Effects of temperature rise and water-table-level drawdown on greenhouse gas fluxes of boreal sedge fens

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As potential outcomes of climate change, we examined the effects of environmental warming and drying on instantaneous CO₂, CH₄ and N₂O fluxes in three sedge fens situated in the northern and middle boreal zones. Warming was induced by means of open top chambers (OTCs) and drying through drainage via ditching. OTCs raised the air temperature by 0.2–2 °C, whereas short-term drainage dropped the water-table level (WTL) by 5–10 cm and long-term drainage by 10–30 cm. The impact of simulated warming was rather negligible as warmer and drier conditions caused net ecosystem exchange (NEE) to decrease only at one of the two mid-boreal sites. Otherwise, the temperature rise alone or paired with WTL drawdown did not alter gas fluxes at any of the sites. Instead, the drainage effect overrode that of warming. Primarily WTL drawdown accounted for the differences in fluxes detected, but this was more apparent at the mid-boreal sites than our northern-boreal one. Notably, the northernmost Lompolojänkkä sedge fen, which was both the coolest and wettest of the three sites, was least sensitive to temperature rise and drainage; there, only CH₄ emissions were affected by WTL drawdown.

Introduction

Biological activity in boreal mires is currently restricted by low seasonal temperatures and high water-table levels, thus being highly sensitive to changes in climate (Gorham 1991). Globally, boreal mires comprise over half of the total peatland area (Joosten and Clarke 2002), containing almost 60% of all carbon stored in mires (Sampson et al. 1993) and even one-third of the total global soil carbon store, i.e., 270–455 Pg (1 Pg = 10¹⁵ g) (Gorham 1991, Turunen et al. 2002), which constitutes 34%–46% of the amount of CO₂ present in the atmosphere (IPCC 2007). Therefore, disturbance to carbon cycling in boreal mires may markedly affect the atmospheric carbon dioxide (CO₂) concentration, consequently acting as a positive or negative feedback for climate change (Gorham 1991, Bridgham et al. 1995, Moore et al. 1998). Other greenhouse gases (GHGs) emitted from mires, methane (CH₄) and nitrous oxide (N₂O) are 25 and 298 times stronger GHGs than CO₂ (100-year time span), respectively (IPCC 2007).
The increase of GHG in the atmosphere is expected to instigate warming in high northern latitudes, especially during winter (Kattenberg et al. 1996, IPCC 2007, Moss et al. 2010). However, summer temperatures are likewise expected to rise by the end of the century, although not as much as the winter ones (IPCC 2007, Moss et al. 2010), possibly causing the seasonal water-table level (WTL) in mires to fall. In pristine peatlands of Finland, it has recently been estimated that climatic warming and drying will decrease total CO$_2$ sequestration by 41% while increasing total CH$_4$ emission by 9%, with the greatest changes in CO$_2$ and CH$_4$ exchange occurring in fens (Gong et al. 2013).

Microbes responsible for heterotrophic soil respiration are sensitive to temperature alterations (Dorrepaal et al. 2009). Nevertheless, the sensitivity of soil microbes to temperature is also dependent on soil moisture (Nadelhoffer et al. 1991, Moorhead and Reynolds 1993). Hence, a temperature rise alone is not always regarded as a remarkable factor influencing soil carbon balance (Oechel et al. 1998). Yet, if soil moisture conditions are favourable for heterotrophic microbes as on mires, the enhancing effect of temperature rise on heterotrophic respiration may be large (Larcher 2003). Dorrepaal et al. (2009) reported that a seasonal temperature rise of just 1 °C increased soil heterotrophic respiration in a subarctic fen already by more than 50%. Thus, if all boreal and subarctic mires respond to a 1 °C seasonal temperature rise in the same fashion, even 100 Mt of carbon could be released from mires into the atmosphere (Dorrepaal et al. 2009). On the other hand, many recent paleoecological studies on boreal peatlands suggest that warming may also increase plant productivity and therefore carbon sequestration (Charman et al. 2013, Loisel and Yu 2013). Further, warmer and drier climate conditions may simultaneously decrease CH$_4$ fluxes and increase N$_2$O fluxes from mires (Heymann and Reichstein 2008).

The water-table levels (WTL) in boreal mires are predicted to fall by 14–22 cm due to global warming (Roulet et al. 1992). A weak but positive relationship between WTL drawdown and intensified CO$_2$ emission has been observed in both laboratory and field experiments (Svensson 1980, Moore and Dalva 1993, Bridgham et al. 2008, Aurela et al. 2009). In the two-year study of Chivers et al. (2009), a WTL drawdown of just 5–8 cm significantly decreased net primary production and therefore also the ecosystem’s ability to sequester carbon. In their study, WTL drawdown transformed the study site from carbon sink to source already by the second year of monitoring. Furthermore, Riutta et al. (2007) found that a WTL drawdown of 14 cm decreased gross photosynthesis 14% but increased ecosystem respiration by 18%, whereas WTL drawdown to 22 cm decreased gross photosynthesis by 22% while increasing ecosystem respiration 20%. In the aforementioned study, heightened ecosystem respiration was primarily attributed to increased peat respiration. However, WTL drawdown has also been reported to increase primary production (Strack et al. 2006a, 2006b) and increases in the abundance and productivity of trees are also likely to occur (e.g., Munir et al. 2014).

Water-table-level drawdown generally enhances the growth of vascular plants, especially dwarf shrubs, while sedating that of Sphagnum mosses (Bubier et al. 2007, Riutta et al. 2007, Limpens et al. 2008). The gradual shift in vegetation alters litter production, accumulation, type and quality, and consequently litter decomposition rates (Dorrepaal et al. 2005, Straková et al. 2010, 2012). In the short term (several years), net C loss from the soil is likely as the direct effects of drawdown still prevail, e.g., better aeration favouring organic matter decay combined with more or less unchanged quantities of inputs (Straková et al. 2010, 2012). During this period, changes in the composition and structure of the plant community are slight. In the long term (decades), however, WTL drawdown spawns dramatic compositional changes in the vegetation community, which may very well offset increased decomposition rates through heightened litter input and accumulation (Straková et al. 2010, 2012). Hence, these indirect effects of the environmental change (i.e., drawdown) override the direct ones during long-term hydroseral succession, which means the carbon sink function is not necessarily lost (Straková et al. 2010, 2012).

The aim of this study was to quantify the effects of short-term (three years) temperature rise and both short-term (three years) and long-
Effects of warming and drying on GHG fluxes of fens

We hypothesized that warmer and drier conditions will decrease short-term NEE of sedge fens, thus hampering the ability of the sites to function as carbon sinks. Meanwhile, we proposed that the coupling of warming and drying would decrease CH$_4$ fluxes, but increase those of N$_2$O. Furthermore, we expect stronger responses in the drainage and warming treatment than in the warming only treatment.

Material and methods

Study sites

The study was carried out on three oligo-mesotrophic sedge fens similar in hydrology. Two of the fens (Lakkasuo, Orivesi and Närhinneva, Virrat) were situated in the middle-boreal coniferous-forest zone (61°47´N, 24°18´E and 62°13´N, 23°23´E, respectively), whereas the third (Lompolojänkkä, Kittilä) in the northern-boreal zone (67°59´N, 24°12´E) (Fig. 1). The long-term (1981–2011) mean annual temperature and precipitation were ca. 3.5 °C and 700 mm, respectively, and the accumulative temperature sum (+5 °C) ca. 1050 degree days for the middle-boreal sites. Correspondingly, the figures for the northern-boreal site were –1.4 °C, 511 mm and 700 degree days. Furrow ditches, approximately 20–25 cm deep, for the short-term water-table-level drawdown treatment were dug manually in early May 2008 at the middle-boreal sites and one month later at Lompolojänkkä. Drainage operations aimed at long-term water-table-level drawdown were implemented in 1961 at Lakkasuo, 1979 at Närhinneva, and 1972 at Lompolojänkkä. Compared with long-term averages, the climate was exceptionally warmer and wetter in 2008 at the middle-boreal sites and one month later at Lompolojänkkä. Drainage operations aimed at long-term water-table-level drawdown were implemented in 1961 at Lakkasuo, 1979 at Närhinneva, and 1972 at Lompolojänkkä. Compared with long-term averages, the climate was exceptionally warmer and wetter in 2008 at all three sites (Fig. 2). In 2009, annual temperatures were near average at the mid-boreal sites, which however experienced exceptionally low rainfall that year. The climate at the northernmost site was also considerably drier in 2010, although the air temperature was near average there.

The soil of the sites consisted of Carex–Sphagnum peat, ranging in depth from 50 to 200 cm. Lakkasuo harboured the thickest peat layer while Närhinneva the thinnest. The internal variation in peat thickness was greatest at Lompolojänkkä, from 50 to 150 cm. In order to provide a general characterization of the vegetation present at the sites studied, coverage was visually estimated as a percentage of plot surface area in two layers, ground (mosses) and field (vascular plants) in late July–early August during the initial season of the study (2008).
Over the decades, long-term drainage had left its imprint on the vegetation at the middle boreal sites as Scots pine (*Pinus sylvestris*) had become firmly established as a stand with dwarf shrubs and upland forest mosses becoming more common. While the pristine sections of these sites were almost treeless, stand volume in the sections subjected to long-term WTL drawdown had reached 190 m³ ha⁻¹ at Lakkasuo and 55 m³ ha⁻¹ at Närhinneva. At the northern-boreal site, vegetation changes resulting from long-term drainage were rather small as compared with the pristine section, as evidenced by the negligible development of the tree stand, amounting to merely 5 m³ ha⁻¹.

### Experimental design

In order to simulate the potential seasonal WTL drawdown scenarios caused by global warming, three 150 m² main plots were created at each site: pristine (P), short-term drainage (SD), and long-term drainage (LD). Short-term drainage spanned a period of three years, whilst long-term drainage several decades. Within each main plot, six subplots were established and assigned to one of two warming treatments: control (ambient temperature) and seasonal warming. Thus, the warming treatments were replicated in triplicate in each main plot. To simulate a moderate global warming effect, i.e., a seasonal temperature rise of 0.5–1 °C (see Chivers *et al.* 2009), air and surface soil temperatures were manipulated in the seasonal warming subplots by placing hexagonal open top chambers on them (Chivers *et al.* 2009). The OTCs were constructed from durable transparent polycarbonate and had a projected area of 1.5 m². In order to measure the temperature rise in both soil and air, temperature data loggers (iButton, Maxim, U.S.A.) were placed in each measurement plot 5 cm below and 20 cm above (*T* ₉₀⁺₂₀) the soil surface. Temperature was monitored at two-hour intervals during the growing season. Eighteen GHG measurement plots were established and organized according to a split-plot design at each site for studying the fluxes of carbon dioxide (CO₂), methane (CH₄) and nitrous oxide (N₂O). GHG exchange measurements encompassed the interface between the
soil, field and ground layers of vegetation, and air. Due to methodological constraints, tree vegetation was excluded, thus having consequences for the interpretation of ecosystem CO$_2$ exchange and respiration in the wooded long-term drainage treatments at the middle boreal sites, which are elaborated on in the Results. The simulation of a warming effect using an open top chamber (OTC) did not permit inclusion of entire trees.

In preparation for gas flux measurements, measurement plots were demarcated by first chainsawing the outline of a 60 × 60 cm aluminium collar into the ground and thereafter shoving the collar’s 30-cm-long sleeve into the trench. This trenching procedure prevented the infiltration, production, and respiration of (new) roots into the delimited area from beyond the bounds of the collar. The superficiality of most of the roots in peatlands (e.g., Finér and Laine 2000) justifies the suitability of the 30 cm trenching depth as a means of accomplishing this. Dying roots within the collar are known to cause a clear CO$_2$ pulse during the first years after collar insertion (e.g., Minkkinen et al. 2007, Mäkiranta et al. 2007).

### Table 1. Vegetation coverage (percentage of area) according to drainage treatment at the mid-boreal (Lakkasuo and Närhinneva) and northern-boreal (Lompolojänkkä) fen sites. All species with coverage ≥ 1% are listed. Coverage determined in late July 2008 at Lakkasuo and Närhinneva, and early August at Lompolojänkkä. Abbreviations: P = Pristine, SD = Short-term drainage, LD = Long-term drainage. Each mean is based on species coverage in six subplots per drainage treatment.

<table>
<thead>
<tr>
<th>Vascular plants</th>
<th>Lakkasuo</th>
<th>Närhinneva</th>
<th>Lompolojänkkä</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>P</td>
<td>SD</td>
<td>LD</td>
</tr>
<tr>
<td>Andromeda polifolia</td>
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</tr>
<tr>
<td>Betula spp.</td>
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</tr>
<tr>
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<td>1</td>
</tr>
<tr>
<td>Calluna vulgaris</td>
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<td>Vaccinium oxyccocus</td>
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<td>1</td>
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<tr>
<td>Vaccinium vitis-idaea</td>
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<td>Dicranum polysetum</td>
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<td>Pleurozium schreberi</td>
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<td>4</td>
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<tr>
<td>Polytrichum strictum</td>
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<td>2</td>
</tr>
<tr>
<td>Sphagnum spp., lawn</td>
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<td>64</td>
<td>90</td>
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<tr>
<td>Sphagnum spp., hummock</td>
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<td>7</td>
<td>31</td>
</tr>
<tr>
<td>Warnstorffia exannulata</td>
<td></td>
<td></td>
<td>1</td>
</tr>
</tbody>
</table>
al. 2008), but the effect was regarded as equal in each plot within a given site and treatment. Vegetation inside the collar was not impaired. Boardwalks were constructed around the plots to minimize disturbance to gas fluxes during measurements. Perforated PVC tubes for determining the WTL relative to the soil surface were installed beside the collared plots.

Due to Sphagnum growth, the depth of temperature loggers progressively increased over the years. Therefore, we could not vouch for the actual depth in the soil from which continuous temperature measurements were recorded. Further, a portion of the original air temperature data (recorded plotwise and bihourly) from the mid-boreal sites was corrupted during storage. Only sister files containing calculations of daily, treatment-level means could be salvaged in such cases. For these reasons, we rely simply on treatment-level, mean $T_{air+20}$ in divulging the OTC warming effect in the following.

**CO$_2$ exchange measurement**

Prior to gas measurement employing the closed-chamber method (Alm et al. 2007), water was poured into the collar groove to ensure an airtight seal of the measurement system upon gas chamber placement. Instantaneous net ecosystem CO$_2$ exchange (NEE) in each plot was measured with a transparent plastic chamber (60 x 60 x 30 cm) equipped with a fan and a portable infra-red gas analyzer (EGM-4, PP Systems, UK). During a measurement campaign, measurements lasting 90–180 s were conducted under a clear sky (full sunlight) and thereafter under one artificial shade that reduced the amount of incoming light by 40%–60%. All measurements in a campaign were made during a single day. Solar radiation varied no more than 20% between treatment plots or during the measurement period (90–180 s) of a single treatment plot. These precautions were taken in order to ensure as similar conditions as possible for all treatment plots at a site over a campaign. However, the scattered measurement occasions and the use of only one artificial shade did not capture photosynthesis intensities under the lowest levels of solar radiation, in particular. Nevertheless, this was the case for all treatment plots (and sites); thus, the comparability of treatments was not compromised.

During the measurements, CO$_2$ concentration in the chamber headspace, photosynthetically active radiation (PAR) under the chamber roof, and chamber temperature were recorded at 15-s intervals. After the measurements in light, the transparent chamber was removed and replaced with a metal chamber of the same size and the ecosystem respiration (ER) in the dark was measured. Please note that in the case of the LD treatment at both mid-boreal sites, only forest-floor net exchange (NE$_{ff}$) and respiration ($R_{ff}$) were measured.

Altogether 16 CO$_2$ flux measurement campaigns were carried out from late May to late September 2008–2010 at Lakkasuo, and 17 times over the same period at Närhinneva. About 80% of the measurements at both mid-boreal sites were made in June–July. At the northern-boreal site, fluxes were measured 11 times during the period June–September 2008–2010. Although two observations of NEE from each sample plot on every measurement occasion were acquired, some had to be rejected due to irregular (e.g., nonlinear) CO$_2$ concentration change. After cleaning the data sets, the total numbers of observations of NEE per treatment were 48 at Lakkasuo, 66 at Närhinneva, and 57 at Lompolojänkkä. For respiration, the respective numbers were 48, 51, and 33.

Immediately after each gas measurement event, soil temperature at 5 cm depth ($T_{soil-5}$) was measured to the nearest 0.1 °C from the middle of each plot with a TES-1312A digital thermometer with K type thermocouple input sensor (TES, Taiwan, R.O.C) and stainless steel temperature probe. In conjunction, the WTL to the nearest cm was recorded for each plot by inserting a battery-operated, water sensitive rod into the respective PVC tube and reading the device’s metric scale upon hearing a beep. These two variables were measured in order to relate the fluxes to the prevailing environmental conditions.

NEE and ER (NE$_{ff}$ and $R_{ff}$) were calculated as the linear change in the CO$_2$ concentration as a function of time by fitting a linear regression line. Positive values of net CO$_2$ exchange indicate net uptake of CO$_2$ into the ecosystem (or forest floor) and negative ones net loss of
CO₂ into the atmosphere. Respiration values are stated as negative indicating CO₂ emission, i.e., source.

**CH₄ and N₂O flux measurement**

CH₄ and N₂O fluxes were determined using the vented static chamber method (Alm et al. 2007). For gas sampling, a 30-cm-high metal chamber equipped with a fan and air temperature sensor was set on the collar in the same manner as in CO₂ measurements. Over a 35-minute period, four gas samples were drawn from the chamber headspace via transfer tubes into 35 ml polypropylene syringes after 5, 15, 25, and 35 minutes had elapsed. CH₄ and N₂O concentrations of gas samples were then analysed in the laboratory within 2–3 days using a gas chromatograph equipped with FI and EC detectors. The concentrations used as standards for CH₄ were 8.2 and 82 µl l⁻¹, and for N₂O 0.82 and 1.64 µl l⁻¹. The gas fluxes were calculated based on the slope of the linear regression between gas concentration and measurement time. All measured fluxes were usable. Positive slopes equated with emission, negative ones consumption. Slightly positive or negative fluxes were common in the data, but zero fluxes were rare. All were included at face value in the data.

Altogether six CH₄/N₂O flux measurement campaigns were carried out during the period June–August 2008–2010 at each of the mid-boreal sites (3 sample plots per treatment × 6 measurements = 18 observations per treatment). At the northern-boreal site, fluxes were measured seven times during the period June–October 2008–2010 (3 sample plots per treatment × 7 measurements = 21 observations per treatment).

**Statistical analysis**

Due to the limited amount of data both annually and overall, we could not reliably model fluxes on which to base simulations of seasonal estimates of carbon balance, CH₄ and N₂O exchange. Therefore, we concentrated on testing the significance of the drainage and warming effects on instantaneous NEE (NEₑ), ER (Rₑ), CH₄ and N₂O fluxes separately for each site. In doing so, we sought to verify whether or not OTC warming had a significant impact on fluxes and if any notable interaction with WTL drawdown occurred at the sites.

Since repeated observations were made on the same subjects (i.e., measurement plots) over a period of time (three growing seasons), the observed responses were correlated. As opposed to repeated measures ANOVA, linear mixed models have been designed to handle correlated data with unequal variances from normal distributions (Pan and Connett 2002). Thus, the analyses of instantaneous flux rates were based on fixed effects models with restricted maximum likelihood (REML) estimation method using the linear MIXED procedure in SPSS Statistics ver. 20 (IBM Corp., U.S.A.). Drainage treatment (pristine, short-term WTL drawdown, long-term WTL drawdown), warming treatment (control, OTC), and time were treated as fixed effects. The models defined a split-plot structure with warming as a split-plot treatment. A first-order autoregressive (AR1) covariance structure was assumed for the time correlation. The LSD adjustment method was applied to the confidence intervals and significance values to account for multiple comparisons. A log transformation was performed on the ER data from Lompolojänkkä to fulfil normality criteria before applying the fixed effects model. Test results were considered significant at p < 0.05.

**Results**

**Impacts on temperature and water-table level**

At all sites, the air temperature at 20 cm above the soil surface was principally higher in OTC plots than in control ones (Fig. 3). During the summer months (June–August), Tₑ⁻air20 was on average 0.2 to 2 °C higher in OTC plots. At the mid-boreal sites, the greatest differences in Tₑ⁻air20 occurred within the pristine treatment, while the smallest in the long-term drainage plots (Fig. 3). Shading by the forest stand at both Lakkasuo and
Närhinneva minimised the difference between LD and LDOTC. This was especially evident at Lakkasuo, where stand volume was over three times greater than at Närhinneva. Oppositely, at the cooler northern-boreal site, the differences in \( T_{\text{air}+20} \) between OTC and control plots were greatest in both drainage regimes, but smallest in the pristine treatment (Fig. 3). All in all, \( T_{\text{air}+20} \) tended to be lowest in plots under long-term drainage regardless of site.

In general, warming of the soil at 5 cm depth was also apparent in response to OTC based on manual measurements made in conjunction with \( \text{CO}_2 \) flux determination (Fig. 4). However, the differences in \( T_{\text{soil},5} \) were smaller than for \( T_{\text{air}+20} \), particularly at Lakkasuo. Unfortunately, these discontinuous measurements of \( T_{\text{soil},5} \) do not adequately account for the inherent temporal variation associated with it. Nonetheless, shading by the forest canopy was also reflected in soil temperature at the middle boreal sites, where long-term drainage accounted for the lowest mean summertime \( T_{\text{soil},5} \).

Short-term and long-term drainage progressively lowered the WTL relative to the pristine treatment at all sites, but these effects were most pronounced at Lakkasuo (Fig. 4). Short-term drawdown lowered the WTL the least at Närhinneva, whereas long-term drawdown did so at Lompolojänkkä. The highest mean WTLs for all treatments occurred namely at the northern-boreal site, all lying within 9 cm of each other. Hence, this fen was the wettest of all the sites.

**Net \( \text{CO}_2 \) Exchange**

While the main effects of drainage treatment and OTC warming were both significant at Lakkasuo, only drainage had a significant effect at the other mid-boreal site, Närhinneva (Table 2). Contrary to the mid-boreal sites, neither WTL drawdown nor warming influenced NEE at the northern-boreal site.

At Lakkasuo, where the mean WTLs under the pristine, short-term, and long-term drainage
regimes contrasted most sharply, drainage progressively and significantly reduced NEE (and $\text{NEF}_f$) relative to the pristine treatment (Fig. 5). In addition, $\text{NEF}_f$ in the long-term drainage treatment was significantly lower than NEE in the short-term WTL drawdown treatment. Just like drainage, OTC warming also diminished the rate of NEE (and $\text{NEF}_f$) overall as compared with the values for the control plots at Lakkasuo; this trend was evident specifically under both WTL drawdown regimes there, although interaction between the drainage and warming effects was not significant (Table 2 and Fig. 5).

At Närhinneva, only the decreasing effect of long-term WTL drawdown on $\text{NEF}_f$ was apparent, which led to significantly lower rates with respect to NEE of the other treatments (Fig. 5). As opposed to those in Lakkasuo, the WTLs in the pristine and short-term drainage treatments at Närhinneva differed little, which likely contributed to the similarity in NEE between the two. Admittedly, the drop in the WTL resulting from the short-term drainage procedure failed to meet expectations as the plots remained wetter than desired. At the northern-boreal site, Lompolojänkkä, the distinctly similar NEEs between treatments were rather expected considering that the mean WTLs lay within close range of each other as well as being the highest of all sites (Figs. 4 and 5). In contrast to Närhinneva, however, the limited WTL drawdown achieved via both drainage regimes at Lompolojänkkä was purely a consequence of climatic factors. Despite comprehensively warmer air temperatures at 20 cm above ground with OTC than without at all three fen sites (Fig. 4), the achieved warming was of no perceivable consequence for NEE (or $\text{NEF}_f$) at two of them, Närhinneva and Lompolojänkkä.

### Table 2

<table>
<thead>
<tr>
<th>Independent variable</th>
<th>Lakkasuo</th>
<th>Närhinneva</th>
<th>Lompolojänkkä</th>
</tr>
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<tbody>
<tr>
<td></td>
<td>df</td>
<td>$F$</td>
<td>$p$</td>
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<tr>
<td><strong>Net CO$_2$ exchange</strong></td>
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<td></td>
<td></td>
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<tr>
<td>D</td>
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<td>W</td>
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<tr>
<td>D $\times$ W</td>
<td>2</td>
<td>2.43</td>
<td>0.112</td>
</tr>
<tr>
<td><strong>Respiration</strong></td>
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<td></td>
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<tr>
<td>D</td>
<td>2</td>
<td>13.33</td>
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<tr>
<td>W</td>
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<tr>
<td>D $\times$ W</td>
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<td>0.407</td>
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<tr>
<td><strong>CH$_4$ flux</strong></td>
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<tr>
<td>D</td>
<td>2</td>
<td>14.10</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>W</td>
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<tr>
<td>D $\times$ W</td>
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<tr>
<td><strong>N$_2$O flux</strong></td>
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<td></td>
<td></td>
</tr>
<tr>
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<td>2.86</td>
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<tr>
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</tr>
<tr>
<td>D $\times$ W</td>
<td>2</td>
<td>0.53</td>
<td>0.598</td>
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</table>

Respiration

The trends present in net CO$_2$ exchange were mostly reiterated in respiration (Table 2 and Fig. 5). Only long-term drainage significantly increased (forest floor) respiration at the middle boreal sites, which consequently exceeded ER rates in the other treatments (Fig. 5). $R_f$ excludes tree crown respiration, thus ecosystem-level respiration for LD/LDOTC at these two sites would naturally be higher (i.e., more negative). At Lompolojänkkä, as with NEE, ER rates were likewise similar in all treatments.

No effect of OTC warming on respiration was found, thus the presence of OTC did not alter CO$_2$ emission from pristine, short-term or
long-term drainage plots anywhere (Table 2 and Fig. 5). While a similar magnitude of NEE was shared by all sites, ecosystem respiration was clearly lower at the northern-boreal site as compared with that at the mid-boreal ones.

**CH$_4$ flux**

With respect to the pristine treatment, short-term WTL drawdown decreased methane emissions significantly at Lakkasuo and Lompolojännäkä (Table 2 and Fig. 6). Long-term WTL drawdown suppressed the release of CH$_4$ most of all, and the significance of this effect could be detected at all three sites. Once again, OTC warming as such or coupled with drainage brought forth no apparent consequences on CH$_4$ fluxes anywhere.

Although NEE and ER were not affected by WTL drawdown at the northern-boreal site, the drop in the WTL under both drainage regimes sufficed to significantly reduce CH$_4$ emissions there. At Närhinneva, however, the short-term WTL drawdown achieved was insufficient to alter CH$_4$ fluxes in addition to NEE and RE. Furthermore, when considering the magnitude of fluxes amongst the three sites, the lowest mean CH$_4$ emissions occurred at Lakkasuo and the highest at Lompolojännäkä, and this applied to all treatments.

**N$_2$O flux**

At the mid-boreal sites, WTL drawdown generally tended to increase nitrous oxide emissions...
relative to the pristine treatment, but such was not the case for the northern-boreal site (Fig. 6). However, significant differences between treatment differences were found only at Närhinneva, where short-term drainage increased N$_2$O emission most clearly (Table 2 and Fig. 6). All sites and treatments considered, the impact of OTC warming on N$_2$O fluxes was indiscernible. The long-term drainage treatment at the mid-boreal site, Lakkasuo, accounted for the highest mean N$_2$O emissions.

Discussion

The degree of warming achieved via temperature manipulation using OTCs and the difference in average WTLs between the pristine and short-term drainage treatments in this study were close to those presented by Chivers et al. (2009). In addition, the increases in air and soil temperatures caused by OTCs here corresponded with the results of Munir and Strack (2014), although here we did not statistically test the differences in air or soil temperatures. In general, instantaneous rates of NEE and ER (and NEff and Rff) in our study roughly corresponded to those measured in earlier studies on pristine and drained peatland sites (Frolking et al. 2002, Riutta et al. 2007, Aurela et al. 2009, Chivers et al. 2009, Drewer et al. 2010, Ojanen et al. 2010, Badorek et al. 2011). In our data, the impacts of long-term drainage stood out from those initiated by short-term drainage or OTC warming. (1) OTC warming had little effect on CO$_2$ fluxes and no effect on CH$_4$ or N$_2$O fluxes. (2) No drainage effects were observed in the northernmost and wettest site except on CH$_4$ fluxes. (3) A more straightforward effect of drainage decreasing CH$_4$ emissions was apparent. Since the carbon exchange and respiration results for the long-term drainage treatment at the mid-boreal sites do not apply to the whole ecosystem, rather just the forest floor, they will be dealt with separately here.

Lakkasuo was the only site where ecosystem CO$_2$ fluxes were notably affected by short-term WTL drawdown and warming. Short-term drainage decreased NEE, which coincides with the findings of Riutta et al. (2007) from the same site as well as Chivers et al. (2009) from an Alaskan rich fen. However, ecosystem respiration in our study remained unchanged, which conflicts with the heightened ER found by Riutta et al. (2007) as well as by Ballantyne et al. (2013) in a poor fen in northern Michigan. The latter-mentioned study reported no significant change in NEE, though. Similar to our results, Chivers et al. (2009) found no difference in ER between control and lowered water table treatments. They attributed this phenomenon to reduced plant C uptake (and thus plant growth), suggesting that autotrophic respiration declined while heterotrophic respiration rose, thereby offsetting any change in ER. The significant overall effect of warming on NEE found at Lakkasuo, in turn, conflicted with the results of Chivers et al. (2009). In their study, proportionally similar increases (16%) in both gross photosynthesis and ER overall due to warming were observed, therefore NEE was unaltered; here, on the other hand, warming at Lakkasuo caused a notable reduction in NEE overall because gross photosynthesis decreased while ER continued steadfastly. Our results from Lakkasuo thus seem to demonstrate that the combined influence of short-term WTL drawdown and warming had unfavourably altered the growing conditions of the vegetation community present hence forcing it into an adjustment phase, as evidenced by lowered NEE (and gross photosynthesis). Although we cannot attest to any changes in community composition and structure as we did not monitor them in this experiment, functional disruption to the community had evidently occurred. Gradually, dwarf shrubs would benefit from the drier environment becoming more abundant (Riutta et al. 2007, Badorek et al. 2011), but given the brief time scale of our study, their influence on CO$_2$ fluxes would have been minor. On a poor fen, Strack and Waddington (2007) found no significant difference in CO$_2$ exchange after short-term WTL drawdown relative to the control, but demonstrated differential responses of carbon cycling to drawdown between microforms (hummocks, lawns, hollows). They also emphasized that the vegetation communities inhabiting different microforms were still undergoing change, which means their full response had yet to be determined.

The small change in the WTL resulting from short-term drainage largely accounted for the
lack of differences in NEE and ER at the other mid-boreal site (Närhinneva), and high moisture levels proceeded to reduce temperature sensitivity of C fluxes as has been documented in a number of studies (e.g., Moore and Dalva 1993, Mäkiranta et al. 2010, Pearson et al. 2012). Our northern-boreal site, on the other hand, highlighted how geographical location and climate can dictate the response of ecosystem CO₂ fluxes to environmental change, i.e., altered hydrology and temperature do not necessarily affect boreal fens in the same way. In contradiction with the findings of Oechel et al. (1998) from wet sedge tundra ecosystems, CO₂ fluxes at Lompolojänkkä were insensitive to both drainage and warming with no indication of any interaction. In Oechel et al. (1998), principally drainage, but also elevated temperature, intensified particularly ER. The divergence of our results becomes even more intriguing when considering the difference in the thickness of the organic soil layer: 50–150 cm in this study, and 15–30 cm in Oechel et al. (1998). Although we must exercise restraint in our interpretation due to the limited size of our dataset, obviously the high water-table levels in both the short-term as well as long-term drainage plots kept ER in check at Lompolojänkkä by limiting the thickness of the aerobic soil layer and thus decomposition (Strack et al. 2006b). We suspect that these results may also be related to Lompolojänkkä’s methane budget. Previously, Drewer et al. (2010) identified methane as the dominant GHG there. In our study, methane emissions continued at a rather high level despite drainage (Fig. 6), which indicates the continued release of organic material into the anaerobic peat layers and consequent anaerobic respiration of microbes in addition to CH₄ transport through the root-shoot pathway. Moreover, this ecosystem has been characterized as highly N limited (Lohila et al. 2010), which sets restrictions on plant growth, while potentially hampering the activity of methanotrophs (Bodelier and Laanbroek 2004). In any case, CO₂ fluxes remained stable over the short term at this high-latitude fen, with the climate there seemingly acting as a buffer against drastic environmental change.

As described in Material and methods, the net CO₂ exchange measured in the long-term drainage treatments at both mid-boreal sites is only representative of non-tree vegetation on the forest floor. This explains the net losses of carbon from LD/LDOTC as seen in Fig. 5; as both sites are wooded, carbon is also stored in tree stems in addition to accumulating in soil via above and belowground tree litter input, but this has been ignored here. Furthermore, Rᵣ measured (which consequently affects NEᵣ) includes decomposition of fallen tree needles and leaves, as these were not removed from the plots during the study, as well as tree root litter at least at the start. These forested sites should not however be erroneously interpreted as carbon sources. While this methodological handicap obviously hinders interpretation of the effects of LD/LDOTC on ecosystem carbon fluxes, incorporating the forest stand into the experimental framework and calculations is far from straightforward. In any case, the contributions of these above-mentioned factors to the NEᵣ and Rᵣ rates registered would presumably be the same in both LD and LDOTC plots. At the northern-boreal site, on the other hand, no such interpretational quandary exists since long-term WTL drawdown had had a negligible effect on tree establishment and growth there, remaining almost treeless.

Based on our instantaneous measurements, the forest floor typically constituted a source of CO₂ to the atmosphere because photosynthesis of the ground vegetation was surpassed by respiration from autotrophic (ground vegetation and some tree roots) and heterotrophic sources (i.e., decomposition of litter and peat). In one of the few studies examining the role and contribution of forest floor vegetation in peatland forest C dynamics, Badorek et al. (2011) made the same observation in a nutrient-poor, forestry-drained peatland site in southern Finland. Furthermore, they reported that the forest floor was responsible for 20%–30% of all the CO₂ assimilated by the forest ecosystem. In comparison, the coverage of mosses and dwarf shrubs in the plots subjected to long-term WTL drawdown at our mid-boreal sites was considerably smaller, especially at Lakkasuo, than in Badorek et al. (2011), thus in our case the forest floor would likely account for a lower proportion of the C sequestered by the whole ecosystem. Despite similar species of vegetation as in the site studied by Badorek et al. (2011), Lakkasuo and Närhinneva were some-
what richer sites, which in part may explain why instantaneous rates of forest floor respiration were also several times greater. Moreover, forest floor vegetation occurred in patches at Lakkasuo due to shading by the forest canopy, while being continuous in the better lighted conditions at Närhinneva. As a result, measured rates of $\text{NE}_\text{f}$ were nearly always negative (i.e., net release of $\text{CO}_2$) in the long-term drainage plots at Lakkasuo, but positive rates (i.e., net uptake of $\text{CO}_2$) were not uncommon at Närhinneva. Just as Badorek et al. (2011) surmised, since litter input was overlooked and some degree of tree root respiration (and root litter decomposition) is included in these $\text{CO}_2$ exchange measurements, the results presented plausibly overestimate respiration and underestimate photosynthesis of the forest floor. Indeed, a number of methodological challenges exist in estimating the carbon fluxes of wooded forestry-drained peatland sites in response to simulated warming and water-table-level drawdown. Ideally, any simulated warming should also target the tree crown, instead of just root systems. Further, the OTC treatment we applied was only short in duration, as opposed to drainage in the long term which had already spanned decades.

Mean daily methane fluxes at the mid-boreal sites were in line with those found by Nykänen et al. (1998), and those for Lompolojänkkä agreed with the findings of Huttunen et al. (2003) and Drewer et al. (2010). As has been noted in numerous previous studies on peatlands (e.g., Roulet et al. 1992, Nykänen et al. 1998, Turetsky et al. 2008, Ojanen et al. 2010), drainage curtailed methane emissions considerably at all three of our sites. Although peat temperature positively correlates with $\text{CH}_4$ emission (Bubier et al. 1995, Nykänen et al. 1998, Huttunen et al. 2003), simulated warming with OTC produced no discernible impact on fluxes anywhere. However, it is unclear as to whether the warming treatment applied here, which was not only short in duration (three years) but limited in extent (i.e., each OTC covering an area of 1.5 m$^2$), would have affected soil temperature lower down in the peat profile; for instance, using the same methodology Chivers et al. (2009) perceived no influence on soil temperature below 2 cm from the soil surface. On the other hand, in examining the effects of WTL drawdown and warming on $\text{CH}_4$ fluxes in a dry boreal bog, Munir and Strack (2014) found that OTCs significantly warmed air temperatures as well as soil temperatures at 5 cm while also noting an effect, though not significant, on temperatures to 30 cm depth. However, they still found no significant effect of OTCs on $\text{CH}_4$ emissions. Furthermore, only small increases in $\text{CH}_4$ emissions resulted from soil warming in the WTL drawdown treatment on a rich fen in the study by Turetsky et al. (2008). Similarly, soil warming did not affect $\text{CH}_4$ fluxes in fen mesocosms, while WTL clearly acted as the dominant control (White et al. 2008). Nevertheless, White et al. (2008) noted major indirect effects of warming and WTL on pore water chemistry and plant productivity, which were deemed important secondary factors in explaining $\text{CH}_4$ fluxes. In congruence with Huttunen et al. (2003), $\text{CH}_4$ emissions in our study were higher from the northern-boreal site than its mid-boreal counterparts apparently due to both high levels of moisture and fertility.

$\text{N}_2\text{O}$ emissions from pristine peatlands are generally low (Regina et al. 1996, Song et al. 2009, Drewer et al. 2010, Lohila et al. 2010) and our study likewise confirms this. $\text{N}_2\text{O}$ fluxes in the pristine treatment at all sites were well within the range measured by Lohila et al. (2010) and Drewer et al. (2010), but flux rates at Lakkasuo and Närhinneva exceeded those of both Nykänen et al. (1995) and Regina et al. (1996) from middle boreal fens. WTL drawdown typically leads to increased emission of $\text{N}_2\text{O}$ in minerotrophic peatland sites (Regina et al. 1996, Ojanen et al. 2010) and this could also be witnessed here at both mid-boreal sites. Although the slight lowering of the water table over the short term at Närhinneva generated no noticeable effect on $\text{CO}_2$ or $\text{CH}_4$ fluxes, it nonetheless increased the release of $\text{N}_2\text{O}$ by almost twofold compared to the pristine state. This would appear to indicate increased mineralization and nitrification of the N pool wrapped up in the organic matter, hence providing nitrate for denitrification and enhanced $\text{N}_2\text{O}$ emission (Maljanen et al. 2012). Since we did not partition OM decomposition from ecosystem respiration, we cannot verify its specific impact on $\text{CO}_2$ emission, but ER nonetheless remained unchanged. The lower
N\textsubscript{2}O emissions of the pristine treatment could be due to either the low availability of nitrate and/or reduction of N\textsubscript{2}O to N\textsubscript{2} caused by greater soil moisture (higher WTL) and consequently low oxygen availability (Lohila et al. 2010, Maljanen et al. 2012). The margin between production and consumption of N\textsubscript{2}O in soil is not absolute, for the processes of nitrification and denitrification may occur in thin, abutting layers of soil (Flechard et al. 2005, Pihlatie et al. 2007, Lohila et al. 2010). Thus, even though the drop in the WTL was ostensibly small under the short-term drainage regime, it may have been significant from the aspect of microbes involved in these processes. Furthermore, the topmost organic soil layer, which is the recipient of incoming N via atmospheric deposition or organic matter decomposition, is known to be crucial in the soil–atmosphere exchange of N\textsubscript{2}O (Regina et al. 1998, Pihlatie et al. 2007, Lohila et al. 2010). Additionally, soil acidity possibly accounts for some of the observed enhancement of N\textsubscript{2}O emission; the oligotrophic Närhinneva fen represented the poorest of our three sites, purportedly having a lower pH. Previously, acidic soil has been associated with the highest N\textsubscript{2}O emissions in a Swedish forestry-drained peatland (Andert et al. 2012). During denitrification, soil pH has likewise been demonstrated to negatively correlate with N\textsubscript{2}O:N\textsubscript{2} product ratios (Simek and Cooper 2002, Dannenmann et al. 2008). On the contrary, Macrae et al. (2013) suggested that soil water retention above the water table following drawdown (up to 20 cm) limits the effects of drainage on microbial activity and nutrient cycling because the soil moisture content remains largely unchanged.

Just as with CO\textsubscript{2} fluxes, N\textsubscript{2}O fluxes at our northern-boreal site, Lompolojänkkä, did not respond to WTL drawdown or warming. Since the change in the WTL after drainage remained small, we suppose that oxygen availability in the peat was not affected enough to alter the N cycle.

Previously at this nutrient-rich sedge fen, Lohila et al. (2010) attributed the relatively low N\textsubscript{2}O fluxes to the low nitrate concentration of the peat and high water-table level. The former restricts microbial denitrification, while the latter creates an anaerobic soil environment which leads to a shift in the end product of denitrification from N\textsubscript{2}O to N\textsubscript{2} as N\textsubscript{2}O is used by microbes in the absence of oxygen (Davidson et al. 2000, Lohila et al. 2010). Furthermore, in their analysis Lohila et al. (2010) found that the peat consumed N\textsubscript{2}O at a depth of 15 cm. Although a considerable amount of organic N is stored in the peat at Lompolojänkkä, atmospheric N deposition is low and mineralized nitrogen scarce (Drewer et al. 2010, Lohila et al. 2010). All of these factors probably contributed to the lack of effects on N\textsubscript{2}O dynamics we observed there.

Conclusions

If we reflect on our hypotheses, we find that our study provided rather modest evidence to support them. All sites and gases considered, the impact of simulated warming was for the most part neutral, the only exception being one of the two mid-boreal sites, where warmer and drier conditions caused NEE to decrease. Otherwise, the temperature rise alone or coupled with WTL drawdown did not alter CO\textsubscript{2}, CH\textsubscript{4} or N\textsubscript{2}O fluxes at the mid-boreal or northern-boreal sites. Instead, the drainage effect seemed to override that of simulated warming. Primarily WTL drawdown accounted for the differences in fluxes detected, but this was more apparent at the mid-boreal sites than our northern-boreal one. In fact, the northernmost Lompolojänkkä sedge fen was least sensitive to temperature rise and drainage; there, we could only attest to the curbing of CH\textsubscript{4} emissions in response to WTL drawdown. As controls of microbial processes, the cooler and wetter conditions and N limitation at this site appeared to buffer it against environmental change — warming and drying — over the short term. However, due to the limitations of our dataset, this study serves chiefly as a stepping stone to intensive, future studies on the subject which should consider, e.g., the annual C balance, long-term influence on fluxes, and tree stand component (on forested sites).

References


Larcher W. 2003. *Physiological plant ecology: ecophysiol-


Simek M. & Cooper J.E. 2002. The influence of soil pH on denitrification: progress towards the understanding of...
this interaction over the last 50 years. European Journal of Soil Science 53: 345–354.


