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### **Warming impacts on boreal fen CO<sub>2</sub> exchange under wet and dry conditions**

Running title: Warming impacts on boreal fen CO<sub>2</sub> exchange

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## Abstract

Northern peatlands form a major soil carbon (C) stock. With climate change, peatland C mineralization is expected to increase, which in turn would accelerate climate change. A particularity of peatlands is the importance of soil aeration, which regulates peatland functioning and likely modulates the responses to warming climate. Our aim is to assess the impacts of warming on a southern boreal and a sub-arctic sedge fen carbon dioxide (CO<sub>2</sub>) exchange under two plausible water table regimes: wet and moderately dry. We focused this study on minerotrophic treeless sedge fens, as they are common peatland types at boreal and (sub)arctic areas, which are expected to face the highest rates of climate warming. In addition, fens are expected to respond to environmental changes faster than the nutrient poor bogs. Our study confirmed that CO<sub>2</sub> exchange is more strongly affected by drying than warming. Experimental water level draw-down (WLD) significantly increased gross photosynthesis and ecosystem respiration. Warming alone had insignificant impacts on the CO<sub>2</sub> exchange components, but when combined with WLD it further increased ecosystem respiration. In the southern fen, CO<sub>2</sub> uptake decreased due to WLD, which was amplified by warming, while at northern fen it remained stable. As a conclusion, our results suggest that a very small difference in the WLD may be decisive, whether the C sink of a fen decreases, or whether the system is able to adapt within its regime and maintain its functions. Moreover, the water table has a role in determining how much the increased temperature impacts the CO<sub>2</sub> exchange.

## Keywords

carbon dioxide, ecosystem respiration, gross photosynthesis, OTC, peatland, warming, water level drawdown

## Introduction

Northern peatlands are a major soil carbon (C) stock of  $500 \pm 100$  Gt (Yu, 2012).

Consequently, the responses of peatland ecosystem C exchange to the changing climate is – or should be – of great concern. The climate of northern Eurasia, where peatlands are a common ecosystem type (Joosten 2010), is expected to become warmer and gradually wetter (Arzhanov, Eliseev, & Mokhov, 2012; Monier, Sokolov, Schlosser, Scott, & Gao, 2013).

Earlier predictions on the future of northern peatlands that were based on  $2 \times \text{CO}_2$  climate scenarios and temperature increase only, suggested an 8 to 22 cm drop in the water tables (Gorham, 1991; Roulet, Moore, Bubier, & Lafleur, 1992). However, the precipitation rates likely increase as well, although more during winters than during summers (e.g., IPCC, 2013; Screen, 2013; Wu & Roulet, 2014). The summer precipitation patterns may vary regionally, and the frequencies of both droughts and floods may increase (Pal, Giorgi, & Bi, 2004;

Lehtonen, Ruosteenoja, & Jylhä, 2014). Thus, in spite of the generally increasing rates of precipitation, it is still probable that due to increased evaporation and increased frequencies of droughts some northern peatlands will experience a drop in the water table, but possibly less than previously predicted. During drought, precipitation frequency regulates surface moisture, which can be important for the C uptake of important peatland *Sphagnum* mosses that are a significant component of peatland vegetation (Nijp et al. 2014). According to palaeoecological studies peatlands respond to increasing temperature depending on their moisture regime; warm and wet periods have been linked with rapid expansion of peatlands (Loisel et al. 2014), while under warm and dry conditions decreased rates of C sequestration have been observed (e.g. Mathijssen et al. 2014). Consequently, responses of northern peatland C cycling to climate warming should be evaluated under both wet and dry future scenarios.

Temperature is a central regulator of the C cycle: it controls metabolic processes linked with photosynthesis (e.g. Jones 1992; Medlyn et al. 2002) as well as plant and soil respiration (e.g. Singh & Gupta 1977; Jones 1992). In peatlands, the water table (WT) level that defines the limits of oxic and anoxic peat layers may, however, be a stronger driver of community composition and ecosystem functions than rising temperature alone (Mäkiranta et al. 2018). Peatland plant and soil communities are adaptations to the generally high WT levels that define the existence of these ecosystems (Sottocornola, Laine, Kiely, Byrne, & Tuittila, 2009; Andersen et al. 2011). Consequently, changes in the WT are likely to shape these communities and through them, ecosystem functioning. There are indications that drop in the water table favors vascular plants, especially woody species, over *Sphagnum* mosses that rely on capillarity for moisture supply (Malmer, Svensson, & Wallén, 1994; Laine et al 1995).

Warming has been shown to have similar impacts as vascular plants are able to take advantage on increasing temperatures better than mosses (Weltzin et al. 2000; Bragazza et al. 2013; Dieleman et al. 2015). Such community changes have been linked with alterations in several ecosystem functions such as decreased carbon accumulation (Riutta, Laine, & Tuittila, 2007; Bragazza et al 2016) and increased decomposition of organic matter (Straková, Penttilä, Laine, & Laiho, 2012). In addition to the indirect impact of the WT drop via community composition, the well-aerated soils support many-fold more efficient soil respiration than what occurs in anoxic conditions (e.g. Silvola, Alm, Ahlholm, Nykänen, & Martikainen, 1996; Minkkinen et al. 2007; Maljanen et al. 2010; Bragazza et al. 2016; Chimner, Pypker, Hribljan, Moore, & Waddington, 2017).

Impacts of warming on peatland vegetation and different ecosystem functions have been experimentally studied with increasing frequency since around 2000 using open top chambers (OTC) (e.g., Wiedermann, Nordin, Gunnarsson, Nilsson, & Ericson, 2007; Turetsky et al.

2008; Dorrepaal et al. 2009; Chivers, Turetsky, Waddington, Harden, & McGuire, 2009; Johnson, Pypker, Hribljan, & Chimner, 2013; Ward et al. 2013; Munir & Strack 2014; Munir, Perkins, Kaing, & Strack, 2015; Buttler et al., 2015; Pearson et al. 2015; Voigt et al. 2017; Gill, Giasson, Yu, & Finzi, 2017; Mäkiranta et al. 2018) or mesocosms (e.g. Weltzin, Bridgham, Pastor, Chen, & Harth, 2003; Dieleman, Branfireun, McLaughlin, & Lindo, 2015). In studies addressing CO<sub>2</sub> exchange, warming has generally increased ecosystem respiration (Table S1.1.; e.g., Dorrepaal et al. 2009; Ward et al. 2013; Voigt et al. 2017), but impacts on gross photosynthesis and on net ecosystem CO<sub>2</sub> exchange have been more variable ranging from decreased to increased flux rates (Chivers et al. 2009; Johnson et al. 2013; Ward et al. 2013; Pearson et al. 2015; Voigt et al. 2017; Gavazov et al. 2018). It is yet hard to conclude what causes the differences as the available studies are still few and carried out at different peatland types, dominated by mosses, shrubs or graminoids. In addition, the length of the experiments have varied so that in some studies, the ecosystem may have been at the preliminary stress stage, while in others an adjustment to the new conditions or even a regime shift to a new type of ecosystem has occurred depending on the onset of the experiments relative to the timing of the measurements.

It is evident that the impacts of increased temperature are modulated by water table that defines the level of soil aeration, as the wet and mostly anaerobic soil conditions are suboptimal for most plants and decomposers (e.g. Davidson & Janssens, 2006; Munir & Strack 2014; Munir et al. 2015; Buttler et al., 2015). However, studies combining both temperature and water table manipulation treatments are rare and focus on different ecosystem processes such as vegetation composition and productivity (Weltzin et al. 2003, Cornelius, Heinichen, Drösler, & Menzel, 2014; Dieleman et al. 2015; Mäkiranta et al. 2018), or methane emissions and related microbial processes (Munir & Strack 2014; Peltoniemi et

al. 2015; 2016). To our knowledge there are only four studies that examined CO<sub>2</sub> exchange (Table S1.1; Oechel, Vourlitis, Hastings, Ault, & Bryant, 1998; Chivers et al. 2009; Pearson et al. 2015; Munir et al. 2015). All these studies that were carried out at different types of peatlands implicate that experimental water level drawdown (WLD) has a stronger impact than warming on CO<sub>2</sub> exchange. Pearson et al. (2015) who studied the initial impacts of WLD and warming treatments (first two years) in our study set-up, reported altogether insignificant changes in net ecosystem CO<sub>2</sub> exchange (NEE) and ecosystem respiration (R<sub>ECO</sub>). WLD, as such, increased R<sub>ECO</sub> and decreased CO<sub>2</sub> sink in a wet sedge tundra (Oechel et al. 1998), rich fen (Chivers et al. 2009) and treed bog (Munir et al. 2015). Munir et al. (2015) found that warming alone increased all CO<sub>2</sub> flux components, while under WLD conditions warming slightly decreased the CO<sub>2</sub> sink. Chivers et al. (2009) reported that warming increased gross photosynthesis (P<sub>G</sub>) and R<sub>ECO</sub> equally and that the impact was similar under the WLD. Oechel et al. (1998) on the other had showed that warming decreased photosynthesis under WLD. The variation in the responses of the different CO<sub>2</sub> exchange components may reflect, e.g., the impacts of initial WT, climatic conditions, or peatland type, but the data are still too scarce for generalizations.

Minerotrophic fens receive nutrient-rich water from surrounding mineral soils and bedrock (Gore 1983), while ombrotrophic bogs are only rainwater-fed. The adaption to continuous flow of water makes fens and their plants poorly adapted to periods of drought and vulnerable to a drop in the water table, while bog species regularly experience dry periods (e.g. Thormann, Bayley & Szumigalski, 1997). The higher nutrient status of fens, compared to bogs, gives more advantage to invading species if environmental conditions change (Eskelinen & Harrison, 2014). Likely for these reasons, fens respond to changes in WT faster and stronger than bogs (Laine, Vasander & Laiho, 1995; Komulainen, Tuittila, Vasander, &

Laine, 1999; Jaatinen, Fritze, Laine, & Laiho, 2007; Gong et al., 2013; Wu & Roulet, 2014).

Due to the demand of high effective precipitation ( $P - ET$ ) (Ruuhijärvi 1982) fens have their highest abundance at boreal and (sub) arctic areas (Joosten, Tannenberger, & Moen, 2017), which are expected to face the highest rates of climate warming (e.g., Prowse et al. 2006, Kjellström et al. 2018).

Due to the expected sensitivity, we focused this study on fens. Our aim was to assess the impacts of warming on boreal sedge fen  $CO_2$  exchange under two plausible moisture regimes, ambient, and moderate water level drawdown (WLD) of less than 10cm, which is approximately doubling the distance from the moss surface to the WT in these wet ecosystems.

We hypothesized that gross photosynthesis ( $P_G$ ) increases under warmer conditions, as warming is generally linked with increased production of plant groups with higher photosynthetic capacity (vascular plants vs. mosses, Weltzin et al. 2000; Bragazza, Parisod, Buttler, & Bardgett 2013; Dieleman et al. 2015). We hypothesize the increase to be stronger under the WLD treatment where conditions allow higher nutrient availability due to amplified decomposition. However, based on our previous results showing very moderate treatment impacts on leaf area and biomass production (Mäkiranta et al. 2018), we expected the increase in  $P_G$  to be moderate as well. Secondly, we hypothesized that ecosystem respiration ( $R_{ECO}$ ) increases due to warming, as both autotrophic and heterotrophic respiration are temperature dependent (Singh & Gupta 1977; Jones 1992) and current temperatures are below optimum. We expected the increase to be stronger under the dry condition at which the conditions are more favorable for decomposers (e.g. Silvola et al. 1996; Minkkinen et al. 2007; Maljanen et al. 2010; Chimner et al. 2017). Thirdly, we hypothesized that as the net effect of warming in ambient wet conditions the  $CO_2$  sink function will strengthen due to increased photosynthesis that will compensate for the increased seasonal carbon effluxes, but

when warming is accompanied with water-level drawdown the fen will turn into a source of CO<sub>2</sub>.

To address these hypotheses, we carried out a study at two sedge fens located at southern and northern Finland. At both sites we used an experimental set-up constituting of control and WLD plots, into which open-top chambers were installed to induce warming. At this paper we report P<sub>G</sub>, R<sub>ECO</sub> and NEE fluxes measured during the third and fourth experimental years. Previously the treatment impacts on microbial community and methane dynamics have been reported by Peltoniemi et al. (2015 and 2016) and the impacts on vegetation community, biomass production and leaf area by Mäkiranta et al. (2018). In addition, Pearson et al. (2015) reported the treatment impacts on NEE and R<sub>ECO</sub> for the first two year after the initiation of the experiment.

## Materials and Methods

### Study sites and experimental design

Our two study sites were located in Southern and Northern Finland, namely in Orivesi (the Southern fen, Lakkasuo, 61°48' N 24°19' E) and Kittilä (the Northern fen, Lompolojänkämä, 67°60' N 24°12' E). In the Southern fen the long-term (1981 - 2011) mean annual temperature and precipitation were ca. +3.5 °C and 700 mm respectively, and the temperature sum (+5 °C threshold) was ca. 1050 degree days (d.d.). Corresponding values for the Northern fen were -1.4 °C, 511 mm and 700 d.d., respectively. During the study period, 2011 – 2012, the environmental conditions varied both between the Southern and Northern fens and between the two growing seasons (see Supplementary 2 for a detailed description). At the Southern fen, the temperature sum and the cumulative sum of photosynthetic photon flux density (PPFD) were higher, while the water table (WT) was naturally deeper than at the



Northern fen (Southern fen: PPF<sub>D</sub> 5417 and 4362 mol m<sup>-2</sup>, temperature sum 1333 and 1132 °C, average WT 12 cm and 6 cm below surface, for 2011 and 2012, respectively; Northern fen: PPF<sub>D</sub> 3911 and 3940 mol m<sup>-2</sup>, temperature sum 947 and 803 °C, average WT 9 cm and 7cm below surface, for 2011 and 2012, respectively). Both summers had a higher temperature sum than the long-term average, but summer 2012 was cooler, less sunny and wetter than 2011, particularly at the Southern fen.

Both sites were sedge fens. Altogether, the vegetation composition was rather uniform throughout the sites so that the microtopography was not pronounced. Even though the vegetation type was quite similar at the two sites, there were some differences in the species composition. At the Southern fen the field layer was characterized by sedges such as *Carex lasiocarpa*, *C. chordorrhiza* and *C. limosa*, along with dwarf shrubs *Andromeda polifolia* and *Vaccinium oxycoccos* and the herb *Menyanthes trifoliata*. In the moss layer, *Sphagnum papillosum* and *S. flexuosum* were the most abundant species in the Southern fen with small patches of *S. fallax*, *S. subfulvum* and *S. subnitens*. At the Northern fen the vegetation differed so that *C. rostrata* was the most abundant sedge, and *V. oxycoccos* was more abundant than in the Southern fen. In addition, herbs *Equisetum fluviatile* and *Comarum palustre* occurred. The moss layer was patchier than in the Southern fen and consisted mainly of *S. fallax*, *S. riparium* and *S. flexuosum*, along with some *S. jensenii*. In addition, the Northern fen was somewhat richer in surface peat (5-15 cm) calcium, potassium, magnesium and phosphorus, while the Southern fen had more total nitrogen (Peltoniemi et al. 2015). A detailed description of the study sites, experimental design, vegetation patterns and peat characteristics is found in Pearson et al. (2015) and Peltoniemi et al. (2015).

The experimental sites were established in 2008 to test the impacts of warming under different moisture regimes. In both locations, the experimental sites consisted of two moisture regime plots, one with an undisturbed wet moisture regime, and the other with moderately dry regime that was achieved with a shallow, ca. 30 cm deep, drainage ditch. The latter is referred to as the water- level drawdown (WLD) treatment.

At both sites, six sample plots were established within each moisture regime plot as sample plot pairs, so that within each pair one sample plot received no temperature manipulation (i.e. ambient-T) and the other received seasonal artificial warming with open top chambers (OTC). All sample plots were located at similar sedge lawn communities that dominated the fens. The hexagonal OTCs were 60 cm tall with 76 cm long sides (max. diagonal distance of 131 cm). The side panels were inclined 60° to improve the transmittance of solar radiation and help trap heat (Peltoniemi et al. 2015).

Measurements of environmental conditions and leaf area index, and impacts of WLD and warming treatments on them

Instantaneous environmental conditions were measured manually during the CO<sub>2</sub> exchange measurement and recorded continuously with data loggers. Soil temperatures inside the moss canopy (1-2 cm depth), and 5 and 15 cm below the moss surface were measured at each sample plot with a temperature probe right after the CO<sub>2</sub> exchange measurement. Soil temperatures at 5 and 15 cm depths and air temperature at 30 cm height were continuously recorded beside each sample plot at 2h time step (iButton, Maxim Integrated, U.S.) and interpolated to hourly values, and averages of warmed and ambient-T plots were calculated for each treatment combination. The water table depth (WT; relative to the moss surface) was measured manually from permanently installed perforated PVC tubes (diameter ~2cm) beside

each sample plot after the CO<sub>2</sub> exchange measurement, on average once per week.

Additionally, WT was monitored from one location at each water table treatment plot continuously at 1 to 3-hour intervals with data loggers (WT-HR 64K, Intech Instruments Ltd, NZ). The position of each manual WT measurement point was levelled, and based on this information continuous data was created for each point separately. The 1 to 3-hour gaps on the continuous WT data was linearly interpolated into hourly values and hourly treatment averages were calculated. Hourly values of PPFD at the Northern fen were recorded on site, and some longer data gaps during summer 2011 were filled by data from a weather station located 3 km from the site (Kenttäröva); at Southern fen PPFD data from Hyytiälä SMEAR II station (Junninen et al. 2009; ~10km from the site) was used. The continuous WT, temperature, and PPFD data were used to reconstruct the seasonal P<sub>G</sub> and R<sub>ECO</sub> for each sample plot.

The development of leaf area index (LAI) over the growing seasons was measured and modelled by Mäkiranta et al. (2018). Briefly, from each plot, the number of leaves per species was counted and the average leaf size of each species was measured 5 to 7 times per growing season. The species specific LAIs were summed to form a total LAI (LAI<sub>tot</sub>) for each measurement date and sample plot. To reconstruct the seasonal LAI<sub>tot</sub> dynamics, a nonlinear mixed effect model with a log-normal function was fitted to the data with the day number as explanatory factor. We used the fixed part of the model to estimate hourly LAI<sub>tot</sub> for each sample plot over the two growing seasons (Mäkiranta et al. 2018).

OTCs increased the average daily air temperature during the growing season by 1.5 °C at 15 cm above the peat surface. As compared to ambient-T sample plots, the effective temperature sum in the OTCs increased by 320 and 200 degree days in the Southern and Northern fens,

respectively (Fig. S2.1 c). Temperature differences between ambient and OTC plots were not observed in peat layers deeper than 5 cm below the surface. During the two-year period, the WLD plots had on average 6 and 3 cm lower WT than the undisturbed plots in the Southern and Northern fen, respectively (Fig. S2.1 d & e). The treatment impacts on total LAI of vascular plants were rather complex (Fig. S2.2). LAI was decreased by WLD treatment under ambient temperature conditions, but the decrease was somewhat compensated by warming treatment. Under wet regime, warming on the other hand, somewhat decreased LAI<sub>tot</sub>. While the WLD lengthened the growing season to some extent, the seasonal pattern of LAI was rather similar under all treatments (Fig. S2.2).

#### CO<sub>2</sub> exchange measurements

Measurements were done weekly during snow free seasons (May/June – October) 2011 and 2012, that is, third and fourth growing season after the onset of the experiments. At each sample plot, a permanent gas flux measurement plot was established in 2008 by inserting a metal collar (60 × 60 cm in area) that had 30-cm-long sleeve into the peat. Altogether, 24 gas flux measurement plots were included in the study, three per treatment combination per site. CO<sub>2</sub> exchange was measured with a transparent plastic chamber (60x60x30 cm) that was connected to a portable infrared gas analyser (EGM-4, PP Systems, UK). The chamber was equipped with a fan and a thermostatic cooling system that maintained the chamber air temperature within ±2 °C of ambient (Alm et al. 2007). The measurement routine at each measurement plot consisted of four measurements: first, instantaneous CO<sub>2</sub> exchange was measured under stable full light, then under one or two shades that reduced the amount of incoming light by 40–50% and 75–90%, and finally, the chamber was covered with an opaque hood and the CO<sub>2</sub> exchange in the dark was measured. After each measurement that

lasted 90–180s, the chamber was lifted and ventilated to restore the ambient CO<sub>2</sub> concentration. During the measurements, the CO<sub>2</sub> concentration, PPFD and air temperature in the chamber headspace were recorded at 15s intervals.

The net CO<sub>2</sub> exchange (NEE, g CO<sub>2</sub> m<sup>-2</sup> h<sup>-1</sup>) was calculated from the linear change in the CO<sub>2</sub> concentration in the chamber headspace, as a function of the chamber headspace volume and surface area, and the mean chamber air temperature during the measurement. Dark measurements were used as an estimate of instantaneous ecosystem respiration (R<sub>ECO</sub>). Gross photosynthesis (P<sub>G</sub>) in full light and shaded conditions was calculated as NEE+R<sub>ECO</sub>. In our sign convention both P<sub>G</sub> and R<sub>ECO</sub> get positive values and NEE is positive when the ecosystem is a CO<sub>2</sub> sink from the atmosphere.

#### CO<sub>2</sub> exchange modelling

We applied nonlinear mixed-effects modelling to quantify how warming and WLD impacted P<sub>G</sub> and R<sub>ECO</sub>, and to reconstruct these fluxes over the two growing seasons. The model building was based on known properties of the natural process, where the effects of treatments and environmental factors on the model parameters were concurrently analysed and added sequentially to the model in order of importance based on prior studies. The possible predictors of the models included location (Southern vs. Northern fen), WLD treatment, warming treatment (OTC), LAI (sample plot level estimates from the LAItot model described above), WT, air temperature (T<sub>air</sub>) and soil temperature at 5 and 15 cm of depth (T<sub>5</sub> and T<sub>15</sub>, respectively). To account for the self-shading of leaves through Beer-Lambert's law (Wilson 1959) LAI was included in the P<sub>G</sub> model as transformation  $LAI2=1-\exp(-LAI)$ . Temperature was included either as a linear predictor of the parameters or as first and second powers using a transformation  $\max(T, r)$ , which assumes that P<sub>MAX</sub> remains

constant at temperatures below  $r$  ( $^{\circ}\text{C}$ ) and has a second-order polynomial response to temperature above this limit. The limit was found using a grid search.

$P_G$  model was based on the hyperbolic light saturation curve (e.g. Lappi & Oker-Blom 1992):

$$P_{Gijklmn} = \frac{P_{MAXijklmn} PPF_{Dijklmn}}{\alpha_{ijklmn} + PPF_{Dijklmn}} + e_{ijklmn} \quad (1)$$

where the response  $P_{Gijklm}$  is the observed  $P_G$  ( $\text{g CO}_2 \text{ m}^{-2} \text{ h}^{-1}$ ), and the predictor  $PPF_{Dijklm}$  ( $\mu\text{mol m}^{-2} \text{ s}^{-1}$ ) on measurement  $n$  of day  $m$  of year  $l$  of sample plot  $k$  at plot pair  $j$  at moisture regime plot  $i$ . The parameters to be estimated are  $P_{MAXijkl}$  ( $\text{g CO}_2 \text{ m}^{-2} \text{ h}^{-1}$ ) that is the photosynthetic capacity, i.e., the maximum rate of light-saturated gross photosynthesis and  $\alpha_{ijkl}$  ( $\mu\text{mol m}^{-2} \text{ s}^{-1}$ ) that is the maximum quantum yield of  $\text{CO}_2$  assimilation, i.e., light use efficiency at low light. The residual ( $e_{ijklm}$ ) is normally distributed with mean zero and constant variance. Parameters  $P_{MAXijkl}$ , and  $\alpha_{ijkl}$  were written as linear functions of fixed predictors and random effects. These submodels were:

$$P_{MAXijkl} = \beta^{P_{MAX}} \cdot \mathbf{x}_{ijkl}^{P_{MAX}} + a_i^{P_{MAX}} + b_{ij}^{P_{MAX}} + c_{ijk}^{P_{MAX}} + d_{ijkl}^{P_{MAX}} + f_{ijklm}^{P_{MAX}} \quad (2)$$

$$\alpha_{ijkl} = \mu^{\alpha} + a_i^{\alpha} + b_{ij}^{\alpha} + c_{ijk}^{\alpha} + d_{ijkl}^{\alpha} + f_{ijklm}^{\alpha} \quad (3)$$

The predictors ( $\mathbf{x}_{ijkl}^{P_{MAX}}$ ) used in the submodel of  $P_{MAX}$  were location, WLD and warming treatment, LAI2 and Tair using a transformation  $\max(\text{Tair}, 9)$ . We also included interactions between WLD and warming, and between location and warming and between location and the transformations of Tair to allow separate optima for the two locations. The parameter  $\alpha_{ijkl}$  was described by intercept and random effects only (eq. 3), as WLD or warming did not significantly impact it, and there was no reason to expect the experiments to cause such shading that would change  $\alpha_{ijkl}$ .

The  $R_{ECO}$  model was based on the Arrhenius-type function by Lloyd and Taylor (1994):

$$Reco_{ijklm} = R_{10ijklm} \exp \left[ E_{0ijklm} \left( \frac{1}{T_{refijklm} - T_{0ijklm}} - \frac{1}{T_{ijklm} - T_{0ijklm}} \right) \right] + e_{ijklm} \quad (4)$$

where  $R_{ECO\ ijklm}$  is the observed  $R_{ECO}$  ( $\text{g m}^{-2} \text{h}^{-1}$ ) and  $T_{ijklm}$  is the air temperature measured simultaneously with the flux measurements on day  $m$  of year  $l$  at sample plot  $k$  of plot pair  $j$  at moisture regime plot  $i$ . The unit of  $T$  in the Eq. (4) is K.  $T_{refijklm}$  is the reference temperature set at 283.15 K (i.e., 10 °C) and parameter  $T_{0ijkl}$  is the temperature minimum constant at which respiration reaches zero, set at 227.13 K (Lloyd and Taylor, 1994). The parameters to be estimated are  $R_{10ijklm}$  ( $\text{g CO}_2 \text{ m}^{-2} \text{h}^{-1}$ ) that is the soil respiration rate at 10 °C, and  $E_{0ijklm}$  (K) that is an exponential parameter depicting the temperature sensitivity of soil respiration. Parameters  $R_{10ijklm}$  and  $E_{0ijklm}$  were written as linear functions of fixed predictors and random effects. These submodels are:

$$R_{10ijkl} = \beta^{R10} \cdot \mathbf{x}_{ijkl}^{R10} + a_i^{R10} + b_{ij}^{R10} + c_{ijk}^{R10} + d_{ijkl}^{R10} \quad (5)$$

$$E_{0ijkl} = \beta^{E0} \cdot \mathbf{x}_{ijkl}^{E0} + a_i^{E0} + b_{ij}^{E0} + c_{ijk}^{E0} + d_{ijkl}^{E0} \quad (6)$$

The predictors used in the  $R10$  submodel were location, WLD and warming treatment, LAI, WT, T15, interaction between WLD and warming, and interaction between location and warming. The predictors used in the  $E0$  submodel were location, WLD and warming treatment, interaction between WLD and warming, and interaction between location and warming.

For the models of both  $P_G$  and  $R_{ECO}$ , the random effects at each nested level of grouping were assumed to be independent, with mean zero and common variance-covariance matrix. The accuracy of estimated effects were analyzed using conditional F-tests and confidence intervals (Pinheiro and Bates 2000) and Akaike information criterion (AIC). Models were fitted using the nlme package of R (R Core Team 2016), following Pinheiro and Bates (2000). As the data includes rather small number of replicates (especially for the moisture

regime plots) regardless of the extensive investment on data collection, we report the estimated effects and their confidence intervals regardless of their statistical significance. Due to the experimental design, especially due to the low number of WLD treatment replicates, the effect of WLD should be much higher than that of warming to become statistically significant..

### Reconstructing seasonal CO<sub>2</sub> fluxes

We used the P<sub>G</sub> and R<sub>ECO</sub> models (eq. 1-6) to predict the instantaneous (g CO<sub>2</sub> m<sup>-2</sup> h<sup>-1</sup>) fluxes and to compute the seasonal cumulative fluxes. Seasonal net ecosystem CO<sub>2</sub> exchange (NEE) was calculated as the difference between P<sub>G</sub> and R<sub>ECO</sub>.

We reconstructed fluxes for period 1 May to 30 September. We acknowledge that gas exchange occurs also during the time period not included here but we do not want to extrapolate outside the time period when our measurements were made. This period covers the typical growing season of the studied locations. Fluxes were calculated for each sample plot and two-way ANOVA tests were used to compare treatment differences in P<sub>G</sub>, R<sub>ECO</sub> and NEE separately for each year.

## Results

The measured CO<sub>2</sub> exchange

The CO<sub>2</sub> exchange measured under full day light ranged from -0.98 (release) to 1.47 (uptake) g m<sup>-2</sup> h<sup>-1</sup>, with an average of 0.37 g m<sup>-2</sup> h<sup>-1</sup>; the highest uptake was measured at the warmed WLD plot of the Southern fen (Fig. S3.1). The measured R<sub>ECO</sub> ranged from 0.03 to 1.37 g m<sup>-2</sup>



$\text{h}^{-1}$ , with an average of  $0.35 \text{ g m}^{-2} \text{ h}^{-1}$  (Fig. S3.1); highest rates were measured from the WLD plots of both Southern and Northern fen.

#### Modelled gross photosynthesis ( $P_G$ )

$P_G$  was modelled via hyperbolic light response curve (Fig. 1a, d) and the light response curve parameter maximum photosynthesis ( $P_{MAX}$ ) was further explained by treatments and environmental variables. Out of the measured environmental variables,  $P_{MAX}$  was best explained by LAI (Fig. 1 b, e) that was transformed as LAI2, and by air temperature (Fig. 2c, f, Table 1.). The two locations differed from each other, the Northern fen having lower  $P_{MAX}$  (Fig. 1). In addition, the  $P_{MAX}$  of the Southern fen had higher temperature optimum ( $32 \text{ }^\circ\text{C}$ ) than the Northern fen ( $24 \text{ }^\circ\text{C}$ ), which appeared to be less sensitive to variation in temperature (Fig. 2c, f). WLD increased  $P_{MAX}$  especially at Southern fen, and modified the  $P_{MAX}$  response to LAI, so that higher  $P_{MAX}$  was attained with lower LAI in WLD than under wet conditions (Fig. 1b, e). Warming alone had no general impact on  $P_{MAX}$ . However, an interaction between warming and location (Southern vs Northern fen) for  $P_{MAX}$  (Table 2.) indicated that the sites seemed to react differently on warming: In the Northern fen warming slightly increased and in the Southern fen decreased  $P_{MAX}$ .

#### Modelled ecosystem respiration

$R_{ECO}$  increased with increasing air temperature, increasing total leaf area, deepening water table and increasing soil temperature (Fig. 2). The modelled parameter R10 (respiration rate at the air temperature of  $10^\circ\text{C}$ ) increased with increasing LAI<sub>tot</sub>, T15 and deepening measurement-period WT (Table 3). WLD treatment increased R10, while the impacts of

warming treatment and location were negligible (Tables 3 and 4). The temperature sensitivity of soil respiration ( $E_0$ ) was increased by WLD and the Northern fen was less temperature sensitive than Southern fen (Tables 3 and 4). While the impact of warming as such was small, warming had an interaction with WLD. Therefore, the increased sensitivity to temperature caused by WLD alone was diminished by warming (Tables 3 and 4).

#### Seasonal cumulative $P_G$ , $R_{ECO}$ and NEE

The cumulative seasonal (May to September)  $P_G$  was highest at the Southern fen under WLD treatment (Fig. 3) but warming and WLD did not significantly impact  $P_G$  at either site.

Similarly to  $P_G$ , the seasonal  $R_{ECO}$  was highest at the Southern fen under WLD treatment.

Unlike for  $P_G$ , WLD and warming treatment increased seasonal  $R_{ECO}$  in both years at the Southern fen (Fig. 3, ANOVA, warming  $p=0.085$  and  $p=0.028$  and WLD  $p=0.009$  and  $p=0.015$  for years 2011 and 2012, respectively).

The between treatment differences in cumulative NEE were not statistically significant, though the decrease caused by WLD alone at the Southern fen had  $p=0.083$  and  $p=0.07$  at 2011 and 2012. At the Southern fen, warming seemed to decrease the NEE, especially under the WLD treatment (Fig. 4). At the Northern fen, NEE varied only little between the treatments (Fig. 4).

## Discussion

### Impacts of warming under contemporary wet conditions

Effects of warming on peatland CO<sub>2</sub> exchange components have been rather widely studied, but still, the results seem to escape attempts for broad generalizations. Earlier reports from warming experiments on peatlands have given very variable results with increasing or decreasing P<sub>G</sub>, generally increasing R<sub>ECO</sub> and differing responses of NEE (Table S1.1). Contributing to this variability, we did not observe significant warming impacts on P<sub>G</sub>, R<sub>ECO</sub> or NEE in our open, sedge-dominated fens under ambient wet conditions after three to four years warming. No changes in the CO<sub>2</sub> exchange components were observed during the two very first years after the initiation of our experiment either (Pearson et al. 2015). The large variability in results may be due to, e.g., differences in studied peatland site types, dominated by mosses, shrubs or graminoids, in the initial moisture regime, and in the length of the experiments. There are few long-term studies (Table S1.1), even ours should still be considered short-term. While the microbial communities may be modified faster (Peltoniemi et al. 2015), it may take close to a decade before peatland vegetation responds even to more drastic changes in their environment than our experimental modifications (Wiedermann et al. 2007). This lag may well be reflected in the response of the CO<sub>2</sub> exchange. We still need a better understanding of the responses of different vegetation components to increased temperature to be able to draw general conclusions about the potential extent and pace of changes in peatland CO<sub>2</sub> exchange induced by warming under the scenario where these wetlands remain as wet as they are currently. While our study adds valuable components to the metadatabase of warming studies on peatlands, there are still collectively too few replicate studies per peatland type for rigorous meta-analysis or modelling.

As only minor warming impacts on vegetation and especially on the total leaf area had been found for our set-up (Mäkiranta et al. 2018, see also Supplementary 3), it is quite reasonable that warming as such did not significantly alter the CO<sub>2</sub> exchange in our sites. Leaf area is generally an integral component in both P<sub>G</sub> and R<sub>ECO</sub> models (e.g., Laine, Riutta, Juutinen, Väiliranta, & Tuittila, 2009, Järveoja, Nilsson, Gažovič, Crill, & Peichl, 2018), and maximum photosynthesis is primarily driven by species composition and vegetation phenology (Peichl et al 2018). Similarly, LAI was the main driver for both P<sub>G</sub> and R<sub>ECO</sub> models in our study. It seems that the high water table typical of pristine fens dampens the warming impact on vegetation that could otherwise be expected (Mäkiranta et al. 2018). In wet conditions, decomposition is constrained by anoxia, and thus does not allow more nutrients to be released to support any significant increase in growth (Davidson & Janssens, 2006). In long-term warming could have potential to increase growth rate sedges (Elmendorf et al. 2012), but such was not observed within the four study years in our study set-up (Mäkiranta et al. 2018).538-

Another consequence of the wet conditions is that the low availability of oxygen also limits soil respiration. While the warming of the air obtained with the OTCs may enhance plant respiration, soil organic matter decomposition that is constrained by anoxia may not respond to an extent that would be seen as higher heterotrophic soil respiration. Further, the minor changes in the vegetation may not affect the quality and quantity of plant litter that are the most important factors influencing decomposition, and thereby heterotrophic respiration, in peatlands (Strakova et al. 2012). More so, as the experimental warming did not impact the soil temperature it may be expected that soil respiration is not affected. Varying impacts on soil temperatures by warming with OTCs have been observed earlier (e.g, Buttler et al. 2015).

The constant, albeit slow water inflow across our fen sites may have maintained soil temperatures below 5 cm depth under the OTCs similar to the surrounding fen. Also,

increased evapotranspiration under the OTCs may in principle have had a soil cooling impact, as discussed by, e.g., Buttler et al. (2015). Whether or not fen soils become warmer under climate change, which at least to some extent will depend on the temperature of the groundwater inputs, may influence the future development of these ecosystems. However, under wet conditions, anoxia will still constrain decomposition.

### Impacts of warming under dry conditions

Warming under dry conditions increased ecosystem respiration more than WLD alone. At the Southern fen, the increase in  $R_{\text{ECO}}$  caused a decrease in seasonal NEE. In the same study set up, these changes in  $\text{CO}_2$  exchange were not yet observed during the two first years of the experiment (Pearson et al. 2015). Vegetation structure was altered by the combined warming and drying (Mäkiranta et al. 2018), and the  $\text{CO}_2$  exchange components may have been modified through these changes. Especially the shrub *Betula nana* benefited more from warming under dry conditions than the dry conditions as such (Mäkiranta et al. 2018), which is interesting, as in another warming experiment the increased growth of this species has been connected to large release of labile C from plant roots (Voigt et al. 2018). Labile C is not only an important energy source for decomposers but can also enhance the decomposition of more recalcitrant carbon compounds (de Vries & Caruso, 2016). The increased abundance of *Betula nana* after some years of warming under dry conditions could thus be one reason for the simultaneous increase in  $R_{\text{ECO}}$ . Other studies that have considered the warming impact under experimentally dried field conditions at peatlands (Table S1.1; Oechel et al. 1998; Chivers et al. 2009; Munir et al. 2015) mainly report increased respiration and decreased NEE, similarly to the Southern fen of our study. Interestingly, results from the Northern fen contradict this pattern. At that site, NEE remained stable even following warming under dry

conditions. Whether this difference depends on the northern, colder location, or the still quite high WT remains unresolved, unfortunately. In both sites WLD as such did cause an increase in temperature sensitivity ( $E_0$ ), but this effect was weakened by warming. Such acclimatization of temperature sensitivity has been observed previously from warming experiment from several ecosystem types, but is not a consistent phenomenon (Luo, Wan, Hui, & Wallace, 2001, Carey et al. 2016).

#### Direct impacts of drying

Earlier predictions that suggested 8 to 22 cm drop of water table (Gorham, 1991; Roulet, Moore, Bubier, & Lafleur, 1992) did not account for the possible increase in precipitation (e.g., IPCC, 2013; Screen, 2013; Wu & Roulet, 2014). Therefore, the moderate WLD in the studied sites is quite realistic in terms of the latest climate change projections. In the Southern fen, WLD increased photosynthesis and respiration, which is in line with most previous studies (Table S1.1.). This impact of WLD on respiration can be expected as oxic conditions are a prerequisite for efficient soil organic matter decomposition (Laiho 2006). In addition, the temperature sensitivity of respiration increased after WLD. Although the changes in vegetation structure were relatively small (WLD decreased maximum leaf area but not the aboveground biomass production; forbs were replaced by evergreen shrubs, but the cover of sedges that are the major plant functional type at the sites remained rather stable; Mäkiranta et al. 2018)) the new community had higher photosynthesis. The higher oxygen and nutrient availability to plant roots in drier conditions may have enhanced the photosynthetic performance of the plants. Obviously, the WLD in this study was moderate enough not to cause a severe moisture stress that would have reduced the rate of photosynthesis, as has been observed in some studies (Alm et al. 1999; Griffis, Rouse, & Waddington, 2000; Weltzin et al. 2000).

## Differences between the two fens

Against our expectations, the treatment impacts on CO<sub>2</sub> exchange were stronger at the Southern than at the Northern fen. Northern ecosystems are often considered to be more temperature limited and therefore more sensitive to climatic changes (Post et al. 2009; Seddon, Macias-Fauria, Long, Benz, & Willis, 2016). Further, in our study set-up, it was previously observed that the microbial community of the Northern fen reacted to WLD or combined WLD and warming treatments more strongly than that of the Southern fen (Peltoniemi et al. 2015). Despite this, NEE remained stable in the Northern fen, but decreased in the Southern fen, and the difference was evident already during the first years since commencement of the experiment (Pearson et al. 2015). The difference in the WLD impact between the two sites may explain part of this response. Despite the similar drainage ditches, the realized WLD at the two sites were on average 6 and 3 cm, which means an average WT of 15 and 11 cm below moss surface at WLD plots of Southern and Northern fen, respectively. It was more difficult to drain the northern fen, where the lateral flow of water into the site is more abundant and more continuous than in the southern fen. With only two study sites it is unfortunately not possible to say whether the differences between the sites are caused by differences in WLD or climate, or by site specific factors.

In general, the measured rates of the different CO<sub>2</sub> exchange components ( $P_G$ ,  $R_{ECO}$ , NEE) of both fens fit within the range measured previously from boreal and sub-arctic fens, with the Southern fen rates being at the high end of the range (e.g. Alm et al. 1997; Griffis et al. 2000; Aurela, Laurila, & Tuovinen, 2002; Heikkinen, Maljanen, Aurela, Hargreaves, & Martikainen, 2002; Riutta et al. 2007a,b; Peichl et al. 2014). Of the two sedge fens studied here, the Southern one showed higher CO<sub>2</sub> sequestration under current weather conditions during both of the two study seasons. In line with the reckoning that moist conditions are

advantageous for peatland CO<sub>2</sub> sequestration, NEE was somewhat higher during the wetter and cooler year 2012 than during 2011.

Moderate environmental change did not lead to regime shift

Our results indicate that change in WT is likely to be, in the nearest future, a stronger driver of CO<sub>2</sub> exchange in northern sedge fens than warming. Both P<sub>G</sub> and R<sub>ECO</sub> were more impacted by WLD than warming. When combining our NEE values with the slightly reduced CH<sub>4</sub> emissions (Peltoniemi et al. 2016), the results suggest that the current moderate warming under the ambient WT regime will lead to slightly higher C sequestration in sedge fens, while under the WLD scenario the C sequestration may remain rather stable. Our results imply that in case of moderate environmental change the fen ecosystem may be able to adapt within its regime and maintain its functions. However, to define the level of change in temperature and water level needed for the regime shift, there is clearly a need for more studies and a data compilation from peatlands with different nutrient status and vegetation structures.

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## References

- Alm, J., Talanov, A., Saarnio, S., Silvola, J., Ikkonen, E., Aaltonen, H., Nykänen, H. & Martikainen, P. J. (1997). Reconstruction of the carbon balance for microsites in a boreal oligotrophic pine fen, Finland. *Oecologia*, 110(3), 423-431.
- Alm, J., Schulman, L., Walden, J., Nykänen, H., Martikainen, P. J., & Silvola, J. (1999). Carbon balance of a boreal bog during a year with an exceptionally dry summer. *Ecology*, 80(1), 161-174.
- Alm, J., Shurpali, N. J., Tuittila, E. S., Laurila, T., Maljanen, M., Saarnio, S., & Minkkinen, K. (2007). Methods for determining emission factors for the use of peat and peatlands flux measurements and modelling. *Boreal environment research*, 12, 85–100.
- Andersen, R., Poulin, M., Borcard, D., Laiho, R., Laine, J., Vasander, H., & Tuittila E.-T. 2011: Environmental control and spatial structures in peatland vegetation. *Journal of Vegetation Science*, 22, 878-890
- Arzhanov, M. M., Eliseev, A. V., & Mokhov, I. I. (2012). A global climate model based, Bayesian climate projection for northern extra-tropical land areas. *Global and Planetary Change*, 86, 57-65.
- Aurela, M., Laurila, T., & Tuovinen, J. P. (2002). Annual CO<sub>2</sub> balance of a subarctic fen in northern Europe: importance of the wintertime efflux. *Journal of Geophysical Research: Atmospheres*, 107(D21), ACH-17.

Bragazza, L., Buttler, A., Robroek, B. J., Albrecht, R., Zaccone, C., Jasey, V. E., & Signarbieux, C. (2016). Persistent high temperature and low precipitation reduce peat carbon accumulation. *Global Change Biology*, 22(12), 4114-4123.

Bragazza, L., Parisod, J., Buttler, A., & Bardgett, R. D. (2013). Biogeochemical plant–soil microbe feedback in response to climate warming in peatlands. *Nature Climate Change*, 3(3), 273.

Buttler, A., Robroek, B. J., Laggoun- Défarge, F., Jasey, V. E., Pochelon, C., Bernard, G., ... & Bragazza, L. (2015). Experimental warming interacts with soil moisture to discriminate plant responses in an ombrotrophic peatland. *Journal of vegetation science*, 26(5), 964-974.

Carey, J. C., Tang, J., Templer, P. H., Kroeger, K. D., Crowther, T. W., Burton, A. J., ... & Jiang, L. (2016). Temperature response of soil respiration largely unaltered with experimental warming. *Proceedings of the National Academy of Sciences*, 113(48), 13797-13802.

Chimner, R. A., Pypker, T. G., Hribljan, J. A., Moore, P. A., & Waddington, J. M. (2017). Multi-decadal changes in water table levels alter peatland carbon cycling. *Ecosystems*, 20(5), 1042-1057.

Chivers, M. R., Turetsky, M. R., Waddington, J. M., Harden, J. W., & McGuire, A. D. (2009). Effects of experimental water table and temperature manipulations on ecosystem CO<sub>2</sub> fluxes in an Alaskan rich fen. *Ecosystems*, 12(8), 1329-1342.

Cornelius, C., Heinichen, J., Drösler, M., & Menzel, A. (2014). Impacts of temperature and water table manipulation on grassland phenology. *Applied vegetation science*, 17(4), 625-635.

Davidson, E. A., & Janssens, I. A. (2006). Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. *Nature*, 440(7081), 165.

de Vries, F. T., & Caruso, T. (2016). Eating from the same plate? Revisiting the role of labile carbon inputs in the soil food web. *Soil Biology and Biochemistry*, 102, 4-9.

Dieleman, C. M., Branfireun, B. A., McLaughlin, J. W., & Lindo, Z. (2015). Climate change drives a shift in peatland ecosystem plant community: implications for ecosystem function and stability. *Global change biology*, 21(1), 388-395.

Dorrepaal, E., Toet, S., van Logtestijn, R. S., Swart, E., van de Weg, M. J., Callaghan, T. V., & Aerts, R. (2009). Carbon respiration from subsurface peat accelerated by climate warming in the subarctic. *Nature*, 460(7255), 616-619.

Elmendorf, S. C., Henry, G. H., Hollister, R. D., Björk, R. G., Bjorkman, A. D., Callaghan, T. V., Collier, L. S., Cooper, E. J., Cornelissen, J. H., Day, T. A., Fosaa, A. M., Gould, W. A., Grétarsdóttir, J., Harte, J., Hermanutz, L., Hik, D. S., Hofgaard, A., Jarrad, F., Jónsdóttir, I. S., Keuper, F., Klanderud, K., Klein, J. A., Koh, S., Kudo, G., Lang, S. I., Loewen, V., May, J. L., Mercado, J., Michelsen, A., Molau, U., Myers-Smith, I. H., Oberbauer, S. F., Pieper, S., Post, E., Rixen, C., Robinson, C. H., Schmidt, N. M., Shaver, G. R., Stenström, A., Tolvanen, A., Totland, Ø., Troxler, T., Wahren, C., Webber, P. J., Welker, J. M. and Wookey, P. A. (2012), Global assessment of experimental climate warming on tundra vegetation: heterogeneity over space and time. *Ecology Letters*, 15, 164-175.

Eskelinen, A., & Harrison, S. (2014). Exotic plant invasions under enhanced rainfall are constrained by soil nutrients and competition. *Ecology*, 95(3), 682-692.

Gill, A. L., Giasson, M. A., Yu, R., & Finzi, A. C. (2017). Deep peat warming increases surface methane and carbon dioxide emissions in a black spruce- dominated ombrotrophic bog. *Global change biology*, 23(12), 5398-5411.

Gong, J., Kellomäki, S., Wang, K., Zhang, C., Shurpali, N., & Martikainen, P. J. (2013). Modeling CO<sub>2</sub> and CH<sub>4</sub> flux changes in pristine peatlands of Finland under changing climate conditions. *Ecological modelling*, 263, 64-80.

Gore AJP (1983) Introduction. In: Gore AJP (ed) Ecosystems of the world, vol 4a. Elsevier, Amsterdam, pp 1-34

Gorham, E. (1991). Northern peatlands, role in the carbon cycle and probable responses to climatic warming. *Ecological applications*, 1(2), 182-195.

Griffis, T. J., Rouse, W. R., & Waddington, J. M. (2000). Scaling net ecosystem CO<sub>2</sub> exchange from the community to landscape- level at a subarctic fen. *Global Change Biology*, 6(4), 459-473.

Heikkinen, J. E., Maljanen, M., Aurela, M., Hargreaves, K. J., & Martikainen, P. J. (2002). Carbon dioxide and methane dynamics in a sub- Arctic peatland in northern Finland. *Polar Research*, 21(1), 49-62.

Jaatinen, K., Fritze, H., Laine, J., & Laiho, R. (2007). Effects of short- and long- term water- level drawdown on the populations and activity of aerobic decomposers in a boreal peatland. *Global Change Biology*, 13(2), 491-510.

Johnson, C. P., Pypker, T. G., Hribljan, J. A., & Chimner, R. A. (2013). Open top chambers and infrared lamps, A comparison of heating efficacy and CO<sub>2</sub>/CH<sub>4</sub> dynamics in a northern Michigan peatland. *Ecosystems*, 16(5), 736-748.

Jones, H. G. (1992). *Plants and microclimate* 2nd edn. *Cambridge University Press*, Cambridge, UK. 428pp

Joosten, H., Tannenberger, F. & Moen, A. (2017). *Mires and peatlands of Europe* (780pp). Schweizerbart Science Publishers,

Junninen, H., Lauri, A., Keronen, P., Aalto, P., Hiltunen, V., Hari, P., Kulmala, M. 2009.

Smart-SMEAR: on-line data exploration and visualization tool for SMEAR stations. *Boreal Environment Research* 14, 447–457.

Järveoja, J., Nilsson, M. B., Gažovič, M., Crill, P. M., & Peichl, M. (2018). Partitioning of the net CO<sub>2</sub> exchange using an automated chamber system reveals plant phenology as key control of production and respiration fluxes in a boreal peatland. *Global Change Biology*, 24, 3436-3451.

Kjellström, E., Nikulin, G., Strandberg, G., Christensen, O. B., Jacob, D., Keuler, K., Lenderink, G., van Meijgaard, E., Schar, C., Somot, S., & Sørland, S. L. Teichmann, C., & Vautard, R. (2018). European climate change at global mean temperature increases of 1.5 and 2 degrees C above pre-industrial conditions as simulated by the EURO-CORDEX regional climate models. *Earth System Dynamics*, 9(2), 459-478.

Komulainen, V. M., Tuittila, E. S., Vasander, H., & Laine, J. (1999). Restoration of drained peatlands in southern Finland, initial effects on vegetation change and CO<sub>2</sub> balance. *Journal of applied ecology*, 36(5), 634-648.

Laiho, R. (2006). Decomposition in peatlands: Reconciling seemingly contrasting results on the impacts of lowered water levels. *Soil Biology and Biochemistry*, 38(8), 2011-2024.

Laine, A., Riutta, T., Juutinen, S., Välianta, M., & Tuittila, E. S. (2009). Acknowledging the spatial heterogeneity in modelling/reconstructing carbon dioxide exchange in a northern aapa mire. *Ecological Modelling*, 220(20), 2646-2655.

Laine, J., Vasander, H., & Laiho, R. (1995). Long-term effects of water level drawdown on the vegetation of drained pine mires in southern Finland. *Journal of Applied Ecology*, 32, 785-802.

Lappi, J. & Oker-Blom, P. (1992.) Characterizing photosynthetic radiation response or other output function as a mean of element responses. *J. Theor. Biol.*, 154, 371–389.

Lehtonen, I., Ruosteenoja, K. and Jylhä, K., (2014). Projected changes in European extreme precipitation indices on the basis of global and regional climate model ensembles.

*International Journal of Climatology*, 34(4), pp.1208-1222.

Lloyd, J., & Taylor, J. A. (1994). On the temperature dependence of soil respiration.

Functional ecology, 8, 315-323.

Loisel, J., Yu, Z., Beilman, D. W., Camill, P., Alm, J., Amesbury, M. J., ... & Belyea, L. R.

(2014). A database and synthesis of northern peatland soil properties and Holocene carbon and nitrogen accumulation. *the Holocene*, 24(9), 1028-1042.

Luo, Y., Wan, S., Hui, D., & Wallace, L. L. (2001). Acclimatization of soil respiration to warming in a tall grass prairie. *Nature*, 413(6856), 622.

Maljanen, M., Sigurdsson, B. D., Guðmundsson, J., Óskarsson, H., Huttunen, J. T., &

Martikainen, P. J. (2010). Greenhouse gas balances of managed peatlands in the Nordic countries—present knowledge and gaps. *Biogeosciences*, 7(9), 2711-2738.

Mathijssen, P., Tuovinen, J. P., Lohila, A., Aurela, M., Juutinen, S., Laurila, T., Niemelä, E.,

Tuittila, E.-S., & Väiliranta, M. (2014). Development, carbon accumulation, and radiative forcing of a subarctic fen over the Holocene. *The Holocene*, 24(9), 1156-1166.

Medlyn, B. E., Dreyer, E., Ellsworth, D., Forstreuter, M., Harley, P. C., Kirschbaum, M. U.

F., Le Roux, X., Montpied, P., Strassmeyer, J., Walcroft, A., Wang, K. & Loustau, D.

(2002). Temperature response of parameters of a biochemically based model of photosynthesis. II. A review of experimental data. *Plant, Cell & Environment*, 25(9), 1167-1179.

Minkinen, K., Laine, J., Shurpali, N. J., Mäkiranta, P., Alm, J., & Penttilä, T. (2007).

Heterotrophic soil respiration in forestry-drained peatlands. *Boreal Environmental Research* 12, 115–126.

Monier, E., Sokolov, A., Schlosser, A., Scott, J., & Gao, X. (2013). Probabilistic projections of 21st century climate change over Northern Eurasia. *Environmental Research Letters*, 8(4), 045008.

Munir, T. M., & Strack, M. (2014). Methane flux influenced by experimental water table drawdown and soil warming in a dry boreal continental bog. *Ecosystems*, 17(7), 1271-1285

Munir, T. M., Perkins, M., Kaing, E., & Strack, M. (2015). Carbon dioxide flux and net primary production of a boreal treed bog: Responses to warming and water-table-lowering simulations of climate change. *Biogeosciences*, 12, 1091–1111

Mäkiranta, P., Laiho, R., Mehtätalo, L., Straková, P., Sormunen, J., Minkkinen, K., Penttilä, T., Fritze, H., & Tuittila, E. S. (2018). Responses of phenology and biomass production of boreal fens to climate warming under different water-table level regimes. *Global Change Biology*, 24, 944–956.

Nijp, J. J., Limpens, J., Metselaar, K., van der Zee, S. E. A. T. M., Berendse, F. and Robroek, B. J. M. (2014). Can frequent precipitation moderate the impact of drought on peatmoss carbon uptake in northern peatlands?. *New Phytologist*, 203(1): 70–80.

Oechel, W. C., Vourlitis, G. L., Hastings, S. J., Ault, R. P. & Bryant, P. (1998). The effects of water table manipulation and elevated temperature on the net CO<sub>2</sub> flux of wet sedge tundra ecosystems. *Global Change Biology*, 4: 77-90.

Pal, J.S., Giorgi, F., & Bi, X. (2004). Consistency of recent European summer precipitation trends and extremes with future regional climate projections. *Geophysical Research Letters* 31(13), <https://doi.org/10.1029/2004GL019836>

Pearson, M., Penttilä, T., Harjunpää, L., Laiho, R., Laine, J., Sarjala, T., Silvan, K. & Silvan, N. (2015). Effects of temperature rise and water-table-level drawdown on greenhouse gas fluxes of boreal sedge fens. *Boreal environment research* 20: 489–505.

Peichl, M., Öquist, M., Löfvenius, M. O., Ilstedt, U., Sagerfors, J., Grelle, A., Lindroth, A., & Nilsson, M. B. (2014). A 12-year record reveals pre-growing season temperature and water table level threshold effects on the net carbon dioxide exchange in a boreal fen. *Environmental Research Letters*, 9(5), 055006.

Peichl, M., Gažovič, M., Vermeij, I., De Goede, E., Sonnentag, O., Limpens, J., & Nilsson, M. B. (2018). Peatland vegetation composition and phenology drive the seasonal trajectory of maximum gross primary production. *Scientific reports*, 8(1), 8012.

Peltoniemi, K., Laiho, R., Juottonen, H., Kiikkilä, O., Mäkiranta, P., Minkkinen, K., Pennanen, T., Penttilä, T., Sarjala, T., Tuittila, E.-S., Tuomivirta, T., & Fritze, H. (2015). Microbial ecology in a future climate: effects of temperature and moisture on microbial communities of two boreal fens. *FEMS Microbiology Ecology*, 91(7).

Peltoniemi, K., Laiho, R., Juottonen, H., Bodrossy, L., Kell, D. K., Minkkinen, K., ... & Tuittila, E. S. (2016). Responses of methanogenic and methanotrophic communities to warming in varying moisture regimes of two boreal fens. *Soil Biology and Biochemistry*, 97, 144-156.

Post, E., Forchhammer, M. C., Bret-Harte, M. S., Callaghan, T. V., Christensen, T. R., Elberling, B., et al., (2009). Ecological dynamics across the Arctic associated with recent climate change. *Science*, 325(5946), 1355-1358.

Prowse, T. D., Wrona, F. J., Reist, J. D., Gibson, J. J., Hobbie, J. E., Lévesque, L. M., & Vincent, W. F. (2006). Climate change effects on hydroecology of Arctic freshwater ecosystems. *AMBIO: A Journal of the Human Environment*, 35(7), 347-358.

Riutta, T., Laine, J., Aurela, M., Rinne, J., Vesala, T., Laurila, T., Haapanala, S., Pihlatie, M. & Tuittila, E.-S. 2007: Spatial variation in plant community functions regulates carbon gas dynamics in a boreal fen ecosystem. *Tellus* 59B: 838-852. doi: 10.1111/j.1600-0889.2007.00302.x



Riutta, T., Laine, J., & Tuittila, E. S. (2007). Sensitivity of CO<sub>2</sub> exchange of fen ecosystem components to water level variation. *Ecosystems*, 10(5), 718-733.

Roulet, N. T. (1991). Surface level and water table fluctuations in a subarctic fen. *Arctic and Alpine Research*, 303-310.

Roulet, N., Moore, T. I. M., Bubier, J., & Lafleur, P. (1992). Northern fens: methane flux and climatic change. *Tellus B*, 44(2), 100-105.

Ruuhijärvi, R. (1982). Mire complex types in Finland. (In) Laine, J (Ed.) Peatlands and their utilization in Finland. Finnish Peatland Society and Finnish National Committee of the International Peat Society, Helsinki. 24-28 pp.

Screen, J. A. (2013). Influence of Arctic sea ice on European summer precipitation. *Environmental Research Letters*, 8(4), 044015.

Seddon, A. W., Macias-Fauria, M., Long, P. R., Benz, D., & Willis, K. J. (2016). Sensitivity of global terrestrial ecosystems to climate variability. *Nature*, 531(7593), 229–232.

Silvola, J., Alm, J., Ahlholm, U., Nykanen, H., & Martikainen, P. J. (1996). CO<sub>2</sub> fluxes from peat in boreal mires under varying temperature and moisture conditions. *Journal of Ecology*, 84, 219-228.

Singh, J. S., & Gupta, S. R. (1977). Plant decomposition and soil respiration in terrestrial ecosystems. *The botanical review*, 43(4), 449-528

Sottocornola, M., Laine, A., Kiely, G., Byrne, K. A., & Tuittila E. S. (2009). Vegetation and environmental variation in an Atlantic blanket bog in South-western Ireland. *Plant Ecology*, 203, 69–81.

Straková, P., Penttilä, T., Laine, J., & Laiho, R. (2012). Disentangling direct and indirect effects of water table drawdown on above- and belowground plant litter decomposition: consequences for accumulation of organic matter in boreal peatlands. *Global Change Biology*, 18(1), 322-335.

Thormann, M. N., Bayley, S. E., & Szumigalski, A. R. (1997). Effects of hydrologic changes on aboveground production and surface water chemistry in two boreal peatlands in Alberta:

Implications for global warming. *Hydrobiologia*, 362(1-3), 171-183.

Turetsky, M. R., Treat, C. C., Waldrop, M. P., Waddington, J. M., Harden, J. W., & McGuire, A. D. (2008). Short- term response of methane fluxes and methanogen activity to water table and soil warming manipulations in an Alaskan peatland. *Journal of Geophysical Research, Biogeosciences*, 113(G3).

Ward, S. E., Ostle, N. J., Oakley, S., Quirk, H., Henrys, P. A., & Bardgett, R. D. (2013). Warming effects on greenhouse gas fluxes in peatlands are modulated by vegetation composition. *Ecology letters*, 16(10), 1285-1293.

Weltzin, J. F., Bridgham, S. D., Pastor, J., Chen, J., & Harth, C. (2003). Potential effects of warming and drying on peatland plant community composition. *Global Change Biology*, 9(2), 141-151.

Weltzin, J. F., Pastor, J., Harth, C., Bridgham, S. D., Updegraff, K., & Chapin, C. T. (2000). Response of bog and fen plant communities to warming and water- table manipulations. *Ecology*, 81(12), 3464-3478.

Wiedermann, M. M., Nordin, A., Gunnarsson, U., Nilsson, M. B., & Ericson, L. (2007). Global change shifts vegetation and plant–parasite interactions in a boreal mire. *Ecology*, 88(2), 454-464.

Wilson, J. W. (1959). Analysis of the spatial distribution of foliage by two- dimensional point quadrats. *New phytologist*, 58(1), 92-99.

Voigt, C., Lamprecht, R. E., Marushchak, M. E., Lind, S. E., Novakovskiy, A., Aurela, M., Martikainen, P. J. & Biasi, C. (2017). Warming of subarctic tundra increases emissions of all three important greenhouse gases—carbon dioxide, methane, and nitrous oxide. *Global Change Biology*, 23(8), 3121-3138.

Wu, J., & Roulet, N. T. (2014). Climate change reduces the capacity of northern peatlands to absorb the atmospheric carbon dioxide: The different responses of bogs and fens. *Global Biogeochemical Cycles*, 28(10), 1005-1024.

Yu, Z. C. (2012). Northern peatland carbon stocks and dynamics: a review. *Biogeosciences*, 9(10), 4071-4085.

## Tables

Table 1. ANOVA results of the nonlinear mixed effect model, of Gross Photosynthesis (Eq. 1-3). LAI2 is the plot level modelled leaf area transformed as  $1-\exp(-\text{LAI})$ , WLD= water level drawdown experiment, Warming = warming treatment with OTC's.

		numDF	denDF	F-value	p-value
PMAx	LAI2	1	711	414.19	0.000
	Air Temperature	4	711	29.54	0.000
	WLD	2	711	2.46	0.087
	Warming	3	711	1.98	0.115

Table 2. Parameter estimates with lower and upper confidence intervals, and random effects of the nonlinear mixed effect model of Gross photosynthesis ( $P_G$ ). LAI2 = is the plot level modelled leaf area transformed as  $\ln(1-\exp(-LAI))$ . Air temperature is described by first and second powers of air temperature using a transformation  $\max(T, 9)$ , which assumes that  $P_{MAX}$  remains constant at temperatures below 9 °C and has a second-order polynomial response to temperature above this limit ( $p_{\max}(T, 9)$  and  $I(p_{\max}(T, 9)^2)$ ). Location separates Southern (So Fen) and Northern (No Fen) fens. WLD denotes for the water level drawdown experiment and Warming to OTC warming experiment. The model includes interaction between location and temperature and between location and warming. In these cases, the estimates are given separately for both locations.

Fixed part		Estimate	Lower	Upper	
$\alpha$	Intercept	216.452	192.917	239.988	
P <sub>MAX</sub>	Location South	-0.843	-1.169	-0.517	
	Location North	-0.232	-0.495	0.030	
	LAI2	1.555	1.405	1.704	
	$p_{\max}(T, 9)$ South	0.097	0.070	0.124	
	$p_{\max}(T, 9)$ North	0.045	0.020	0.070	
	$I(p_{\max}(T, 9)^2)$ South	-0.002	-0.002	-0.001	
	$I(p_{\max}(T, 9)^2)$ North	-0.001	-0.002	0.000	
	WLD	0.171	0.020	0.321	
	WLD x Warming	-0.090	-0.244	0.063	
	Warming South	-0.066	-0.197	0.064	
	Warming North	0.085	-0.048	0.219	
Random part	Moisture regime plot ( $a_i$ )	Plot pair in moisture regime plot ( $b_{ij}$ )	Sample plot in plot pair ( $c_{ijk}$ )	Year in sample plot ( $d_{ijkl}$ )	Day in year ( $f_{ijklm}$ )
var(P <sub>max</sub> )	0.000	$0.073^2$	$0.090^2$	$0.081^1$	$0.203^2$
var( $\alpha$ )	0.000	$28.164^2$	$16.821^2$	-	-
corr(P <sub>max</sub> , $\alpha$ )	0.000	-0.277	1	-	-
Error variance	$0.116^2$				

Table 3. ANOVA results of the nonlinear mixed effect model for  $R_{ECO}$  (Eq. 4-7) that is based on the Arrhenius-type function by Lloyd and Taylor (1994) at which air temperature is used as the explanatory variable. LAI = is the plot level modelled leaf area, WT= water table level, T\_15 = soil temperature at 15 cm depth, WLD= water level drawdown experiment, Location = southern or northern fen, Warming = warming treatment with OTC's.

	numDF	denDF	F-value	p-value
LAI	1	547	55.65	0.000
WT	1	547	7.71	0.006
T15	1	547	57.12	0.000
WLD on all	4	547	6.55	0.000
WLD on R10	2	547	5.20	0.006
WLD on E0	2	547	4.24	0.015
Warming on all	6	547	2.85	0.010
Warming on R10	3	547	2.02	0.110
Warming on E0	3	547	4.72	0.003

Table 4. Parameter estimates and random effects of the nonlinear mixed effect model for Reco (Eq. 4-7). R10 and E0 are the parameters of the Arrhenius-type function by Lloyd and Taylor (1994) at which air temperature is used as the explanatory variable. LAI = is the plot level modelled leaf area, WT= water table level, T\_15 = soil temperature at 15 cm depth, WLD= water level drawdown experiment, Location = southern or northern fen, Warming = warming treatment with OTC's.

		Value	Lower	Upper
R10	Location So Fen	0.053	0.021	0.086
	Location No Fen	0.053	0.021	0.086
	LAI	0.067	0.050	0.084
	WT	0.002	0.001	0.003
	T_15	0.007	0.005	0.009
	WLD	0.035	-0.002	0.072
	Warming South	0.001	-0.022	0.023
	Warming North	0.002	-0.019	0.023
	WLD: Warming	0.025	-0.002	0.053
E0	Location South	201.64	170.62	232.65
	Location North	159.55	127.57	191.54
	WLD	41.32	12.85	69.79
	Warming South	-13.59	-44.67	17.48
	Warming North	13.95	-19.83	47.72
	WLD: Warming	-44.71	-81.46	-7.96
Random part	Moisture regime plot	Plot pair in moisture regime plot	Sample plot in plot pair	Year in sample plot
sd(R10)	0.009	0.022	0.010	0.007
sd(E0)	3.61	5.89	-	-
corr(R10, E0)	-1.00	-0.509	-	-
Residual standard error	0.187 <sup>2</sup> *0.801			

## Figure captions

Fig 1. Visualization of the types of responses used in the  $P_G$  model (Eq1-3, Table 1 and 2).

Adjusted response of  $P_G$  to photosynthetic photonflux density (PPFD), total leaf area ( $LAI_{tot}$ ) and air temperature ( $T_{air}$ ) in the Southern fen (panels a, b and c) and in the Northern fen (panels d, e and f), respectively. The curves show such prediction of the model where one factor at a time is allowed to vary within the true range of the data set and the others are set constant. The used constants were: PPFD = maximum measured values 2052 and 1467  $\mu\text{mol m}^{-2}\text{s}^{-1}$  for Southern and Northern fen, respectively,  $LAI_{tot}$  = maximum value of each WDL x warming x site combination, and  $T_{air}$  = optimum temperature of each location (35 and 25 °C for Southern and Northern fen).

Fig 2. Visualization of the types of responses used in the  $R_{ECO}$  model (Eq 4-6, Tables 3 and 4). Adjusted response of  $R_{ECO}$  to Air temperature ( $T_{air}$ ), total leaf area ( $LAI_{tot}$ ), water table depth (WT) and soil temperature at 15 cm depth ( $T_{soil}$ ) in Southern fen (panels a, b, c and d) and in Northern fen (panels e, f, g and h), respectively. The curves show such prediction of the model where one factor at a time is allowed to vary within the true range of the data set and the others are set constant. The used constants were:  $T_{air}$  and WT = maximum measured from the location,  $LAI_{tot}$  = the maximum value of each WDL x warming x site combination,  $T_{soil}$  = mean of the measured values at each location. The WT values indicate the depth of the water table from the moss surface, i.e. higher values indicate drier conditions.

Figure 3. Seasonal (May to September) cumulative gross photosynthesis ( $P_G$ ) and ecosystem respiration, with standard errors, under warming and water table treatments at Southern (So) and Northern (No) fen during years 2011 and 2012. Warming was induced by open top chambers and dry conditions by experimental water level drawdown (WLD))

Figure 4. Seasonal (May to September) cumulative net ecosystem  $CO_2$  exchange, with standard errors, under warming and water table treatments at Southern (So) and Northern (No) fen during years 2011 and 2012. Warming was induced by open top chambers and dry conditions by experimental water level drawdown (WLD).







