High methane emissions from restored Norway spruce swamps in southern Finland over one growing season

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SUMMARY

Forestry-drained peatlands in the boreal region are currently undergoing restoration in order to bring these ecosystems closer to their natural (undrained) state. Drainage affects the methane (CH_4) dynamics of a peatland, often changing sites from CH_4 sources to sinks. Successful restoration of a peatland would include restoration of not only the surface vegetation and hydrology, but also the microbial populations and thus CH_4 dynamics. As a pilot study, CH_4 emissions were measured on two pristine, two drained and three restored boreal spruce swamps in southern Finland for one growing season. Restoration was successful in the sense that the water table level in the restored sites was significantly higher than in the drained sites, but it was also slightly higher than in the pristine sites. The restored sites were surprisingly large sources of CH_4 (mean emissions of 52.84 mg CH_4 m^{-2} d^{-1}), contrasting with both the pristine (1.51 mg CH_4 m^{-2} d^{-1}) and the drained sites (2.09 mg CH_4 m^{-2} d^{-1}). More research is needed to assess whether the high CH_4 emissions observed in this study are representative of restored spruce mires in general.

KEY WORDS: CH_4 fluxes, drained peatland, greenhouse gas, pristine mire, restoration

INTRODUCTION

Peatlands constitute a large carbon (C) store and are a sink for carbon dioxide (CO_2), but also act as a source of methane (CH_4) (Turunen *et al*. 2002, Yu *et al*. 2010). Drainage for forestry substantially alters the C cycle of a peatland: it suppresses methanogenic activity and increases aerobic decomposition by lowering the water table (Blodau & Moore 2003). Expansion of the aerobic peat layer reduces the activity of methanogenic microbes and, at least initially, increases the activity of methanotrophs (Kettunen *et al.* 1999). As a result, drainage can change sites from sources to sinks of CH_4 (Nykänen *et al.* 1998, von Arnold *et al.* 2005, Ojanen *et al.* 2010), although ditches are an exception and can be large point sources of CH_4 (Roulet & Moore 1995, Minkkinen *et al.* 1997, Minkkinen & Laine 2006). Lowering of the water table also increases the rate of peat mineralisation and CO_2 emissions (e.g. Moore & Knowles 1989, Silvola *et al.* 1996); although, in some cases of successful drainage for forestry, increased tree growth and litter production can offset these losses (e.g. Ojanen *et al*. 2013). In Finland, where the drainage of peatlands for forestry has been widespread (e.g. Vasander *et al.* 2003), approximately 70 % of spruce mires have been drained, making them one of the most endangered biotopes in the region (Raunio *et al.* 2008). Thus, restoration of mires, and of spruce mires in particular, is among the most important measures for the protection and promotion of biodiversity in Finland and elsewhere in the boreal region.

From an ecological point of view, successful restoration in peatlands is most commonly seen as the recovery of peat-forming vegetation (e.g. Rochefort *et al.* 2003) and a subsequent return of the C sink function of the ecosystem (Komulainen *et al.* 1999, Lucchese *et al.* 2010), both facilitated by hydrological conditions similar to those prior to drainage (Maanavilja *et al.* 2014). However, successful restoration of the functionality of the peatland is also determined by the type, abundance and activity of the microbial communities (Andersen *et al.* 2006, 2010), which are reflected in part in the CH_4 dynamics. Thus, the spatio-temporal dynamics of CH_4 emissions in restored peatlands resemble those of pristine mires in some cases (Tuittila *et al.* 2000, Wilson *et al.* 2009), while in other cases significant differences between restored and pristine sites have been observed after both short-term (Waddington & Day 2007) and long-term rewetting (Juottonen *et al.* 2012, Wilson *et al.* 2013, Vanselow-Algan *et al.* 2015). Restoration has been found to result in both higher (Wilson *et al.* 2013, Vanselow-Algan *et al.* 2015) and lower (Juottonen *et al.* 2012)

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CH_4 emissions than the pristine state.

CH_4 dynamics have not been well studied in pristine spruce mires, which makes it difficult to assess the target state for restoration. For example, Huttunen *et al.* (2003) reported both low CH_4 emissions and CH_4 uptake (ranging from -2.9 to 12.6 mg CH_4 m^{-2} d^{-1}) in spruce mires over two consecutive years. Moreover, very low CH_4 emissions have been reported in peatlands that were previously drained for forestry and subsequently rewetted (e.g. Komulainen *et al.* 1998, Juottonen *et al.* 2012). Juottonen *et al.* (2012) suggested that the low CH_4 emissions observed in a study on restored peatland buffer zones could be explained by the poor establishment of methanogen communities during the decade since rewetting. The flux measurement points used in that study were placed solely in the zones between filled-in drainage ditches, where CH_4 emissions were low (Juottonen *et al.* 2012) despite the extensive coverage of *Carex*, *Eriophorum* and *Calamagrostis* species (Väänänen *et al.* 2008). Drainage ditches are a new type of microhabitat characterised by open (and, at times, stagnant) water or bare peat surfaces and higher CH_4 emissions than the 'mid-strip' areas between the drainage ditches (Minkkinen & Laine 2006). Such microhabitats are rare in pristine spruce mires. Whether CH_4 emissions differ between filled-in ditches and mid-strip areas has not previously been assessed in restored forestry-drained sites.

Here we present the results of CH_4 flux measurements taken during a single growing season at two pristine, two drained and three restored spruce mires in the southern boreal region. We assess the differences in CH_4 fluxes between sites, with particular emphasis on emissions from filled-in ditches at the restored sites. We hypothesise that, in restored spruce mires not used as buffer zones, CH_4 fluxes from filled-in ditches are likely to be higher than emissions from mid-strip areas. We address the question of whether the CH_4 dynamics on restored spruce mires resemble those of pristine spruce mires; and assess the need for further research on CH_4 dynamics in spruce mires, in view of a likely increase in areas undergoing restoration in the near future.

METHODS

Measurement sites

Instantaneous CH_4 fluxes (calculated as mg CH_4 m^{-2} d^{-1}) were measured at seven spruce-dominated peatlands in southern Finland (Figure 1) during the summer and autumn (June–September) of 2012. Mean monthly temperatures during the thermic summer of that year (09 May to 20 September; Finnish Meteorological Institute 2015) were between 14.4 and 15.7 °C, and thus 0.3–0.5 °C below the 1981–2010 average for the study areas (Finnish Meteorological Institute 2015). Total precipitation during the thermic summer was between 205 and 244 mm, or 93–113 % of the 1981–2010 average (Finnish Meteorological Institute 2015).

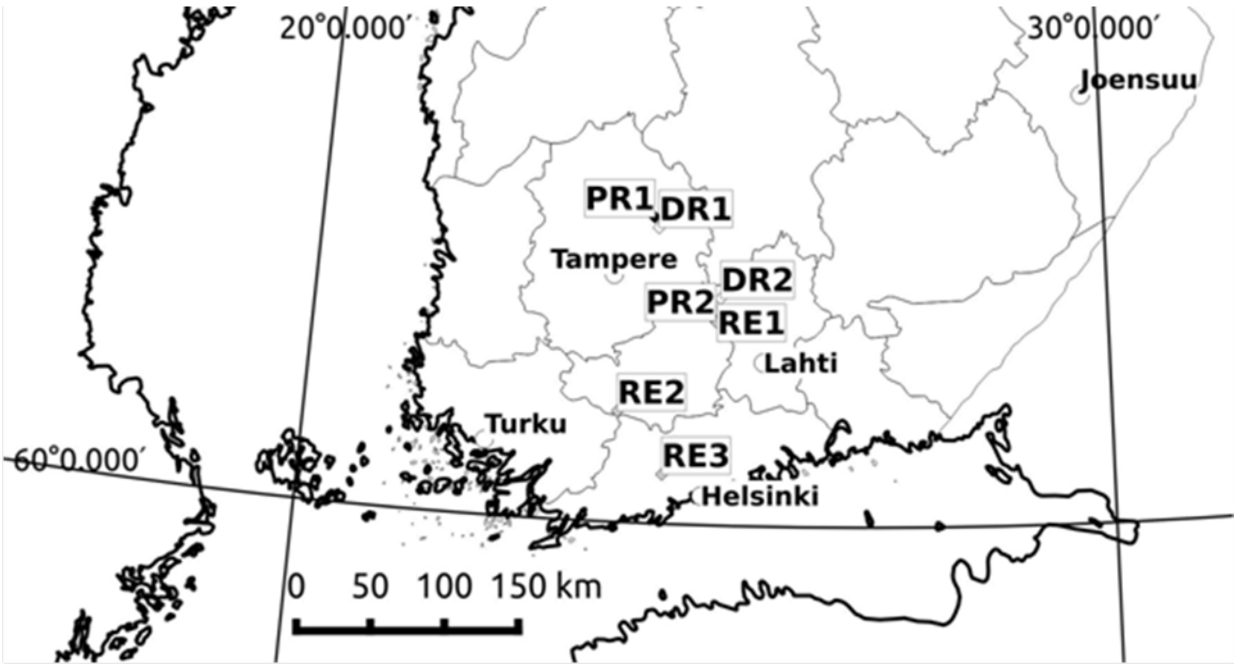

Figure 1. Map of southern Finland showing the measurement site locations. Site management codes: PR = pristine, DR = drained, RE = restored.

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Two sites (PR1, PR2) were pristine (undrained), two (DR1, DR2) were drained for forestry and three (RE1, RE2, RE3) were restored. Both the drained and the restored sites had been in a drained state for more than four decades. The restoration measures at RE1, RE2 and RE3 were conducted 11, 17 and 11 years before the start of our measurement campaign, respectively. The measures included damming of the drainage ditches with peat, but did not involve thinning or clear-felling of the tree stand (Table 1). On two of the restored sites (RE2 and RE3), the Norway spruce (*Picea abies*) stand had largely died due to re-wetting and restoration. Similarly to the pristine sites, the drained and restored sites had been mesotrophic spruce mires before drainage (classified as *Vaccinium myrtillus* spruce swamp; Laine *et al*. 2012). Specific information on peat characteristics such as bulk density (BD) and nutrient content, for sites other than RE3, is presented in Table 2. The methods that we used to assess peat characteristics are presented in Maanavilja (2015).

The vegetation on the measurement plots differed between the management options. On the pristine sites (PR1 and PR2), the moss layer was dominated by *Sphagnum angustifolium* and *S. girgensohnii*. The ground vegetation on Site PR1 was characterised by *Vaccinium myrtillus* and *V. vitis-idaea*, whereas vegetation cover at site PR2 was scarce and consisted mostly of *Carex lasiocarpa*. On the drained sites (DR1 and DR2), moss coverage was 70 % on average and the remainder of the ground layer was unvegetated (i.e. bare peat); the most common moss species were *Pleurozium schreberi*, *Hylocomnium splendens* and *S. angustifolium*. The shrub layer on the drained sites consisted mostly of *V. myrtillus*. On the restored sites (RE1, RE2 and RE3) *S. riparium*, *S. angustifolium* and *S. girgensohnii* were the most common moss species. *Lysimachia thyrsiflora* grew in abundance in the ditch on Site RE3.

The measurements were conducted at four locations on each site, each location comprising two circular measurement plots (diameter = 30 cm). At each of the four locations, living vegetation (which included the moss layer) was removed by clipping on one of the plots, while the other plot was left intact. The four measurement locations were placed in different parts of the peatland with respect to the drainage ditches or, in the case of the pristine sites, to the mire edge (Figure 2), in order to include differences in hydrology (water table level) within the sampling design. Two plots were located on the ditch or mire margin, two were located at a distance of two metres from the ditch (or mire edge), and four were located in the middle of the strip (see Figure 2). The distance between the plots was dependent on the width of the peatland.

Wooden platforms were built adjacent to the sampling locations on the pristine and restored sites in order to minimise disturbance to the soil and the probability of CH_4 ebullition due to soil compression during measurement visits. To ensure a gas-tight connection between the soil and the measurement chamber, a groove with the same diameter as the measurement chamber (30 cm) was carved into the soil on each plot to a depth of 2 cm at the beginning of the measurement period (May 2012). This method of preparing plots for gas measurements without permanent collars has previously been used in other studies (e.g. Ojanen *et al.* 2010).

Two or three perforated PVC pipes (diameter = 16 mm, length = 0.8 m) were inserted into the peat at each site for the measurement of water table level (WTL); one near the mire edge or ditch and the second near the centre of the mire or strip. The WTL was measured manually at each of these wells during every CH_4 measurement round. The altitudes of all WTL wells and CH_4 sampling points were measured relative to a fixed reference point on each site. Each CH_4 measurement was associated with the WTL reading from the well nearest to the sampling point.

Table 1. WGS84 co-ordinates and volume of tree stand (m^3 ha^{-1}) on the sites. Site RE3 was measured in 2007, and the other sites in 2010.

Site	Co-ordinates	*Picea abies*	*Betula pubescens*	Total
PR1	24.24 °E, 61.86 °N	256	3	259
PR2	25.06 °E, 61.24 °N	261	19	280
DR1	24.30 °E, 61.80 °N	278	22	300
DR2	25.11°E, 61.38 °N	258	62	320
RE1	25.07 °E, 61.23 °N	181	1	182
RE2	23.87 °E, 60.67 °N	0	29	29
RE3	24.45 °E, 60.30 °N	126	59	185

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Table 2. Surface peat (top 30 cm) properties (± SD) in the study sites: pH, bulk density (BD, g cm^{-3}), the content of C, N and oxalate-extractable Fe, Al and P (g kg^{-1} dry soil), and CH_4 production potential (μg C h^{-1} g^{-1} dry soil) under anaerobic laboratory conditions. No data are presented for Site RE3. The samples at locations DI and DS were combined for analysis. At location PR, samples were combined for analysis from all sampling locations (i.e. mire edge, 2 m from the edge, mid-mire). Site management codes: PR = pristine, DR = drained, RE = restored, DI = ditch, DS = beside ditch, MID = mid-strip.

Site	location	pH	BD	C	N	Fe_{ox}	Al_{ox}	P_{ox}	CH_4 potential
PR1	PR	4.01 ± 0.04	0.053 ± 0.022	544 ± 5	15.6 ± 1.03	1.12 ± 0.45	1.17 ± 0.18	0.17 ± 0.09	1.90 ± 1.04
PR2	PR	4.02 ± 0.07	0.072 ± 0.012	471 ± 5	16.0 ± 1.13	1.90 ± 0.25	2.50 ± 0.43	0.22 ± 0.02	0.91 ± 0.85
DR1	DI, DS	4.10 ± 0.08	0.146 ± 0.045	325 ± 153	12.0 ± 6.05	1.45 ± 0.20	3.09 ± 1.54	0.17 ± 0.03	0.01 ± 0.00
	MID	3.98 ± 0.05	0.130 ± 0.021	488 ± 11	18.4 ± 2.58	2.28 ± 1.46	0.58 ± 0.21	0.08 ± 0.03	0.03 ± 0.02
DR2	DI, DS	4.20 ± 0.06	0.117 ± 0.017	523 ± 30	21.3 ± 0.28	4.49 ± 2.64	4.33 ± 1.96	0.23 ± 0.06	0.22 ± 0.31
	MID	4.04 ± 0.08	0.095 ± 0.025	505 ± 36	20.4 ± 1.78	3.86 ± 0.47	3.04 ± 0.47	0.37 ± 0.05	0.00 ± 0.00
RE1	DI, DS	4.27 ± 0.09	0.080 ± 0.016	499 ± 2	15.2 ± 0.22	0.74 ± 0.17	1.04 ± 0.23	0.04 ± 0.00	1.80 ± 0.75
	MID	3.96 ± 0.10	0.072 ± 0.021	483 ± 1	15.9 ± 1.54	1.37 ± 0.28	1.63 ± 0.48	0.08 ± 0.03	0.46 ± 0.56
RE2	DI, DS	4.11 ± 0.09	0.104 ± 0.023	556 ± 8	19.5 ± 1.93	3.21 ± 0.56	3.27 ± 0.74	0.28 ± 0.05	14.92 ± 6.86
	MID	4.13 ± 0.11	0.092 ± 0.018	552 ± 3	19.1 ± 0.26	2.21 ± 0.40	2.20 ± 0.32	0.19 ± 0.03	13.97 ± 3.46

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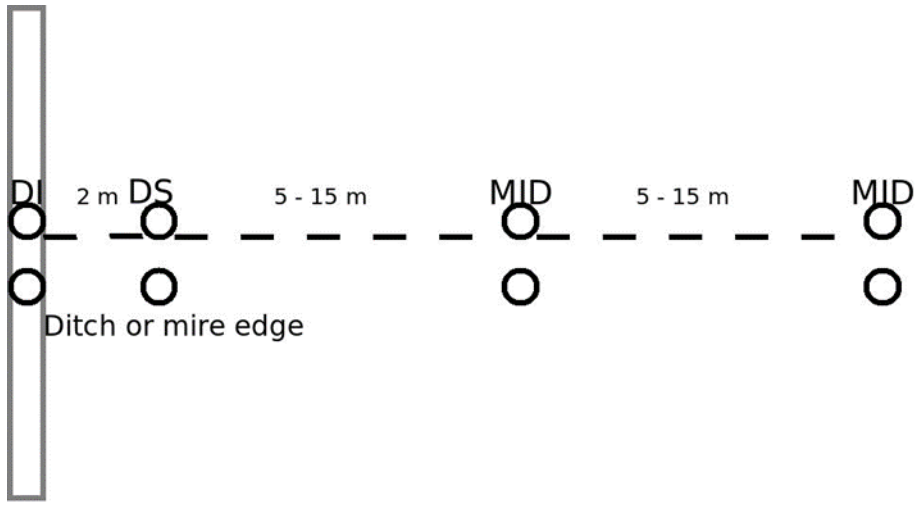

Figure 2. Measurement site sampling design. Open circles represent measurement plots. Abbreviations indicate measurement plot locations: DI = ditch, DS = beside ditch, MID = mid-strip. Dashed line represents the distances between measurement plot groups.

Gas sampling and sample processing

Opaque closed cylindrical chambers (height = 30 cm, diameter = 30 cm) made from galvanised sheet iron were used for the CH_4 flux measurements. A small fan at the top of each chamber mixed the air to ensure that the atmosphere inside the chamber was homogenous. Gas samples were taken from the chamber at 5, 15, 25 and 35 minutes after closure time, with a 60 ml syringe *via* a plastic tube, and injected into 12 ml glass vials with a needle through a rubber septum, flushing the vial first with 20 ml of the sample. The error caused by traces of indoor air in the vials was taken into account during the flux calculation phase by applying a correction coefficient of 0.847, estimated empirically by ventilating 30 vials in a normal indoor atmosphere overnight then injecting (following the method described above) 99.996 % pure helium (He) into 20 of the vials and indoor air into 10 of the vials and analysing their contents for CH_4 concentrations after 24 hours.

Air temperature (°C) inside the chamber was recorded at the beginning and end of the 35-minute measurement period. Chamber headspace volume was also estimated at each measurement round to account for moss growth in the plot. Soil temperature at 5 cm depth (T_{-5}) was measured at the centre of the measurement plot after the CH_4 measurements, using a thin probe (diameter = 3.2 mm). Flux measurements were made approximately twice *per* month from June to September 2012.

The gas samples were analysed at the laboratory of the Finnish Forest Research Institute at Vantaa, Finland using an Agilent Technologies 7980A gas chromatograph with Agilent packed columns 12Ft 1/8 2 mm Hayesep Q 80/100 UM and 6Ft 1/8 2mm Hayesep Q 80/100 UM fitted with an FI-detector for CH_4, and a Gilson GX-271 autosampler. The measurements were run and analysed with the Openlab CDS ChemStation program, Rev. C .01.03.

Flux estimation and statistical analysis

The results were initially filtered by fitting a linear function to the raw data, in order to detect ebullition during the measurement or leaking vials. In cases where there was apparent ebullition at the beginning of the measurement period, indicated by an unrealistically high initial CH_4 concentration (> 2.2 ppm), the measurement was discarded. Similarly, if ebullition was apparent at Samples 2 or 3, the measurement was discarded. If ebullition was apparent only at the end of the measurement period (Sample 4), the last sample was discarded and the flux was calculated using the first three samples. Thus, the data utilised include only the diffusive emissions of CH_4 from the soil. CH_4 emitted by ebullition was not included as we could not be certain that the ebullition was not caused by the measurement procedure itself. If vial leakage was evident, the sample was discarded. A maximum of one discarded sample was allowed per measurement. The percentage of accepted flux measurements was 83 % from a total of 290 measurements.

The change in CH_4 concentration over time (dCH_4/dt) was calculated from the linear fit to the accepted samples of each individual measurement and divided by the aforementioned correction coefficient (0.847) for unevacuated vials. Although the development of CH_4 concentration in the chamber airspace is theoretically nonlinear, the linear regression method for flux estimation has been

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recommended for the estimation of relative differences in trace gas emissions between treatments as it is less sensitive than nonlinear methods to small differences in soil characteristics between the measurement sites (Venterea *et al.* 2009) and is also more robust in the case of a small number of samples per measurement (Levy *et al.* 2011). The CH_4 flux (mg CH_4 m^{-2} d^{-1}) was then calculated as a function of the chamber headspace volume and mean air temperature inside the chamber during the measurement.

The effect of site management (i.e. pristine, drained, restored) on mean CH_4 fluxes was tested with a mixed-effects linear model:

$$F = B_0\mathrm{PR} + B_1\mathrm{DR\text{-}DI} + B_2\mathrm{DR\text{-}DS} + B_3\mathrm{DR\text{-}MID} + B_4\mathrm{RE\text{-}DI} + B_5\mathrm{RE\text{-}BS} + B_6\mathrm{RE\text{-}MID} + e_{ij} \qquad [1]$$

where F is the CH_4 flux (mg CH_4 m^{-2} d^{-1}), and $B_{0\ldots6}$ are the coefficients (parameters) that determine the mean flux values over the study period for the pristine (PR), drained-ditch (DR-DI), drained-beside-ditch (DR-DS), drained-mid-strip (DR-MID), restored-ditch (RE-DI), restored-beside-ditch (RE-DS) and restored-mid-strip (RE-MID) management-plot location pairs; and e_{ij} is the random effect of the measurement plot.

The effect of sampling location (MID, DI, DS) on CH_4 emissions in the drained and restored sites was tested using a pairwise comparison between the appropriate management-location pairs. Due to the small number of sites in the study, the effect of the peat characteristics (Table 2) on the fluxes was not assessed.

The effect of management on WTL was tested with a linear mixed-effects model:

$$W = B_1\mathrm{PR} + B_2\mathrm{DR} + B_3\mathrm{RE} + e_{ij} \qquad [2]$$

where W represents the mean WTL over the measurement period; B_1, B_2 and B_3 are the parameter values for pristine (PR), drained (DR) and restored (RE) management options, respectively; and e_{ij} is the random effect of the site and WTL measurement well. In order to get comparable results for each site type, the WTL values used in model fitting were the measured WTL values from all the measurement wells on each site, excluding the ditches in the drained sites (DR1, DR2). The CH_4 flux data were skewed to the right on all sites, and this is reflected in the high standard errors of the parameters; however, transforming the data can give false estimates of the treatment means (Feng *et al.* 2014). Therefore, in order to obtain meaningful mean values for individual treatments from the models without back-transformation, the flux and WTL values were not transformed for analysis.

The R software v. 3.2.2 (R Development Core Team 2015), with the additional packages Agricolae v. 1.2-2 (de Mendiburu 2015), car (Fox & Weisberg 2011), nlme v. 3.1-122 (Pinheiro *et al.* 2015) and Lattice (Sarkar 2008), was used for all calculations and Figures.

RESULTS

As expected, site management was reflected in the water table levels (WTL). The restored sites had the highest mean WTL (-12 cm on average, S.E. 2.6 cm), although the difference from pristine sites (-18 cm on average, S.E. 3.2 cm) was not statistically significant ($p = 0.22$). The drained sites had the lowest mean WTL (-37 cm on average, S.E. 3.3 cm), and this was significantly lower ($p = 0.01$) than at the pristine sites (Figure 3).

Variations in the CH_4 fluxes at the restored sites (-6.6 to 409.4 mg CH_4 m^{-2} d^{-1}) and in the ditches of the drained sites (-0.8 to 200.4 mg CH_4 m^{-2} d^{-1}) were high, without any clear temporal trend. The highest CH_4 emissions were measured at the restored sites and the lowest at the drained sites (Figure 4). At all sites, occasional uptake of CH_4 was observed during periods of low WTL, with a median uptake of 5.6 mg CH_4 m^{-2} d^{-1}. Uptake was most common on sites DR1 (41 measurements) and PR2 (31 measurements), whereas only three measurements on the restored sites indicated uptake. The fluxes displayed correlation with WTL only at site PR1, where there was a significant ($p = 0.007$) inverse relationship between WTL and CH_4 flux ($F = -1.6 + (-30.3/\mathrm{WTL})$) (Figure 5). There was no correlation between the CH_4 fluxes and T_{-5} at any of the sites.

The mean CH_4 fluxes (± S.E.M) *per* unit area from the different management-location pairs could be divided into two groups. The first group comprised the pristine plots and the beside-ditch and mid-strip plots on the drained sites (which were not significantly different from the pristine plots); and the second group comprised the ditches in the drained and restored sites and the beside-ditch and mid-strip plots on the restored sites (which were significantly different from the pristine plots) (Table 3). According to the pairwise comparison, the CH_4 fluxes on drained sites were significantly higher from ditches than from mid-strip plots, but did not differ between beside-ditch and mid-strip plots (p = 0.02 and 0.09, respectively); whereas at restored sites, there were no significant differences in CH_4 fluxes between the different measurement locations (Table 3, Figure 6).

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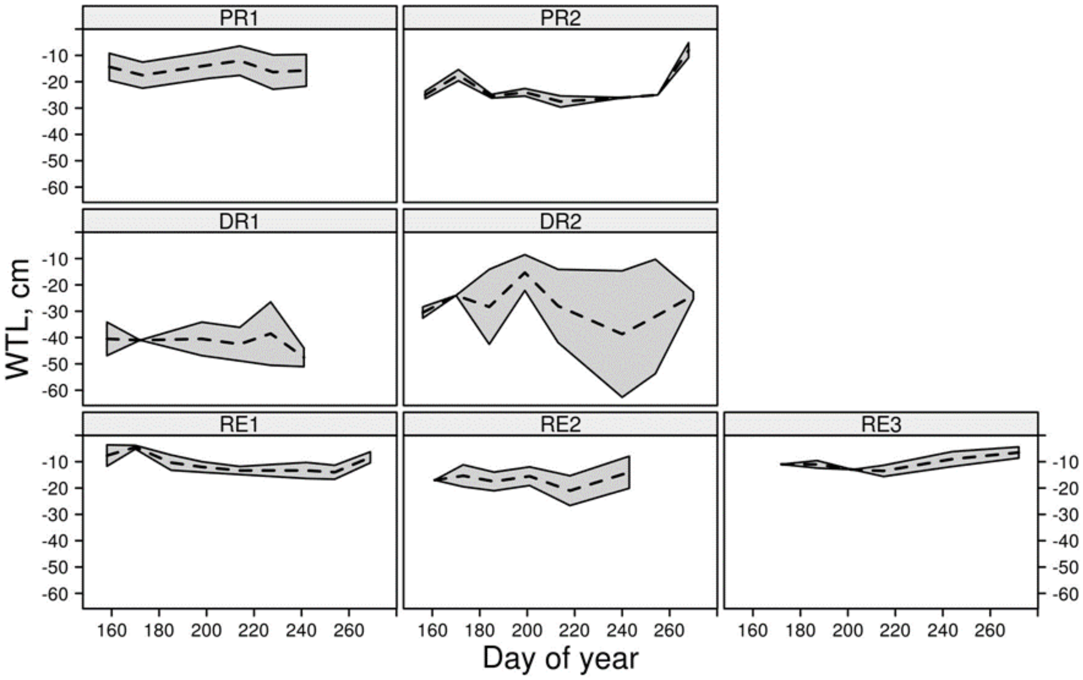

Figure 3. Time series of mean (dashed line) and standard deviation (grey area) of water table level (WTL, cm) in the dipwells at different measurement sites during the summer of 2012 (day of year 160–270). Negative values indicate WTL below the soil surface. Ditch wells in the DR sites are excluded. Site codes: PR = pristine, DR = drained, RE = restored.

DISCUSSION

This is the first time that the effect of restoration of boreal spruce mires drained for forestry on CH_4 emissions has been assessed by measuring the fluxes not only from the areas between the filled-in ditches, but also from the ditches and the areas of disturbed soil beside the ditches. The results show that the restored sites were on average much larger emitters of CH_4 than both pristine and drained sites, and that they were comparable to ditches on drained sites in this regard. Uptake of CH_4 was observed under all management options, and this result is in agreement with previous studies that have reported CH_4 uptake in pristine and drained spruce mires (Huttunen *et al.* 2003, Ojanen *et al.* 2010).

In southern Finland, the prevailing peatland complex type is raised bog (Ruuhijärvi 1982, see Figure 1 in Turunen *et al.* 2002), and spruce mires are found primarily in valleys, around brooks or on the margins of larger mire complexes. Thus, they are usually long and narrow in shape and the ditches, which are made at the edges of the mire, extend over a larger than average area. The mean width of the ditches at our sites was 1.92 metres and the mean strip width between one ditch and the next was 110 metres. We assumed that the areas of disturbed soil on both sides of each ditch had the same width as the ditch itself. Therefore, to obtain area-weighted estimates of mean emissions for the different management classes, we assumed that the ditches comprise 3 %, beside-ditch areas 6 %, and mid-strip areas 91 % of the total land area (Table 3). With these assumptions, the mean fluxes from the drained and restored sites would be 2.09 and 52.84 mg CH_4 m^{-2} d^{-1} (or 2.42 kg CH_4 ha^{-1} and 61.3 kg CH_4 ha^{-1} over the measurement period of 116 days), respectively (Table 3). The fluxes from the pristine sites calculated over the measurement period were 1.51 mg CH_4 m^{-2} d^{-1} (or 1.75 kg CH_4 ha^{-1} over the measurement period of 116 days) (Table 3). The emissions *per* unit area of the restored and drained sites calculated over the measurement period fall within the range of CH_4 emission factors defined by the IPCC Wetlands Supplement for drained and rewetted peatlands (IPCC 2014). While the restored sites in this study were a large source of CH_4 compared to the pristine and drained sites, the results are somewhat surprising because they contrast with the results of an earlier study by Juottonen *et al.* (2012), who concluded that the methanogen communities had changed under the drained state and had not revived in ten years after restoration so that CH_4 emissions from restored sites were only a fraction of those from the corresponding pristine sites. Part of the difference may be explained by the selection of measurement plots by Juottonen *et al.* (2012), as no plots were placed on or beside the filled-in ditches on restored sites. In addition, the

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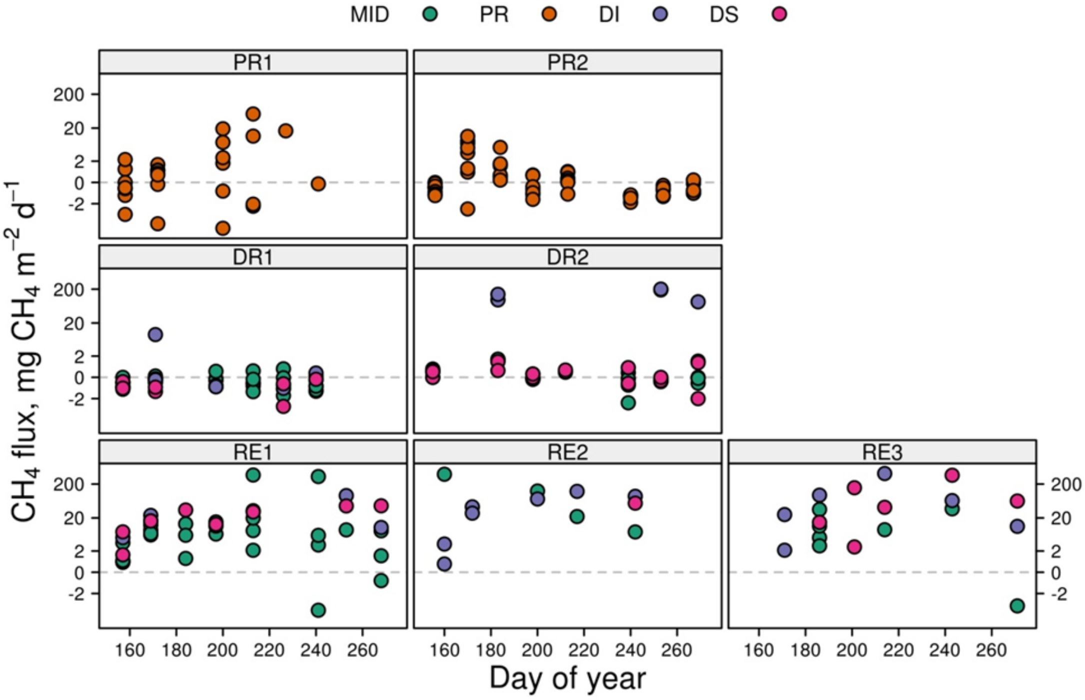

Figure 4. CH_4 fluxes (mg CH_4 m^{-2} d^{-1}) as a time series (day of year) grouped by site (site management codes: PR = pristine, DR = drained, RE = restored). Symbols denote different plot locations within the sites (MID = mid-strip, PR = pristine, DI = ditch, DS = beside-ditch). Note the hyperbolic arc-sine scale of the y-axis. Y-axis values have been back-transformed to show the true measured fluxes.

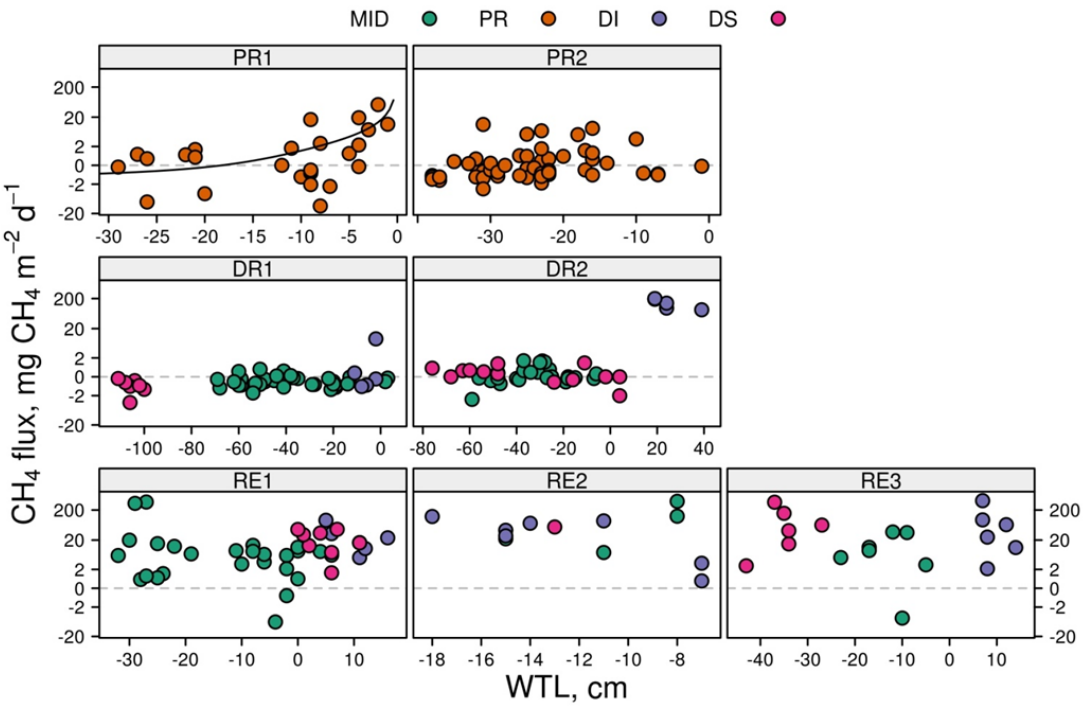

Figure 5. CH_4 fluxes (mg CH_4 m^{-2} d^{-1}) *versus* water table level (WTL, cm) grouped by site (site management codes: PR = pristine, DR = drained, RE = restored). The different colours of the points indicate different plot locations within the sites (MID = mid-strip, PR = pristine, DI = ditch, DS = beside-ditch). Regression curve (solid line) in PR1 shows the inverse relationship between flux and WTL ($F = -1.6 + (-30.3 / WTL)$, $p = 0.007$). Note the hyperbolic arc-sine scale of the y-axis and the different x-axis scale in each panel. Y-axis values have been back-transformed to show the real measured fluxes. Negative values indicate WTL below the soil surface.

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Table 3. Site management options (Management), plot locations, parameter names for each management-location pair (Parameter), parameter values (mg CH_4 m^{-2} d^{-1}) and standard errors (S.E.), significance (*p*) of parameter differences from pristine for Model (1), percentage of area represented by each location (Area represented, %), and area-weighted fluxes *per* management category (flux *per* total area, mg CH_4 m^{-2} d^{-1}).

Management	Plot location	Parameter	Parameter value (mg CH_4 m^{-2} d^{-1})	S.E.	*p*	Area represented (%)	Area flux (mg CH_4 m^{-2} d^{-1})
Pristine (PR)		B_0	1.51	10.86		100	1.51
Drained (DR)	ditch (DI)	B_1	75.83	23.74	0.007	3	
	beside ditch (DS)	B_2	-0.41	20.98	0.936	6	
	mid-strip (MID)	B_3	-0.18	12.85	0.920	91	
	Total					100	2.09
Restored (RE)	ditch (DI)	B_4	52.04	19.28	0.027	3	
	beside ditch (DS)	B_5	66.05	20.90	0.009	6	
	mid-strip (MID)	B_6	51.99	14.70	0.009	91	
	Total					100	52.84

mid-strip plots in our restored sites, in contrast to those studied by Juottonen *et al.* (2012), were also large sources of CH_4. High CH_4 fluxes from mid-strip plots have also been reported for rewetted cut-over peatlands (Wilson *et al.* 2009, 2013) where the WTL was close to or above the soil surface. The mean CH_4 flux from the pristine spruce mires in this study was similar to that measured in an earlier study on spruce mires, although the maximum emission and uptake values that we measured were much higher (see Huttunen *et al.* 2003). The poor correlation between instantaneous CH_4 fluxes and WTL seen here (Figures 4, 5) has also been noted in previous research (e.g. Moosavi *et al.* 1996, Liblik *et al.* 1997, Treat *et al.* 2007). The generally low emissions and the spatial pattern of CH_4 fluxes from our drained sites resemble observations from elsewhere (e.g. von Arnold *et al.* 2005, Minkkinen & Laine 2006, Ojanen *et al.* 2010, IPCC 2014), i.e. high emissions from the ditches and small emissions or uptake in the mid-strip plots.

The spruce mires studied in this short investigation are characterised by a water table well below the soil surface, surface vegetation composed mainly of forest shrubs and herbs, and a relatively large tree stand even in the pristine sites. The main difference in vegetation between a pristine spruce mire and drained spruce peatland forest is in the dominance of peat mosses (mainly *Sphagnum*), which give way to forest mosses after drainage. This makes it easier to understand why the CH_4 fluxes did not differ between the drained and pristine sites in our study. In other treeless and sparsely tree-covered mire types, the water table in the pristine state is at the soil surface and the mire vegetation is distinctly different from the vegetation after the drainage succession, so that drainage causes a significant drop in CH_4 emissions (Nykänen *et al.* 1998, Strack *et al.* 2004, Minkkinen & Laine 2006).

From a hydrological point of view it could be argued that restoration has been successful at our sites because the water table at the restored sites was (perhaps surprisingly) as high as, or higher than, at the pristine sites. This could be partly due to the fact that the dams in the ditches were generally made higher than the surroundings in order to direct water from the ditches onto the undisturbed soil between them. Moreover, peat hydraulic conductivity and water retention capacity are likely to be lower in restored than in pristine sites because of peat decomposition during the period when the peatland was drained (Boelter 1969, Silins & Rothwell 1998, Minkkinen & Laine 1998, Maanavilja 2015). This is reflected in our study by the higher bulk density of peat in the drained and restored sites (Table 2). Thus, the filtration of water through the surface soil in restored sites may be limited, resulting in more overland flow than in pristine sites. Furthermore, the spruce species that grow on pristine sites have root systems that are adapted to waterlogged conditions

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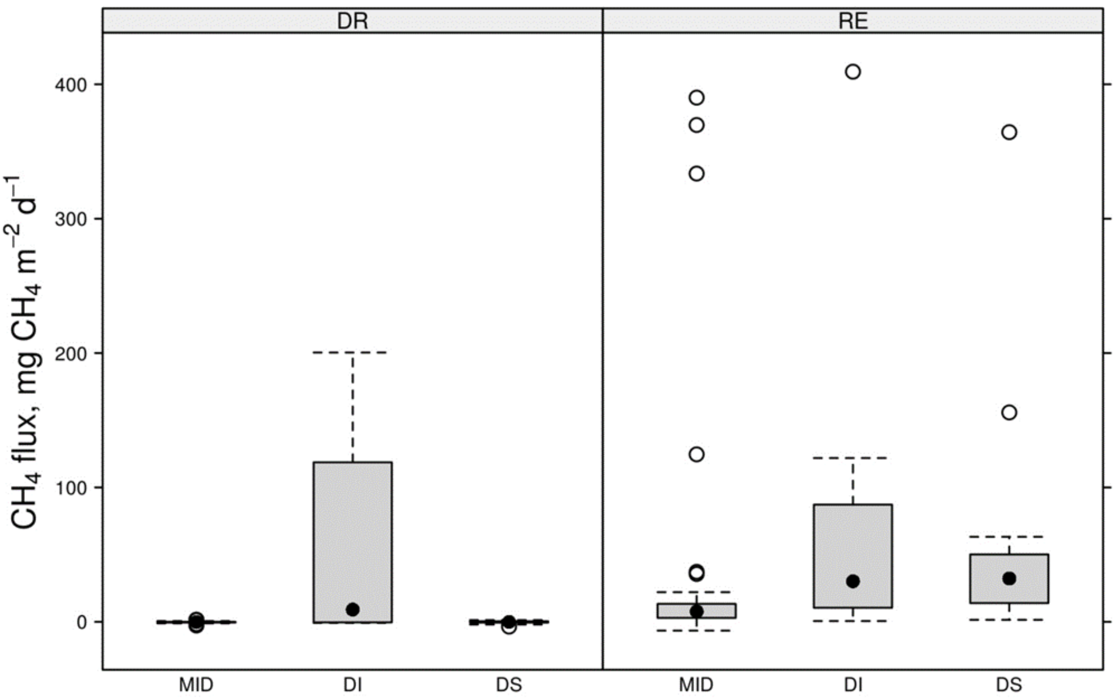

Figure 6: Median (dot), 25th–75th percentile (grey box) ± 1.5 interquartile ranges (dashed umbrellas) of CH_4 fluxes (mg CH_4 m^{-2} d^{-1}) on drained (DR) and restored (RE) sites from mid-strip (MID), ditch (DI) and beside-ditch (DS) plots. Open circles represent observations that lie beyond the 75th percentile + 1.5 interquartile ranges. The number of measurements in each site management-location pair were: DR-MID 60, DR-DI 11, DR-DS 20; RE-MID 37, RE-DI 18 and RE-DS 16.

and, therefore, probably have some capacity for transpiration. This may keep water levels lower than at restored sites, where large-scale death of spruce trees is a general outcome of restoration (as at Sites RE2 and RE3 in this study).

According to the results from our restored sites, high CH_4 emissions from ditches may persist even more than ten years after the ditches are blocked; a result which is supported by research on other mire types (e.g. Cooper *et al.* 2014). However, as the emissions from the mid-strip and beside-ditch plots on our restored sites were also high compared with the emissions from pristine and drained sites, restoration appears to have increased CH_4 emissions well above the level of those in drained or pristine sites. A probable reason is that restoration raised the WTL above the levels in pristine sites and thus induced more anoxic conditions. A fluctuating water table and an abundance of readily available substrate for methanogens in the intermittently inundated surface layer has previously been linked with long-term high CH_4 fluxes on restored bogs (Vanselow-Algan *et al.* 2015), spring-fed forested wetlands (Koh *et al.* 2009) and rewetted degraded fens (Hahn-Schöfl *et al.* 2011). Plant activity has also been linked to CH_4 dynamics on a permanently inundated fen (Koebsch *et al.* 2015). As the growth of *Sphagnum* species on restored spruce mires is rapid (Maanavilja 2015) and the water table on our restored sites was close to the surface (Figure 3), the supply of substrate to methanogens and the conditions required for methanogenic activity could sometimes co-occur, and this may be part of the explanation for the high CH_4 fluxes we observed. Thus, our results indicate that restored spruce mires may in some cases be larger sources of atmospheric CH_4 than previously thought. How long this state might prevail remains unclear as our data covered only one growing season.

Our hypothesis that the filled-in ditches have much higher CH_4 fluxes than the mid-strip area was not confirmed. This was due to high CH_4 emissions from the mid-strip area of the restored site, rather than low emissions from the ditches. The results should prompt more inquiries focusing on why the CH_4 dynamics on mid-strip areas of the restored sites differ from those on the pristine sites (particularly as pristine sites represent the target state for restoration in many cases), and whether restoration methods could be improved to prevent this phenomenon. This is a timely question because the restoration of spruce mires is generally accepted as a prime tool for biodiversity protection in boreal forest landscapes.

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