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Direct and indirect climate change effects on carbon dioxide fluxes in a thawing boreal forest-wetland landscape

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Abstract

In the sporadic permafrost zone of northwestern Canada, boreal forest carbon dioxide (CO_2) fluxes will be altered directly by climate change through changing meteorological forcing and indirectly through changes in landscape functioning associated with thaw-induced collapse-scar bog ("wetland") expansion. However, their combined effect on landscape-scale net ecosystem CO_2 exchange (NEE_{LAND}), resulting from changing gross primary productivity (GPP) and ecosystem respiration (ER), remains unknown. Here, we quantify indirect land cover change impacts on NEE_{LAND} and direct climate change impacts on modeled temperature- and light-limited NEE_{LAND} of a boreal forest-wetland landscape. Using nested eddy covariance flux towers, we find both GPP and ER to be larger at the landscape- compared to the wetland-level. However, annual NEE_{LAND} (-20 g C m^{-2}) and wetland NEE (-24 g C m^{-2}) were similar, suggesting negligible wetland expansion effects on NEE_{LAND}. In contrast, we find non-negligible direct climate change impacts when modeling NEE_{LAND} using projected air temperature and incoming shortwave radiation. At the end of the 21st century, modeled GPP mainly increases in spring and fall due to reduced temperature-limitation, but becomes more frequently light-limited in fall. In a warmer climate, ER increases year-round in the absence of moisture stress resulting in net CO_2 uptake increases in the shoulder seasons and decreases during the summer. Annually, landscape net CO_2 uptake is projected to decline by 25±14 g C m^{-2} for a moderate and 103±38 g C m^{-2} for a high warming scenario, potentially reversing recently observed positive net CO_2 uptake trends across the boreal biome. Thus, even without moisture stress, net CO_2 uptake of boreal forest-wetland landscapes may decline, and ultimately these landscapes may turn into net

CO_2 sources under continued anthropogenic CO_2 emissions. We conclude that NEE_{LAND} changes are more likely to be driven by direct climate change rather than by indirect land cover change impacts.

Introduction

The boreal biome, with its distinct land-atmosphere exchange of sensible heat, water vapor, methane, and carbon dioxide (CO_2), plays an important role in the global and regional climate systems (Chapin *et al.*, 2000). For example, boreal forests represent an important carbon (C) sink of about 0.5 Pg C yr^{-1} (Pan *et al.*, 2011), equivalent to 17±6 % of the global land CO_2 sink (Le Quéré *et al.*, 2015). Climate warming in the boreal biome of northwestern North America has caused widespread permafrost thaw at the southern permafrost limit inducing wetland expansion leading to replacement of boreal forests in lowland regions (e.g.; Helbig *et al.*, 2016a; Lara *et al.*, 2016; Chasmer & Hopkinson, in press). Previous studies have shown that land cover changes in these regions affect regional land-atmosphere interactions by favoring the partitioning of available energy to latent instead of sensible heat (Helbig *et al.*, 2016b) and by enhancing landscape methane emissions (Helbig *et al.*, in press). However, it remains uncertain how climate warming and resulting land cover changes influence net ecosystem CO_2 exchange (NEE), and its component fluxes gross primary productivity (GPP) and ecosystem respiration (ER) (Schuur *et al.*, 2015).

Along the southern limit of the North American permafrost zone, long-term net CO_2 uptake has resulted in large organic C stocks as peat (Robinson & Moore, 1999; Tarnocai *et al.*, 2009; Treat *et al.*, 2016). In these organic-rich boreal landscapes, thawing permafrost makes previously frozen organic C stocks available for decomposition and ER may be enhanced by

warming soils (Schuur *et al.*, 2009; O'Donnell *et al.*, 2012; Natali *et al.*, 2014; Treat *et al.*, 2014; Koven *et al.*, 2015). However, permafrost thaw in organic- and ice-rich landscapes often leads to surface subsidence and increased land surface wetness (e.g.; Osterkamp *et al.*, 2000; Baltzer *et al.*, 2014). Under saturated and anoxic conditions, associated with subsidence, organic matter decomposes more slowly, causing only an attenuated post-thaw increase in ER (Knoblauch *et al.*, 2013). At the same time, GPP might increase due to increased nutrient and soil moisture availability, and warmer soil and air temperatures (e.g.; Turetsky *et al.*, 2000; Camill *et al.*, 2001; Wickland *et al.*, 2006; Turetsky *et al.*, 2007; Keuper *et al.*, 2012; Finger *et al.*, 2016). The combination of changes in both GPP and ER in a warming climate will eventually determine if organic-rich boreal landscapes will continue to be long-term CO_2 sinks exerting a climate cooling effect (Frolking *et al.*, 2006). Since 1985, the land net CO_2 sink in the boreal biome (50° to 60° N, excluding Europe) increased by 8-11 Tg C yr^{-1} (Welp *et al.*, 2016), but it remains unclear if this trend will continue in an increasingly warmer climate.

Recent warming trends in northwestern Canada, in the order of 0.25-0.50 °C per decade (DeBeer *et al.*, 2016), are likely to continue and potentially accelerate during the 21st century (Kirtman *et al.*, 2013). Direct climate change effects result from instantaneous ecosystem responses to these altered meteorological conditions. For example, boreal forest GPP is suppressed at air temperatures (T_a, °C) below the freezing point and increases with both T_a- and light-availability (Tanja *et al.*, 2003; Luyssaert *et al.*, 2007), while ER increases with T_a and soil temperature (T_s, °C) (Dunn *et al.*, 2007; Ueyama *et al.*, 2014). In addition to substantially warmer regional climates at high latitudes, future changes in cloud cover could alter incoming shortwave radiation (SW_{in}, W m^{-2}) in these regions (Kirtman *et al.*, 2013). In contrast, indirect climate change impacts result from changes in ecosystem composition, structure, and function

thus altering how ecosystems may respond to variations in meteorological conditions. For example, a gradual increase in the temperature sensitivity of ER over several years can alter NEE of boreal forests in the absence of any warming trend (e.g., Hadden & Grelle, 2016). The abrupt vegetation changes following permafrost thaw in lowland boreal forests may trigger shifts in ecosystem function (Camill *et al.*, 2001). Thus, both direct and indirect climate change effects on GPP and ER need to be assessed to better constrain the future NEE of organic-rich boreal landscapes in the permafrost zone.

Here, we examine the direct climate change effects of altered meteorological conditions and the indirect effects of thaw-induced wetland expansion on NEE and its component fluxes GPP and ER for a boreal forest-wetland landscape in a rapidly thawing lowland region at the southern limit of permafrost in northwestern Canada (Quinton *et al.*, 2011; Baltzer *et al.*, 2014). We use nested eddy covariance net CO_2 flux measurements to compare NEE of the thawing landscape to NEE of a nearby permafrost-free wetland within the heterogeneous landscape, both exposed to the same meteorological conditions. Downscaled regional climate projections are used to assess the GPP, ER, and NEE response to a changing climate. We analyse

(i) how thaw-induced wetland expansion and associated forest loss indirectly affect NEE, GPP, and ER of the boreal forest-wetland landscape, and

(ii) how these indirect climate change effects compare to direct effects of projected changes in T_a and SW_{in} over the 21st century.

Materials and Methods

Study site

Scotty Creek (61°18' N; 121°18' W) is a 152-km^2 watershed in the sporadic permafrost zone (10-50% of land area underlain by permafrost) near Fort Simpson, NT in the southern Taiga Plains of northwestern Canada. With 70 Pg of soil organic C in the top 3 meters, the Taiga Plains store about 15 % of the total organic C stocks (<3 m) in the North American permafrost zone (data from Hugelius *et al.*, 2013). The dry continental climate of the Fort Simpson region is characterized by a mean T_a of -2.8 °C and a mean total precipitation of 388 mm with 149 mm falling as snow (1981-2010; Environment Canada, 2014). The southern part of Scotty Creek is characterized by a mosaic of forested permafrost (peat) plateaus, wetlands, forested uplands and shallow lakes (Chasmer *et al.*, 2014). Permafrost-free wetlands ("wetlands") occur mainly as collapse-scar bogs dominated by bryophytes (*Sphagnum balticum* and *S. magellanicum*), ericaceous shrubs (*Chamaedaphne calyculata*, *Andromeda polifolia*, *Vaccinium oxycoccos*), pod grass (*Scheuchzeria palustris*), and a few isolated black spruce (*Picea mariana*) and tamarack (*Larix laricina*). In contrast, forested permafrost plateaus ("forests") are characterized by a denser overstorey of black spruce with a shrub understorey and a ground cover comprising ericaceous shrubs (mainly *Rhododendron groenlandicum*), and lichens (*Cladonia* spp.) and bryophythes (*Sphagnum fuscum* and *S. capillifolium*), respectively (Garon-Labrecque *et al.*, 2015). Abiotic and biotic characteristics change abruptly between these two ecosystem types as indicated by contrasting overstorey leaf area index ($\geq$ 1 vs. $\leq$ 0.5 for forest and wetland, respectively) and soil moisture conditions ($\leq$ 30 % for the forests compared to $\geq$ 70 % for the wetlands). An active layer (i.e., seasonally thawed surface soil) of approximately 50 cm overlays near-surface permafrost in the forests. No near-surface permafrost is present in the wetlands

(Baltzer *et al.*, 2014). These changes occur over several meters across transition zones with inundated, warmer peat soils (Bubier *et al.*, 1995; Baltzer *et al.*, 2014; Fig. 1). Warm soils in the wetlands cause lateral thawing of near-surface permafrost underlying the forests and, thus, a rapid expansion of permafrost-free wetlands (Kurylyk *et al.*, 2016). At Scotty Creek, forests and wetlands comprise thick organic peat soils of ≥3 m with a mean total organic C content of 167±11 kg C m^{-2} (n = 3; Pelletier *et al.*, in press). About 20 % of North America's boreal forests grow in the circumpolar permafrost zone on ice-rich permafrost and thick overburden cover, and are thus prone to thaw-induced surface subsidence and to forest loss in a warming climate (Helbig *et al.*, 2016a; Olefeldt *et al.*, 2016).

Eddy covariance measurements

Eddy covariance net CO_2 flux measurements were conducted at a landscape tower at 15.2 m above the mean lichen-moss surface of the permafrost plateau (23 March 2015 to 30 August 2016) and at a nested wetland tower at 1.9 m above the mean moss surface (10 June 2015 to 30 August 2016). At the wetland and the landscape tower, high-frequency (10 Hz) fluctuations of vertical wind velocity and sonic temperature were measured with a sonic anemometer (CSAT3A, Campbell Scientific, Logan, UT) and CO_2 and water vapor densities with a co-located open-path infrared gas analyzer (EC150, Campbell Scientific). At the beginning of the study period (23 March 2015 to 16 August 2015), an enclosed infrared gas analyzer (LI-7200, LI-COR Biosciences, Lincoln, NE) was used for CO_2 and water vapor density measurements at the landscape tower. Differences in net CO_2 fluxes derived from the LI-7200 and the EC150 were less than 5 % and cumulative net CO_2 fluxes over 57 days differed by 8 % (Helbig *et al.*, 2016c). Net ecosystem CO_2 exchange for the landscape (NEE_{LAND}; μmol m^{-2} s^{-1}) and the wetland

tower (NEE_{WET}; μmol m^{-2} s^{-1}) was calculated as the sum of the turbulent net CO_2 flux and a storage term. The storage term was derived from half-hourly CO_2 concentration changes at the measurement heights. We follow the micrometeorological NEE convention where net landscape/ecosystem CO_2 uptake is indicated by a negative sign and net CO_2 release to the atmosphere by a positive sign. Net ecosystem CO_2 exchange was filtered for periods with insufficient turbulence using a landscape tower friction velocity threshold of 0.13 m s^{-1} (95 % confidence interval (CI): 0.10 – 0.21 m s^{-1}), derived according to Papale *et al.* (2006). The 95 % CI was derived by using 100 bootstrapped nighttime NEE time series as input. The same threshold was used for the wetland and the landscape tower as the wetland is nested in the landscape tower footprints (Fig. S1). All flux calculations were done using the EddyPro software (version 6.1.0, LI-COR Biosciences). A more detailed description of the instrumental setup and the flux processing procedure is given in Helbig *et al.* (2016b) and Helbig *et al.* (2016c). For the entire study period, 55 % (daytime: 68 %; nighttime: 39 %) and 43 % (daytime: 56 %; nighttime: 28 %) of NEE passed the quality control at the landscape and wetland tower, respectively.

Assessing indirect climate change impacts on CO_2 fluxes using nested eddy covariance fluxes

Footprint modeling

Half-hourly 2-D flux footprints for the wetland and the landscape tower (defined as half-hourly probability maps of flux contribution per unit area [% per m^2]) were obtained according to Kljun *et al.* (2015). The flux footprints were combined with a land cover classification map (Chasmer *et al.*, 2014), as described by Helbig *et al.* (2016b), to derive sums of half-hourly probabilities of flux contributions for individual land cover types (i.e., flux footprint

contributions from forests and wetlands; Fig. 1). Additionally, transition zones were delineated based on aerial photographs as areas of wetland expansion (and thus of forest loss) since 1977 (see Chasmer *et al.*, 2010). Within a radius of 350 m around the landscaper tower, 21 % of the land surface was classified as transition zone. Their flux footprint contributions were then separately derived for each half-hourly flux measurement. Transition zones are part of the wetland land cover type and their definition is to some extent arbitrary, as a reference year (here 1977, the first year of available aerial photography) is used to differentiate between gradual transition zones and interior wetlands. As the half-hourly variability in transition zone contribution was relatively small (standard deviation: 2 % for wetland tower and 5 % for landscape tower), only their average flux footprint contribution to the two flux towers over the entire study period was analyzed. Wetland NEE was discarded when forest contributions were greater than 5 % and NEE_{LAND} was discarded when contributions from a nearby lake were larger than 5 % (Fig. 1). On average, forest contributions to landscape tower footprints were 48 % whereas wetlands contributed 50 % (48 % from bogs and 2 % from fens). The remaining contributions originated from the nearby lake. The wetland tower was located in a collapse-scar bog and wetlands within the landscape tower footprint consisted to >95% of collapse-scar bogs. In the following, "wetlands" therefore refer to collapse-scar bogs. Fens represent a second permafrost-free wetland ecosystem type covering about 12% of the entire Scotty Creek watershed (Chasmer *et al.*, 2014). Similar to collapse-scar bogs, fens are expanding due to permafrost thaw (Chasmer & Hopkinson, in press). Due to their differing hydrology, vegetation composition, and nutrient availability, CO_2 flux dynamics of fens most likely differ from CO_2 flux dynamics of collapse-scar bogs (e.g.; Bubier, 1995; Yu, 2006; Treat *et al.*, 2016).

Flux partitioning

Gaps in NEE were filled using the marginal distribution sampling method (Reichstein *et al.*, 2005) with SW_{in}, T_a, and water vapor pressure deficit (VPD, kPa) as look-up table variables. We calculated annual NEE for 100 friction velocity thresholds (as derived from bootstrapped nighttime NEE) to derive the 95 % CI of annual NEE.

To partition NEE into its component fluxes, GPP (µmol m^{-2} s^{-1}) and ER (µmol m^{-2} s^{-1}), we used a bulk partitioning approach (e.g.; Runkle *et al.*, 2013). The non-gap-filled, half-hourly daytime NEE (SW_{in} > 5 W m^{-2}) was fit to a bulk model combining a rectangular hyperbola function (for GPP) and an empirical Q_{10} model (for ER):

$$NEE = -GPP + ER = \underbrace{-\frac{GPP_{max}\,\alpha\,SW_{in}}{GPP_{max}+\alpha\,SW_{in}}}_{Term\ A} + \underbrace{ER_{base}Q_{10}^{\frac{T_a-T_{ref}}{\gamma}}}_{Term\ B} \qquad (1)$$

where GPP_{max} (µmol m^{-2} s^{-1}) is the maximum canopy photosynthetic capacity, α (µmol m^{-2} s^{-1} per W m^{-2}) is the initial canopy quantum efficiency, ER_{base} (µmol m^{-2} s^{-1}) is the basal respiration at a reference temperature (T_{ref} = 15 °C), Q_{10} indicates the sensitivity of *ER* to T_a, and γ = 10 °C is a constant (e.g.; Mahecha *et al.*, 2010). For the Q_{10} model, we selected T_a measurements within the forest canopy at 2 m above the lichen-moss surface because T_a represents an integrated temperature measure for the landscape whereas soil temperature varies spatially (laterally and vertically) across the heterogeneous landscape (Helbig *et al.*, in press). We fixed the Q_{10} parameter in a first iteration (Q_{10} = 2.5 [landscape] and Q_{10} = 1.1 [wetland]) before deriving the final GPP_{max}, α, and ER_{base}, as described in Reichstein *et al.* (2005). To derive a complete *ER* time series, we combined gap-filled nighttime NEE (i.e., ER) with the modeled daytime ER (see Term B in Eqn. 1). Ecosystem respiration was then subtracted from measured NEE to derive GPP. By using only daytime NEE to obtain daytime ER, we account for

potential light inhibition of leaf respiration during the day (Wehr *et al.*, 2016) and avoid problems of extrapolating relationships between nighttime T_a and ER to daytime conditions (e.g., Lasslop *et al.*, 2010). We assessed indirect land cover change impacts on CO_2 fluxes by analysing differences between NEE and derived component fluxes from the two eddy covariance flux towers with contrasting flux footprint composition.

Modeling NEE and GPP

In this study, we assess how daily light- and temperature-conditions affect mean daily NEE_{LAND}. Net ecosystem CO_2 exchange is the small difference between its two large component fluxes GPP and ER. Ecosystem respiration is strongly controlled by temperature whereas light and temperature are strong controls on GPP, highlighting the potentially different responses of ER and GPP to changing climatic conditions (e.g., Fang & Moncrieff, 2001; Huxman *et al.*, 2003; Lafleur *et al.*, 2005). We therefore modeled light-regulation of GPP using the rectangular hyperbola function in Eqn. 1 and used a downward regulation scalar [f (T_a) in Eqn. 2] to account for temperature-limitation of GPP. Mean daily GPP was fitted to the following equation with the *nlinfit* function in Matlab (version 8.6.0; The MathWorks, Natick, MA) using daily means of T_a and SW_{in}:

$$GPP = f(T_a)\ x\ \frac{GPP_{max}\ \alpha\ SW_{in}}{GPP_{max} + \alpha\ SW_{in}} \qquad (2)$$

f (T_a) is implemented as a sigmoidal function ranging from 0 to 1 and accounts for instantaneous temperature constraints using mean daily T_a and for seasonal temperature constraints using a moving T_a average (i.e., average of seven preceding days, T_{a_week}; °C). The T_{a_week} constraint accounts for seasonality in biological controls other than the instantaneous GPP response to T_a, such as physiological activity (e.g., Rayment *et al.*, 2002) and thermal

acclimation (e.g., Gea-Izquierdo *et al.*, 2010). According to Liebig's law, we assume that only the more limiting factor controls GPP (e.g.; Yuan *et al.*, 2007):

$$f(T_a) = \min\left(\frac{1}{1+a^{(b-T_a)}}, \frac{1}{1+a^{(c-T_{a\_week})}}\right) \quad (3)$$

where *a, b,* and *c* are model coefficients. Additionally, we constructed an ER model (ER_{MOD}) by fitting a Q_{10}-model (term B in Eqn. 1 based on daily T_a) to mean daily ER. Modeled NEE (NEE_{MOD}) was calculated as the sum of GPP_{MOD} and ER_{MOD}. Thus, NEE_{MOD} only depends on the climatic controls T_a and SW_{in} and does not account for other environmental or biological limitations on NEE (e.g.; soil moisture limitations; Niu *et al.*, 2011; Peichl *et al.*, 2013). Model uncertainties were estimated based on 1000 bootstrapped GPP and ER time series.

To characterize how the potential of NEE_{LAND} (NEE_{POT}) responds to changes in thermal conditions, we defined NEE_{POT} as the most negative daily NEE_{LAND} for given daily T_a (i.e., NEE_{LAND} < 15 percentile per T_a bin with each bin containing 2.5 % of all data). Like NEE_{POT}, we defined the temperature controlled potential of GPP_{LAND} (GPP_{POT_Ta}) as the upper limit of daily GPP_{LAND} for a given daily T_a and T_{a_week}. To characterize the light control on the potential of GPP_{LAND} (GPP_{POT_SWin}), we defined GPP_{POT_SWin} as the upper limit of daily GPP_{LAND} for a given daily SW_{in}. Sigmoidal functions were then fitted to GPP_{POT_Ta} and GPP_{POT_SWin}:

$$GPP_{POT\_i} = \frac{k}{1+l^{(m-x_i)}} + n \quad (4)$$

where GPP_{POT_i} is modeled GPP_{POT} for the variable x_i (i.e., T_a/T_{a_week} and SW_{in}) and *k, m, n,* and *l* are model coefficients. We defined GPP_{POT} as temperature-limited if GPP_{POT_Ta} for the observed daily T_a or T_{a_week} was smaller than GPP_{POT_SWin} for the observed daily SW_{in}. For the opposite case, GPP_{POT} was light-limited. If differences in GPP_{POT_Ta} and GPP_{POT_SWin} were less than 10 %, we assumed that GPP_{POT} was co-limited by temperature and light.

Assessing direct climate change impacts on NEE

To assess direct climate change impacts on NEE_{MOD}, GPP_{MOD}, and ER_{MOD}, we used the modelling approach described above with regionally downscaled climate projections as drivers. We obtained T_a and SW_{in} for the period 2006 to 2015 and 2091 to 2100 from the North American Coordinated Regional Climate Downscaling Experiment (CORDEX; http://www.cordex.org) and extracted daily time series for Scotty Creek. The CORDEX provides downscaled climate projections at 50-km resolution for various combinations of Earth system models (ESM) and regional climate models (RCM). We used the ensemble means of six CORDEX projections for two Representative Concentration Pathways (RCP) scenarios: the medium warming RCP4.5 and the high warming RCP8.5 scenario (for selected RCM/ESM simulations see Fig. S9; https://na-cordex.org/simulations-modeling-group). We used both RCPs to compare the scenario leading to the strongest warming (RCP8.5) with a more moderate scenario (RCP4.5). Currently, global net CO_2 emissions follow the most pessimistic CO_2 emission scenario, but these may potentially be reduced depending on future climate policies (Friedlingstein *et al.*, 2014a). To adjust for potential systematic differences between modeled (CORDEX) and measured T_a, we debiased modeled T_a for each CORDEX projection before calculating ensemble means by regressing it against measurements of daily T_a (Wilby *et al.*, 2004) from the nearest weather station in Fort Simpson (~50 km; 2006-2015; Environment Canada, 2016; http://climate.weather.gc.ca/climate_data/). We constrained the regression to periods when both CORDEX and weather station $T_a > -5$ °C as the root-mean-square-error between modeled and measured T_a for colder periods increased by about 50 % (Fig. S5).

Results

Half-hourly landscape and wetland NEE

Between 10 June 2015 and 30 August 2016 wetlands and forests contributed equally to landscape flux footprints with 50±30 % (±95 % CI) and 47±28 %, respectively (and 3 % from the lake). About a third of the wetland contributions to the landscape flux footprints originated from the forest-to-wetland transition zones (i.e., total transition zone contributions to landscape flux footprints were 18±10 %). In contrast, transitions zones only contributed 3±3 % to the wetland flux footprints. NEE_{LAND} ranged from -7.9 μmol m^{-2} s^{-1} (1 %-ile) to 4.8 μmol m^{-2} s^{-1} (99 %-ile) whereas a smaller range from -5.2 μmol m^{-2} s^{-1} (1 %-ile) to 3.9 μmol m^{-2} s^{-1} (99 %-ile) was observed for NEE_{WET} (Fig. 2a). Positive NEE_{LAND} was more positive (i.e., more net CO_2 release) than NEE_{WET} and negative NEE_{LAND} was more negative (i.e., more net CO_2 uptake) than NEE_{WET} with a total least-squares (TLS) slope between NEE_{WET} and NEE_{LAND} of 1.49±0.03 and an intercept of 0.24±0.03 μmol m^{-2} s^{-1}. Slopes for this relationship were independent of wetland contributions (FP_{WET}; %) to landscape flux footprints. The slope for periods with FP_{WET} smaller than or equal to 50 % (1.50±0.05) was not significantly different ($\alpha = 0.05$) from the slope for periods with FP_{WET} larger than 50 % (1.43±0.03). Slopes were consistently positive for night- and daytime NEE_{LAND} against NEE_{WET} relationships. However, the nighttime slope for low FP_{WET} (1.32±0.18) was significantly smaller than the slope for high FP_{WET} (1.81±0.15), indicating that nighttime NEE_{LAND} differed more from NEE_{WET} when wetland contributions to landscape flux footprints were large. For the daytime NEE_{WET} and NEE_{LAND} relationships, the slope for high FP_{WET} of 1.52±0.05 was significantly smaller than the slope for low FP_{WET} of 1.71±0.07. NEE_{LAND} and NEE_{WET} relationships were independent of wind direction (Fig. S2) as

slopes for periods with northerly winds with overlapping wetland and landscape flux footprints were similar to slopes for periods with non-overlapping footprints (Fig. S2).

Daily landscape and wetland NEE and their component fluxes

Monthly medians of daily NEE_{LAND} and NEE_{WET} were negative from May to August (i.e., net CO_2 uptake period) when minimum daily T_a were generally warmer than 0 °C and positive for the remaining eight months with minimum daily T_a at or below 0 °C for most of the days (Fig. 3a, Fig. S3 & S4). Maximum positive daily NEE_{LAND} and NEE_{WET} were observed in November 2015 with medians of 0.48 μmol m^{-2} s^{-1} and 0.46 μmol m^{-2} s^{-1}, respectively, when T_a was below 0 °C, maximum SW_{in} smaller than 200 W m^{-2}, but soil temperatures in the wetlands (at 32 cm) still between 1 °C and 2.5 °C (Fig. S4). Minimum negative NEE_{WET} and NEE_{LAND} in 2016 occurred in July with -0.86 μmol m^{-2} s^{-1} and -1.01 μmol m^{-2} s^{-1}, respectively. From May to July 2015 monthly medians of daily NEE_{LAND} were more negative than NEE_{WET} (Wilcoxon signed-rank test; $p < 0.05$). In contrast, the median of daily NEE_{LAND} was less negative than NEE_{WET} in August 2015 (Wilcoxon signed-rank test; $p < 0.001$) and not significantly different during the same month in 2016. Monthly medians of daily NEE_{LAND} in September, October, and December were more positive than NEE_{WET} while no significant differences were observed for the remaining winter months. Differences in the derived daily component fluxes GPP and ER were more pronounced with monthly medians of daily GPP_{WET} and ER_{WET} being significantly smaller than GPP_{LAND} and ER_{LAND} from March to November (Fig. 3 b & c). During the winter months between December and April, differences in landscape and wetland GPP and ER were smaller than 0.1 μmol m^{-2} s^{-1}. The largest GPP and ER differences were observed in June 2015 with monthly medians of GPP_{WET} being 1.8 μmol m^{-2} s^{-1} smaller than medians of GPP_{LAND} and

monthly medians of ER_{WET} being 1.6 μmol m^{-2} s^{-1} smaller than medians of ER_{LAND}. In 2016, the largest differences in monthly medians of GPP and ER were observed in July with 1.5 μmol m^{-2} s^{-1} and 1.3 μmol m^{-2} s^{-1}, respectively. Between 2015 and 2016, the patterns and magnitude of NEE, GPP, and ER from both towers were similar for the overlapping months April to August.

Annual landscape and wetland NEE

Annual cumulative NEE_{LAND} and NEE_{WET} (ΣNEE, g C-CO_2 m^{-2}; 1 August 2015 to 31 July 2016) were not significantly different with -20.1 g C-CO_2 m^{-2} (-14.6 to -26.9 g C-CO_2 m^{-2} [95 % CI]) and -23.5 g C-CO_2 m^{-2} (-19.6 to -35.1 g C-CO_2 m^{-2}), respectively (Fig. 4). Both the landscape and the wetland were thus small net CO_2 sinks. Shortly after snowmelt, the landscape and wetland wintertime net CO_2 source switched to a net CO_2 sink. From August 2015 until the end of snowmelt in 2016, ΣNEE_{LAND} was more positive (65.1 g C-CO_2 m^{-2}) than ΣNEE_{WET} (39.3 g C-CO_2 m^{-2}). The following larger landscape net CO_2 uptake between May and July 2016 reduced the annual ΣNEE differences to 3.4 g C-CO_2 m^{-2}. Only in the beginning of January, wetland soil temperature (at 32 cm) dropped near the freezing temperature of water (Fig. S4) and the mean early winter (October to December) respiratory net CO_2 losses at the wetland and landscape tower dropped by more than 50 %, remaining low until snowmelt (January to April). In contrast to ΣNEE_{LAND} and ΣNEE_{WET}, the ΣGPP_{LAND} of 532 g C-CO_2 m^{-2} was larger than the ΣGPP_{WET} of 378 g C-CO_2 m^{-2}. Similarly, the ΣER_{LAND} (512 g C-CO_2 m^{-2}) exceeded the ΣER_{WET} (355 g C-CO_2 m^{-2}, data not shown).

Meteorological controls of potential NEE, GPP, and ER

While both GPP_{LAND} and ER_{LAND} increased consistently with T_a, the largest mean daily net CO_2 uptake (NEE_{LAND}) was observed at mean daily T_a of approximately 15 °C (Tab. 1 & Fig. 5). Daily mean NEE_{POT} was ~0 μmol m^{-2} s^{-1} for mean daily T_a < 2 °C, became increasingly more negative at warmer T_a reaching a minimum of ~-2 μmol m^{-2} s^{-1} at about 15 °C, before it became again slightly less negative for warmer T_a (Fig. 5a). Currently, mean daily T_a at Fort Simpson is below 2 °C on more than 50 % of the days of the year (median of 0.2 °C; 2006-2015). In contrast, only about 43 % of days are projected to be below this threshold at the end of the 21st century for the RCP 8.5 scenario (median of 4.8 °C; 2091-2100). Under the current climate, 15 % of daily T_a exceed the optimum NEE_{POT} temperature of 15 °C. The fraction of days with daily T_a above this threshold is projected to rise to 30 % (RCP8.5) by the end of the 21st century. Both T_a and SW_{in} limit GPP_{POT} (Fig. 5 b - d). Maximum mean daily GPP_{LAND} of ~6 μmol m^{-2} s^{-1} was observed when mean daily T_a and T_{a_week} were warmer than 15 °C and mean daily SW_{in} was larger than ~200 W m^{-2}. Mean daily ER_{LAND} rapidly increased with T_a above the freezing point reaching a maximum ER_{LAND} of ~5 μmol m^{-2} s^{-1} at T_a warmer than 20 °C. The T_a-based Q_{10}-model explained 75 % of the variance in daily ER_{LAND} (root-mean-square error (RMSE): 0.8 μmol m^{-2} s^{-1}; for model parameters see Fig. 6 & Tab. S1). The combined T_a-SW_{in} model of GPP_{LAND} explained 88 % of the variance in daily GPP_{LAND} (RMSE: 0.7 μmol m^{-2} s^{-1}; for model parameters see Tab. S1). Modeled NEE_{MOD} - the difference between GPP_{MOD} and ER_{MOD} - explained 45 % of the variance in mean daily NEE_{LAND} (RMSE: 0.7 μmol m^{-2} s^{-1}).

Temperature- and light-limitation of GPP_{POT}

During the measurement period, GPP_{POT} was mainly temperature-limited in late winter (until early May) with cold T_a suppressing GPP despite high SW_{in} (Fig. 5 d & Fig. 7 a). With warming T_a in June 2016, the fraction of days when GPP_{POT} was T_a-limited dropped to 33 % compared to 94 % in May 2016 (Fig. 7a). In July 2016, GPP_{POT} was co-limited by T_a and SW_{in} on 74 % of days (Fig. 7b). Light-limitation of GPP was rare until July ($\leq$ 10 % of days) and became more frequent in August and October with 19 % and 23 % of days, respectively (Fig. 7c). From July to September, the fraction of days with T_a-limited GPP increased again from 13 % to 87 %.

Until the end of the 21st century (2091-2100), mean daily T_a between April and September at Scotty Creek is projected to increase by 2.5 °C for the RCP 4.5 or by 5.2 °C for the RCP 8.5 scenario compared to the period 2006 to 2015 (Fig. S6a-d). In contrast, mean daily SW_{in} for the same period is projected to decrease by 3 W m^{-2} (RCP 4.5) and by 6.6 W m^{-2} (RCP 8.5), most likely due to increased cloudiness as indicated by concurrent increases in precipitation (Fig. S6 e-l). These projected changes consistently reduce T_a-limitation of GPP_{POT} between April and October. The largest reduction in the fraction of days with T_a-limited GPP_{POT} is expected in June and September with -26 % and -22 % for the RCP 4.5 scenario and with -45 % and -47 % for the RCP 8.5 scenario, respectively. The largest increase in days with co-limited GPP_{POT} is projected for June (+24 % [RCP 4.5] and +40 % [RCP 8.5]). Increases in the fraction of days with SW_{in}-limited GPP_{POT} are most pronounced in September with 14 % (RCP 4.5) and 37 % (RCP 8.5). Between March and July, projected increases in days with SW_{in}-limited GPP_{POT} are smaller than 10 % (RCP 4.5 and RCP 8.5).

Projected changes in GPP_{MOD}, ER_{MOD}, and NEE_{MOD}

By the end of the 21st century, the projected changes in T_a and SW_{in} enhance GPP_{MOD} with maximum increases in May (Fig. 8). For the RCP 8.5 scenario, the projected increase in annual GPP_{MOD} is about twice as large as for the RCP 4.5 scenario. However, the increase in annual ER_{MOD} for the RCP 8.5 scenario is 2.5 times larger than for the RCP 4.5 scenario due to warmer T_a. In contrast to GPP_{MOD}, monthly ER_{MOD} is expected to increase most strongly in August and July. The differences in the timing of increases in GPP_{MOD} and ER_{MOD} result in a more negative NEE_{MOD} early in the summer and less negative NEE_{MOD} in July - the warmest summer month. Annual NEE_{MOD} switches its sign from -9±39 g C-CO_2 m^{-2} (±95 % CI; 2006-2015) to +16±42 g C-CO_2 m^{-2} (2091-2100) for the RCP 4.5 scenario and becomes a significant net CO_2 source with +94±54 g C-CO_2 m^{-2} (2091-2100) for the RCP 8.5 scenario. Similar annual NEE_{MOD} for the wetland (i.e., NEE_{MOD} derived from GPP_{WET} and ER_{WET}) was modeled with projected annual NEE_{MOD} (2091-2100) of -9±27 g C-CO_2 m^{-2} and +60±31 g C-CO_2 m^{-2} for the RCP 4.5 and the RCP 8.5 scenario, respectively (Fig. S7). While climatic changes both in winter and summer contribute to this change in annual NEE_{MOD}, the bulk of the reduction occurs during the summer months (May to September) for the RCP 8.5 scenario (73 %). For the RCP 4.5 scenario, an equal reduction occurs during the cold (October to April) and warm season (May to September).

Discussion

Indirect thaw-induced climate change impact on carbon dioxide fluxes

At Scotty Creek, both half-hourly net CO_2 uptake during the day and net CO_2 release during the night were larger for the boreal forest-wetland landscape compared to the wetland (Fig. 2). However, half-hourly NEE_{LAND} differed more from NEE_{WET} with increasing wetland

contributions to landscape flux footprints. In contrast, sensible and latent heat (Helbig *et al.*, 2016b) and methane fluxes (Helbig *et al.*, in press) were found to scale with wetland contributions at Scotty Creek. An analysis of mean flux footprint contributions from forest-wetland transition zones revealed that these contributions were about six times larger for landscape than for wetland tower flux footprints (Fig. 1 c). The transition zones with higher soil moisture and warmer soil temperatures (Bubier *et al.*, 1995; Baltzer *et al.*, 2014) may be characterized by larger GPP and ER compared to the interior of the wetlands and the forests, both characterized by drier surface soils. Such spatial patterns of GPP and ER have previously been observed in similar permafrost peatlands using chamber methods (Turetsky *et al.*, 2002; Wickland *et al.*, 2006; Myers-Smith *et al.*, 2007). Methane fluxes may be more uniform across the wetland as these are more sensitive to variations in water table position compared to variations in surface soil moisture (e.g., Bubier *et al.*, 1995; Kettunen, 2003). In contrast, the productivity of the dominant plant genus in the wetland, *Sphagnum* spp., is strongly controlled by surface moisture (e.g., Schipperges & Rydin, 1998), potentially explaining the differing spatial patterns of NEE and methane fluxes.

Similar findings were reported for a thawing tundra landscape, where both GPP and ER of actively thawing patches within the landscape were larger than the integrated landscape GPP and ER (Belshe *et al.*, 2012). Permafrost thaw increases the availability of nitrogen (Finger *et al.*, 2016), increases surface soil moisture, and induces vegetation shifts toward more aquatic species (Camill, 1999; Camill *et al.*, 2001), potentially enhancing both productivity and respiration in the transition zones. Compared to the permafrost-free wetland, the larger extent of actively thawing transition zones in the boreal forest-wetland landscape may therefore cause larger GPP_{LAND} and ER_{LAND} (Fig. 2).

In contrast to ΣGPP and ΣER, annual ΣNEE_{LAND} and ΣNEE_{WET} did not differ significantly at Scotty Creek (Fig. 3), suggesting that thaw-induced wetland expansion and forest loss might have a negligible short-term impact on ΣNEE. The long-term negative ΣNEE (i.e., net CO_2 uptake) is a major component of peatland C budgets in addition to the typical C losses due to methane emissions and due to net lateral export of dissolved organic C (e.g.; Roulet *et al.*, 2007). At Scotty Creek, wetlands emit 12 g C-CH_4 m^{-2} per year as opposed to 6 g C-CH_4 m^{-2} at the landscape level (Helbig *et al.*, in press), suggesting a similar wetland and landscape net C uptake of -12 g C m^{-2} yr^{-1} (-24 g C-CO_2 m^{-2} + 12 g C-CH_4 m^{-2}) and -14 g C m^{-2} yr^{-1} (-20 g C-CO_2 m^{-2} + 6 g C-CH_4 m^{-2}), respectively (excluding lateral export of dissolved organic C [DOC]). For a boreal peatland landscape in the discontinuous permafrost zone of Manitoba, Moore (2003) reports small annual DOC exports between 1.7 and 3.2 g C m^{-2} yr^{-1}. If DOC exports at Scotty Creek are of a similar magnitude, a current net C uptake of approximately 10 g C m^{-2} yr^{-1} can be expected. A multi-site synthesis study reports similar long-term C accumulation rates for boreal permafrost peatlands [14 g C m^{-2} yr^{-1}] and for permafrost-free bogs [18 g C m^{-2} yr^{-1}] (Treat *et al.*, 2016). Similarly, growing-season NEE was not significantly different across a thaw chronosequence from a forested permafrost peat plateau to a collapse-scar bog in Alaska (Johnston *et al.*, 2014). For a permafrost peatland landscape in northern Manitoba, aboveground net primary productivity of permafrost peat plateaus and of collapse-scar bogs was similar, but a twofold increase in the accumulation of peat was observed following thaw (Camill *et al.*, 2001). Post-thaw increases in C accumulation have been reported for several thawing permafrost peatlands in Manitoba, Saskatchewan, Alberta, and Alaska (Camill, 1999; Turetsky *et al.*, 2000; Turetsky *et al.*, 2007; Jones *et al.*, 2013). However, enhanced decomposition of thawed forest peat has also been shown to exceed increased C accumulation rates in near-surface collapse-scar

bog peat, inducing a rapid post-thaw net C loss (O'Donnell *et al.*, 2012). Particularly transition zones may be subject to rapid net C losses, before they slowly return to a net C sink after about a decade (Jones *et al.*, 2016). Our findings suggest that thawing boreal forest-wetland landscapes can still act as net CO_2 sinks – and most likely as net C sinks - under the current climate. The continuing net CO_2 sink may be the result of integrating large areas with small net CO_2 uptake (e.g., forested permafrost plateaus and interior of permafrost-free wetlands) and small areas with potentially large net CO_2 loss (e.g., recently thawed transition zones). While the thaw-induced wetland expansion may affect long-term C cycle dynamics through its effect on regional hydrology (Connon *et al.*, 2014), species-specific productivity (Camill *et al.*, 2001), and fire regimes (Camill *et al.*, 2009), the immediate indirect climate warming impact of such land cover change on landscape NEE appears to be small.

Direct climate change impacts on carbon dioxide fluxes

In contrast to the small indirect thaw-induced climate change impact on NEE, direct climate change effects appear to be larger and may depend strongly on the future CO_2 emission trajectories as represented by RCPs (Fig. 8). At Scotty Creek, early summer NEE_{MOD} increases with warming T_a, but decreases later in the summer. Such a seasonal pattern is supported by multi-year observations of NEE at other northern and alpine ecosystems (Huxman *et al.*, 2003; Piao *et al.*, 2008). Mid-summer GPP is often light-saturated and warmer summer T_a only marginally enhances plant productivity. ER is mainly temperature-limited (in the absence of moisture stress) and warmer mid-summer T_a reduces NEE by enhancing ER (Huxman *et al.*, 2003). In a warmer climate with more hot summer days (Fig. 5a), this increase in ER may eventually exceed GPP (Runkle *et al.*, 2013). At the tree level, increased white spruce tree-ring

growth in Alaska has been related to warmer spring temperatures for some individuals but also to decreased growth in response to warmer summer temperatures for other individuals (Wilmking *et al.*, 2004). Similar to this study, recent tree-ring and modelling analyses highlight the negative impacts of warmer summer T_a - and an associated increase in autotrophic respiration - on net primary productivity (i.e., balance between GPP and autotrophic respiration) of black spruce forests (Girardin *et al.*, 2016). Additionally, warmer summer T_a may accelerate evapotranspiration rates, decrease moisture availability, and enhance atmospheric water demand potentially slowing down GPP and/or ER during peak growing season (e.g.; Barber *et al.*, 2000; Kljun *et al.*, 2007; Novick *et al.*, 2016).

In fall, light-limitation of GPP is more frequent than in spring (Niu *et al.*, 2011; Fig. 7), potentially explaining the larger spring response in GPP_{MOD} to warmer T_a. For a subalpine forest, Huxman *et al.* (2003) found two NEE minima in early and late summer with a reduction in net CO_2 uptake in mid-summer. Here, we observed only one NEE minimum in July for the current seasonal NEE pattern at Scotty Creek. However, similar to Huxman *et al.* (2003), projected NEE_{MOD} is characterised by two minima in June and August for the RCP 4.5 scenario. In the RCP 8.5 scenario, the NEE_{MOD} minima in early and late summer are even more pronounced (Fig. 8).

In a recent modeling synthesis study, McGuire *et al.* (2016) found that moderate warming in the northern circumpolar permafrost region increased GPP, and vegetation C stocks, but decreased soil C stocks over a 50-year time period in most ESMs. Atmospheric inversion models indicate an increasing net CO_2 sink in the boreal biome for the period 1985 to 2012 (Welp *et al.*, 2016; 50° - 60° N). These results are supported by site-level NEE measurements for temperate and boreal forests indicating that earlier spring onset (i.e., warmer T_a) consistently increases

GPP, and to a lesser extent ER (Kljun *et al.*, 2007; Richardson *et al.*, 2009; Richardson *et al.*, 2010). However, the positive productivity response of evergreen coniferous forests appears to be smaller compared to deciduous forests (Kljun *et al.*, 2007; Welp *et al.*, 2007; Richardson *et al.*, 2010). In a boreal forest ecosystem in the sporadic permafrost zone, longer growing seasons did not increase net CO_2 uptake as the positive productivity response was offset by enhanced respiration (Dunn *et al.*, 2007). In a boreal forest warming experiment, bud burst of black spruce trees occurred earlier and greater shoot lengths were observed (Bronson *et al.*, 2009). The increase in photosynthetic tissue may therefore enhance aboveground net primary productivity, even in the absence of changes in light-saturated photosynthesis and foliage respiration per m^2 of foliage (Bronson & Gower, 2010). Concurrent observations of decreases in fine root net primary productivity may, however, result in unchanged total net primary productivity (Bronson *et al.*, 2008).

Availability of organic C in permafrost peatland landscapes, such as Scotty Creek, is not limited (Treat *et al.*, 2016). Warmer T_a may therefore gradually increase ER while the dominant temperature-limitation of GPP may switch to a more dominant light-limitation, limiting the productivity benefits of warming T_a (Fig. 6 and 7). Air temperature effects on ER have been shown to exert a strong control on interannual variation of boreal forest NEE, exceeding the impacts of variations in GPP (Ueyama *et al.*, 2009; Ueyama *et al.*, 2014). In boreal forests, the NEE response to T_a often follows a parabolic curve with a temperature-optimum of NEE followed by decreasing net CO_2 uptake with T_a above this threshold (Grant *et al.*, 2009; Niu *et al.*, 2011; Fig. 6a). At Scotty Creek, this T_a-threshold appears to be approximately 15 °C, slightly warmer than the 11-year mean NEE T_a-optimum of 11±2 °C (± one standard deviation) for a boreal forest in the sporadic permafrost zone of northern Manitoba (Niu *et al.*, 2012). It should

be noted that, in the long-term, the NEE temperature-optimum might change with thermal adaptation of the vegetation or species composition shifts (Yuan *et al.*, 2011). In a warmer climate, the T_a-optimum of NEE in boreal landscapes like Scotty Creek is likely to be exceeded more often during the summer (Fig. 5a), potentially decreasing summertime net CO_2 uptake. Our results suggest that, with continuously rising T_a, increases in net CO_2 uptake of boreal forest-wetland landscapes may therefore eventually slow down, and their long-term net CO_2 uptake may potentially decrease depending on the climate-warming scenario.

A decreasing potential of boreal forest-wetland landscapes to sequester CO_2 in a warmer climate is supported by a projected C loss at the southern edge of the boreal biome where ecosystems with low potential for long-term C accumulation are expected to replace current boreal organic C-rich ecosystems (Koven, 2013). A diminishing potential net CO_2 uptake may "push" the current C-accumulating landscapes to an unstable state increasing the potential for an abrupt transition to landscapes with lower C stocks and a loss of their CO_2 sink function (Scheffer *et al.*, 2012). For the RCP4.5 scenario, current climates (i.e., mean annual T_a and total precipitation) similar to the projected end-of-the-century climate of Scotty Creek are found within the boreal biome in northern Alberta. For the RCP8.5 scenario, similar climates are currently found at the limit or south of the boreal biome in Canada and the northwestern United States (Fig. 9 and Fig. S8). In contrast to changes in T_a and precipitation, SW_{in} is more strongly bound to latitude. The limited duration of the period providing sufficient light for photosynthetic CO_2 uptake combined with warmer T_a and more precipitation (Fig. S6) is therefore likely to increase ER more than GPP, particularly for the RCP8.5 scenario (Fig. 8). A shift from permafrost peatland landscapes with large organic C stocks (mean of 106 kg m^{-2} ± 45 [± one standard deviation] for forested permafrost plateaus [n = 158]; 117 kg m^{-2} ± 65 for collapse-scar

bogs [n = 52]; data from Treat *et al.*, 2016) to landscapes with low C stocks would result in large net CO_2 emissions. Our results suggest that the magnitude of these emissions will strongly depend on future anthropogenic CO_2 emission pathways (Fig. 8).

Comparison with Earth system models and CO_2 flux inversion modeling

A comparison with five end-of-21st-century ESM projections of NEE (from the Coupled Model Intercomparison Project [CMIP5; http://cmip-pcmdi.llnl.gov/cmip5/]; Friedlingstein *et al.*, 2014b; Fig. S9) shows that three out of five ESMs project NEE changes similar to our findings. More specifically, for the southern Taiga Plains region, no ESM shows significant changes in mean annual NEE for the moderate RCP4.5 scenario (Two-Sample t-test; $\alpha = 0.05$; $n = 10$). For the warmer RCP8.5 scenario, three out of the five ESMs indicate decreases in net CO_2 uptake (7 to 36 g C-CO_2 m^{-2} less negative NEE with one ESM showing a significant decrease; $p = 0.04$; $n = 10$; see Fig. S9). Two ESMs even indicate a switch from a net CO_2 sink to a net CO_2 source. Similar to our study, all ESMs project the largest monthly increase in net CO_2 uptake between April and June (except for July in the RCP8.5 scenario of one ESM) and smaller increases or even decreases in net CO_2 uptake later in summer.

For the period 2006 to 2015, all five ESMs indicate a mean net CO_2 sink for the southern Taiga Plains region with differences of less than 20 g C-CO_2 m^{-2} to measured annual NEE at Scotty Creek (except for a larger difference for one ESM; Fig. S10). Compared to the annual landscape NEE of -20 g C-CO_2 m^{-2} at Scotty Creek, global CO_2 flux inversions (1° x 1° resolution, CarbonTracker, 2016) suggest a mean annual NEE (2006 – 2015) of -39±52 g C-CO_2 m^{-2} [± one standard deviation] with a similar monthly NEE seasonality and magnitude (Fig. S10a). However, four out of five ESMs overestimate the maximum monthly net CO_2 uptake in

the summer and the maximum monthly net CO_2 loss in the winter. The ESMs simulate both direct and indirect climate change effects on NEE, but their NEE response may vary due to differing representations of land surface processes (e.g., dynamic vegetation models, phenology, CO_2 fertilization, nutrient dynamics) (e.g., Friedlingstein *et al.*, 2014b; Wieder *et al.*, 2015). Disentangling the individual contributions from these processes to diverging NEE projections is difficult due to the complex interactions between the individual model components (e.g., Friedlingstein *et al.*, 2014b). However, an improved understanding of temperature- and light-limitation of NEE may help reducing the wide spread in modeled boreal landscape NEE response to climate change and minimize the deviation between measured and modeled seasonality of NEE.

Potential responses of ecosystem functioning to a changing climate

How vegetation productivity and respiration respond to changes in temperature and light may be affected by factors other than shifts in landscape and ecosystem composition and structure. Rising atmospheric CO_2 concentrations and the related fertilization effect on plant productivity may stimulate and enhance GPP (McGuire *et al.*, 2016). This CO_2 fertilization effect could directly increase GPP through its positive impact on maximum GPP (Ueyama *et al.*, 2016), favoring a larger potential for net CO_2 uptake than projected in this study. However, the magnitude of the CO_2 fertilization effect in boreal forests remains poorly constrained: both no productivity response (Kroner & Way, 2016) and a positive response was observed (Tjoelker *et al.*, 1998) in CO_2 fertilization experiments of Norway spruce (*Picea abies*) and black spruce seedlings. A small, positive GPP response of 0.16 % ppm^{-1} (2002-2014) was estimated for an Alaskan black spruce forest (Ueyama *et al.*, 2016). Net primary productivity of about half of the

black spruce forests in North America (south of 60° N) was projected to decline at the end of the 21st century in a modeling study despite a positive CO_2 fertilization effect on GPP (Girardin *et al.*, 2016). For *Sphagnum* spp. and vascular bog species, only small or negative CO_2 effects on productivity were reported (Berendse *et al.*, 2001; Heijmans *et al.*, 2002). To some extent, plants can acclimate to warmer T_a by modifying their photosynthetic and respiratory apparatus. In warming and CO_2 enrichment experiments, the thermal optimum of light-saturated net CO_2 uptake of both Norway spruce and black spruce seedlings increased in the warming treatments while leaf respiration was suppressed. At the same time, light-saturated net CO_2 uptake was found to decrease for the warmest treatments (+8 °C) (Way & Sage, 2008; Kroner & Way, 2016). A better constraint of the impacts of CO_2 fertilization and thermal acclimation on the productivity of boreal plant species is therefore needed to fully understand the response of boreal forest-wetland landscape CO_2 fluxes to climate change.

Our focus on meteorological controls (temperature and light) of GPP only constrains the GPP_{MOD} response given no other limiting factors. Actual GPP however may be reduced by additional environmental limitations. For example, earlier spring onset in the boreal and temperate forests has been observed to decrease peak summer productivity due to soil moisture deficits later in the summer (Buermann *et al.*, 2013; Wolf *et al.*, 2016). Particularly in late summer and fall, soil moisture deficits can add another environmental constraint on GPP (Niu *et al.*, 2011). In peatlands, fluctuating water levels may also modify the temperature-sensitivity of heterotrophic soil respiration (e.g., Silvola *et al.*, 1996; Hanis *et al.*, 2015) and affect GPP (e.g., Chivers *et al.*, 2009). Changes in net primary productivity may alter C substrate availability to soil microbes through changes in litter fall (Bond-Lamberty *et al.*, 2004; Beier *et al.*, 2008) and changes in GPP may affect autotrophic respiration through the allocation of photosynthates

(Janssens *et al.*, 2001). Such indirect effects of ecosystem acclimation may modify the overall temperature sensitivity of ER and, therefore, additionally affect NEE responses to a changing climate. The temperature-response of ER in a warmer climate could also be attenuated if increasing net C losses diminish the fraction of labile organic C, exposing more recalcitrant organic matter from deeper peat layers, or induce temperature-related changes in soil microbial communities (Hogg *et al.*, 1992; Bradford *et al.*, 2008). Understanding how these environmental controls interact with the warming-related shifts in the seasonality of GPP and ER will help constraining the NEE response to a warmer climate.

Here, we show that thaw-induced wetland expansion and associated boreal forest loss appears to have negligible indirect climate change effects on the observed landscape net CO_2 uptake of ~20 g C-CO_2 m^{-2} yr^{-1}. However, even without moisture stress, net CO_2 uptake of boreal forest-wetland landscapes is likely to decline by the end of the 21st century due to direct climate change impacts of changing meteorological forcing. This projected reduction is about five times larger for a high climate-warming scenario (103 g C-CO_2 m^{-2} yr^{-1}) compared to a moderate scenario (25 g C-CO_2 m^{-2} yr^{-1}). In an exceedingly warmer climate, the recently observed increasing net CO_2 uptake of the boreal biome may therefore turn into a decreasing net CO_2 sink during the 21st century, reducing the ability of boreal landscapes to sequester atmospheric CO_2.

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Supporting information

Fig. S1: Friction velocity and landscape and wetland net ecosystem CO_2 exchange.

Fig. S2: Wind direction and landscape and wetland net ecosystem CO_2 exchange.

Fig. S3: Daily gross primary production (GPP), ecosystem respiration (ER), and net ecosystem CO_2 exchange (NEE)

Fig. S4: Air temperature and soil temperature, incoming shortwave radiation, and snow depth and daily liquid precipitation.

Fig. S5: Daily air temperature at Fort Simpson versus daily air temperature from regional climate/earth system model simulations.

Fig. S6: Projected end-of-the-21st-century changes in near-surface air temperature, incoming shortwave radiation, and precipitation compared to the current conditions.

Fig. S7: Projections of modeled monthly wetland gross primary productivity, ecosystem respiration, and net ecosystem carbon dioxide exchange at Scotty Creek.

Fig. S8: Current analogues of the projected end-of-the-21st-century climate at Scotty Creek for the RCP4.5 scenario and for the RCP8.5 scenario.

Fig. S9: Net ecosystem CO_2 exchange from five Earth System Model simulations from the Coupled Model Intercomparison Project (CMIP5) for the grid cell comprising Scotty Creek (61°18’ N; 121°18’ W).

Fig. S10: Mean monthly and mean annual net ecosystem CO_2 exchange from CarbonTracker and five ESMs for the period 2006 to 2015 for the grid cell comprising Scotty Creek.

Tab. S1: Best fit parameters for the models of gross primary productivity and ecosystem respiration at the landscape- and the wetland-scale.

Tab. 1: Mean daily net ecosystem CO_2 exchange (NEE_{LAND}), gross primary productivity (GPP_{LAND}), and ecosystem respiration (ER_{LAND}) at landscape-level (± one standard deviation) for 5 °C-daily air temperature (T_a) bins between 23 March 2015 and 30 August 2016. Number of days (*n*) for bins for the observation period at Scotty Creek and the percentage of days with T_a within the bins at Fort Simpson between 2006 and 2015 (data from: Environment Canada, 2016; http://climate.weather.gc.ca/climate_data/).

	NEE_{LAND} ± std µmol m^{-2} s^{-1}	GPP_{LAND} ± std µmol m^{-2} s^{-1}	ER_{LAND} ± std µmol m^{-2} s^{-1}	*n*	*days* *%*
$T_a \leq$ -2.5 °C	+0.28±0.22	0.04±0.11	0.33±0.17	169	45.6
-2.5 °C < $T_a \leq$ 2.5 °C	+0.28±0.27	0.21±0.19	0.49±0.22	53	8.5
2.5 °C < $T_a \leq$ 7.5 °C	+0.16±0.56	0.72±0.68	0.88±0.62	52	9.1
7.5 °C < $T_a \leq$ 12.5 °C	-0.45±0.65	2.26±1.32	1.81±1.03	63	10.5
12.5 °C < $T_a \leq$ 17.5 °C	-0.67±0.85	3.74±1.40	3.08±1.06	90	15.2
17.5 °C < $T_a \leq$ 22.5 °C	-0.80±0.58	4.35±1.32	3.55±1.07	86	9.8
$T_a >$ 22.5 °C	-0.59±0.52	5.15±0.59	4.56±0.74	12	1.3

Fig. 1: **(a)** Oblique photograph of an actively thawing transition zone between wetland and forest. **(b)** Oblique photograph of the studied boreal forest-wetland landscape taken from a helicopter. Bright green areas represent visually delineated transition zones (several metres in lateral extent). **(c)** Land cover types in the flux footprints of the wetland (red cross) and the landscape tower (green cross): forested permafrost peat plateaus (dark green) and wetlands [collapse-scar bogs (yellow), fens (light brown), and an upland on post-glacial till (greenish yellow in the top right corner, outside the footprint)]. Wetland areas that have been converted from forested permafrost peat plateaus since 1977 (transition zones as identified using historical aerial photographs) are indicated in light green. Note that the extent of the transition zone map in **(c)** is limited to the east and south. Solid lines show landscape (dark green) and wetland tower (red) 90 % flux footprint climatology.

Fig. 2: Comparison of half-hourly net ecosystem carbon dioxide exchange at the landscape- (NEE_{LAND}) and wetland-scale (NEE_{WET}) for **(a)** all, **(b)** only nighttime, and **(c)** only daytime measurements. Data points are color-coded according to the wetland contribution to landscape flux footprints (FP_{WET}). The solid blue and yellow lines show the total least squares regressions for low (FP_{WET} < 50 %) and high FP_{WET} ($FP_{WET} \geq$ 50 %), respectively.

Fig. 3: **(a)** Daily net ecosystem carbon dioxide exchange (NEE), **(b)** gross primary productivity (GPP), and **(c)** ecosystem respiration (ER) from the wetland and landscape (including wetlands and forests) tower for individual months. Boxes show 25th and 75th percentiles; grey lines inside the boxes show medians. Monthly medians with asterisks are significantly different (Wilcoxon signed-rank test; * α = 0.05 / ** α = 0.01 / ** α = 0.001). Note that data from the wetland tower is missing for April, May, and July 2015 due to sensor malfunctioning.

Fig. 4: Cumulative gap-filled net ecosystem carbon dioxide exchange at the landscape- and wetland-scale (ΣNEE_{LAND} & ΣNEE_{WET}, solid lines). Grey shaded areas indicating 95 % confidence

intervals of ΣNEE between August 2015 and 2016 due to the friction velocity threshold and random errors in NEE measurements.

Fig. 5: **(a)** Mean daily air temperature (T_a) and net ecosystem carbon dioxide exchange at the landscape tower (NEE_{LAND}). Closed circles show measured NEE_{LAND} and open circles show potential NEE. Solid lines indicate the current and projected median of daily T_a between 2006-2015 and 2091-2100. Dashed lines show the respective 10^{th} and 90^{th} percentiles. Mean daily gross primary productivity derived from NEE_{LAND} (GPP_{LAND}) against **(b)** mean daily T_a and **(c)** the seven-day moving average of T_a. Solid lines are best model fits to potential GPP (circles) and shaded areas indicate the 95 % confidence interval. Color-coding of data points represents mean daily incoming shortwave radiation (SW_{in}). (d) GPP_{LAND} against SW_{in}. Color-coding shows T_a.

Fig. 6: Mean daily ecosystem respiration at the landscape tower (ER_{LAND}) against mean daily T_a. Solid line shows the best-fit Q_{10}-model.

Fig. 7: Monthly fraction of days when potential gross primary productivity (GPP_{POT}) is limited by **(a)** air temperature (T_a), **(c)** incoming shortwave radiation (SW_{in}), or **(b)** co-limited by both variables. The dashed line shows GPP_{POT}-limitation for T_a and SW_{in} measured at Scotty Creek between August 2015 and July 2016. Solid lines indicate ensemble mean GPP_{POT}-limitation for the recent and projected modeled T_a and SW_{in} from six combinations of four regional and three global climate models.

Fig. 8: Projections (2091-2100) of monthly modeled gross primary productivity (GPP_{MOD}), ecosystem respiration (ER_{MOD}), and net ecosystem carbon dioxide exchange (NEE_{MOD}) for the landscape at Scotty Creek **(a)** for the RCP 4.5 and **(b)** for the RCP 8.5 scenario. For comparison, narrow white bars show recent (2006-2015) GPP_{MOD}, ER_{MOD}, and NEE_{MOD}. Error bars indicate uncertainties (95 % confidence intervals) in the GPP- and ER-model.

Fig. 9: Current climate analogues (2006-2015) of the projected end-of-21^{st}-century (2091-2100) climate at Scotty Creek **(a)** for the RCP4.5 scenario and **(b)** for the RCP8.5 scenario. Circles show all climate analogues from six different regional/global climate model combinations. The green circle indicates the location of Scotty Creek. Orange circles show locations of current climates similar to the projected climate for Scotty Creek (±10 % difference in mean annual precipitation and ±0.5 °C of mean annual air temperature). Red circles indicate locations where, additionally, differences in annual incoming shortwave radiation (SW_{in}) are ±30 %. Grey shaded area is the current extent of the boreal zone (data from Brandt, 2009).