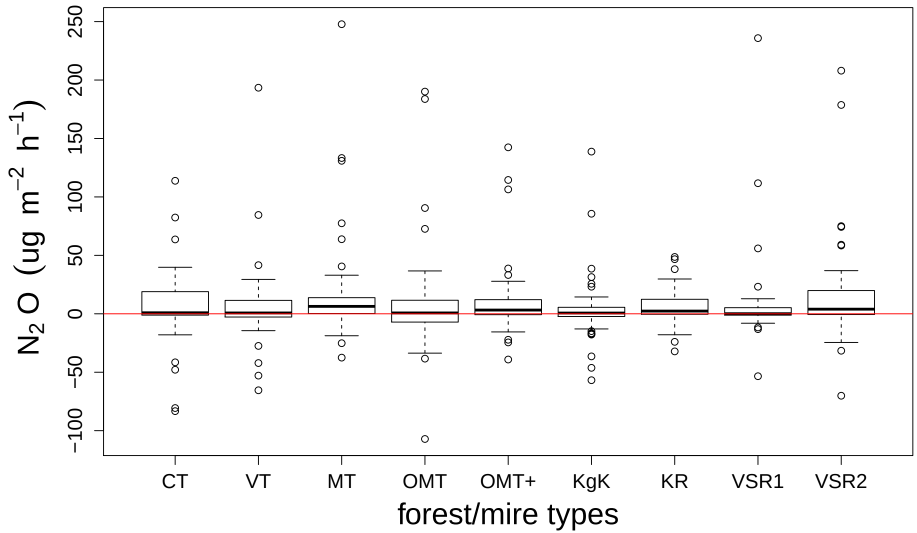

Figure 5. The boxplot of measured forest floor N_2O fluxes (µg m^{-2} h^{-1}) in forest/mire types (uplands – CT, VT, MT, OMT; transitions – OMT+, KgK, KR; and mires – VSR1, VSR2) during the period including typical and dry years. The left–right arrangement of sites mimics the locations on the slope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

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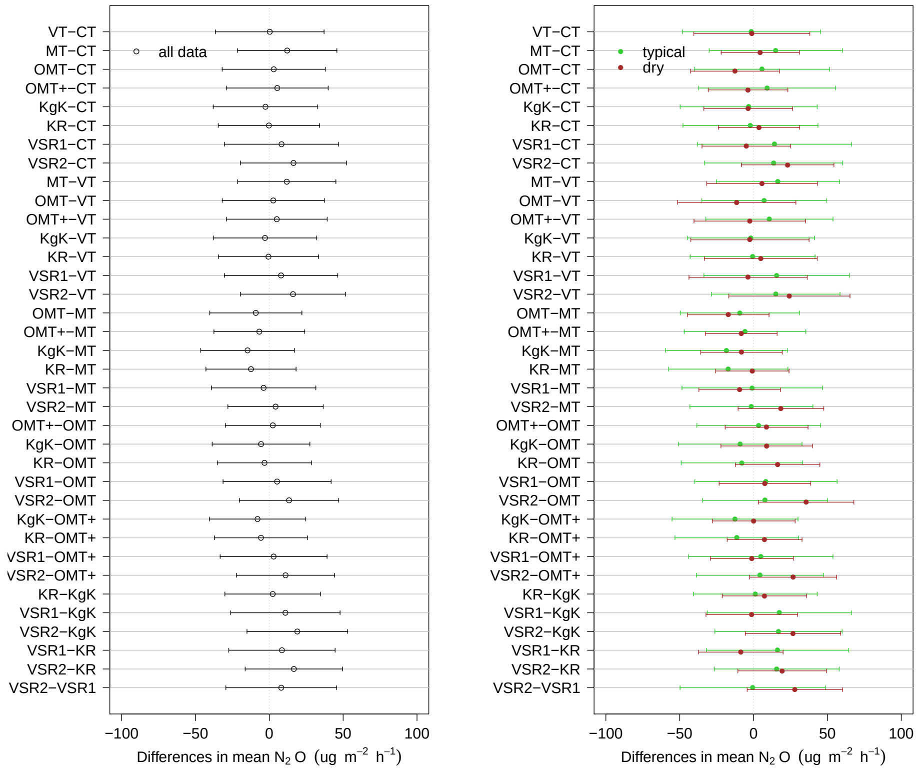

Figure 6. The post-hoc Tukey differences (error bars for 95 % confidence intervals) of mean N_2O ($\mu g\,m^{-2}\,h^{-1}$) fluxes from forest floor for the pair-wise comparisons of forest/mire types (uplands - CT, VT, MT, OMT; transitions – OMT+, KgK, KR; and mires – VSR1, VSR2): (left) the N_2O flux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

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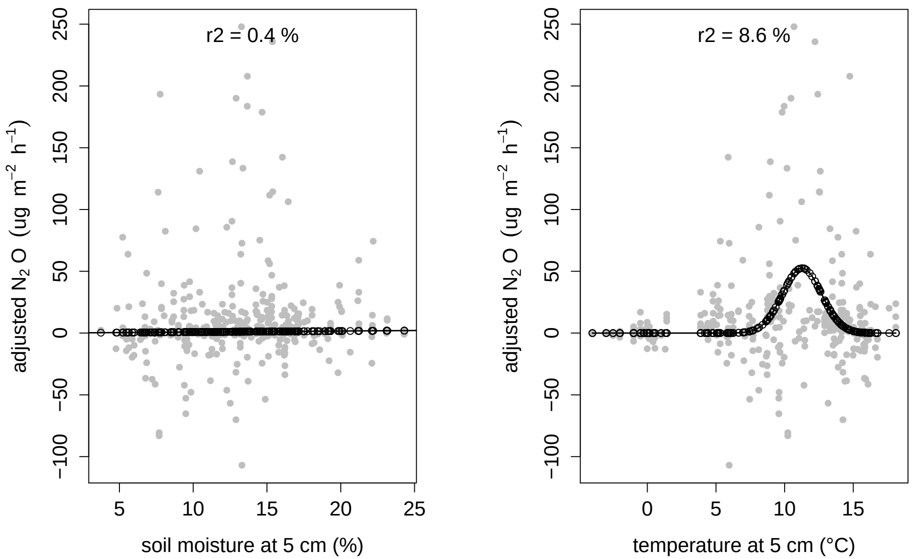

Figure 7. Sensitivity of forest floor N_2O fluxes (µg m^{-2} h^{-1}) of forest/mire types together with environmental factors. Left is N_2O flux response to soil moisture at 5 cm during the period including wet, typical, and dry years. On the right is N_2O flux response to soil temperature at 5 cm. The 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.

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