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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 21$^{st}$ 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
CO₂ sources under continued anthropogenic CO₂ emissions. We conclude that NEE\textsubscript{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 (CO₂), 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 CO₂ 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 CO₂ 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 CO₂ 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 21$^{st}$ 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 21$^{st}$ century.

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Materials and Methods

Study site

Scotty Creek (61°18’ N; 121°18’ W) is a 152-km² 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 bryophytes (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.
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 ($\text{NEE}_{\text{LAND}}$, μmol m$^{-2}$ s$^{-1}$) and the wetland...
tower (NEE_{WET}; \mu\text{mol m}^{-2} \text{s}^{-1}) was calculated as the sum of the turbulent net CO\textsubscript{2} flux and a storage term. The storage term was derived from half-hourly CO\textsubscript{2} concentration changes at the measurement heights. We follow the micrometeorological NEE convention where net landscape/ecosystem CO\textsubscript{2} uptake is indicated by a negative sign and net CO\textsubscript{2} release to the atmosphere by a positive sign. Net ecosystem CO\textsubscript{2} exchange was filtered for periods with insufficient turbulence using a landscape tower friction velocity threshold of 0.13 m s\textsuperscript{-1} (95 \% confidence interval (CI): 0.10 – 0.21 m s\textsuperscript{-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\textsubscript{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\textsuperscript{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

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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, CO₂ flux dynamics of fens most likely differ from CO₂ 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 ($\mu$mol m$^{-2}$ s$^{-1}$) and ER ($\mu$mol 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):

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

where $GPP_{max}$ ($\mu$mol m$^{-2}$ s$^{-1}$) is the maximum canopy photosynthetic capacity, $\alpha$ ($\mu$mol m$^{-2}$ s$^{-1}$ per W m$^2$) is the initial canopy quantum efficiency, $ER_{base}$ ($\mu$mol 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 $\gamma = 10$ °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 $GPP_{max}$, $\alpha$, 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

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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\_\text{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 \textit{nlinfit} function in Matlab (version 8.6.0; The MathWorks, Natick, MA) using daily means of \(T_a\) and \(SW_{in}\):  

\[
GPP = f(T_a) \times \frac{GPP_{max} \times SW_{in}}{GPP_{max} + \alpha SW_{in}} \tag{2}
\]

\(f(T_a)\) 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, \(T_{a,\text{week}}\); °C). The \(T_{a,\text{week}}\) 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

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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):

\[
f(T_a) = \min \left( \frac{1}{1+a(b-T_a)}, \frac{1}{1+a(c-T_{a.week})} \right)
\]

(3)

where \(a\), \(b\), and \(c\) are model coefficients. Additionally, we constructed an ER model (ER\text{MOD}) by fitting a \(Q_{10}\)-model (term B in Eqn. 1 based on daily \(T_a\)) to mean daily ER. Modeled NEE (NEE\text{MOD}) was calculated as the sum of GPP\text{MOD} and ER\text{MOD}. Thus, NEE\text{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\text{LAND} (NEE\text{POT}) responds to changes in thermal conditions, we defined NEE\text{POT} as the most negative daily NEE\text{LAND} for given daily \(T_a\) (i.e., NEE\text{LAND} < 15 percentile per \(T_a\) bin with each bin containing 2.5 % of all data). Like NEE\text{POT}, we defined the temperature controlled potential of GPP\text{LAND} (GPP\text{POT}_Ta) as the upper limit of daily GPP\text{LAND} for a given daily \(T_a\) and \(T_{a.week}\). To characterize the light control on the potential of GPP\text{LAND} (GPP\text{POT}_SWin), we defined GPP\text{POT}_SWin as the upper limit of daily GPP\text{LAND} for a given daily \(SW_{in}\). Sigmoidal functions were then fitted to GPP\text{POT}_Ta and GPP\text{POT}_SWin:

\[
GPP_{POT,i} = \frac{k}{1+4(m-x_i^2)} + n
\]

(4)

where GPP\text{POT}_i is modeled GPP\text{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\text{POT} as temperature-limited if GPP\text{POT}_Ta for the observed daily \(T_a\) or \(T_{a.week}\) was smaller than GPP\text{POT}_SWin for the observed daily \(SW_{in}\). For the opposite case, GPP\text{POT} was light-limited. If differences in GPP\text{POT}_Ta and GPP\text{POT}_SWin were less than 10 %, we assumed that GPP\text{POT} was co-limited by temperature and light.
Assessing direct climate change impacts on NEE

To assess direct climate change impacts on NEE<sub>MOD</sub>, GPP<sub>MOD</sub>, and ER<sub>MOD</sub>, we used the modelling approach described above with regionally downscaled climate projections as drivers. We obtained T<sub>a</sub> and SW<sub>in</sub> 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<sub>2</sub> emissions follow the most pessimistic CO<sub>2</sub> emission scenario, but these may potentially be reduced depending on future climate policies (Friedlingstein <i>et al.</i>, 2014a). To adjust for potential systematic differences between modeled (CORDEX) and measured T<sub>a</sub>, we debiased modeled T<sub>a</sub> for each CORDEX projection before calculating ensemble means by regressing it against measurements of daily T<sub>a</sub> (Wilby <i>et al.</i>, 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<sub>a</sub> > -5 °C as the root-mean-square-error between modeled and measured T<sub>a</sub> 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 (α = 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

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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 $\text{NEE}_{\text{LAND}}$ and $\text{NEE}_{\text{WET}}$ 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 $\text{NEE}_{\text{LAND}}$ and $\text{NEE}_{\text{WET}}$ 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 $\text{NEE}_{\text{WET}}$ and $\text{NEE}_{\text{LAND}}$ 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 $\text{NEE}_{\text{LAND}}$ were more negative than $\text{NEE}_{\text{WET}}$ (Wilcoxon signed-rank test; $p < 0.05$). In contrast, the median of daily $\text{NEE}_{\text{LAND}}$ was less negative than $\text{NEE}_{\text{WET}}$ in August 2015 (Wilcoxon signed-rank test; $p < 0.001$) and not significantly different during the same month in 2016. Monthly medians of daily $\text{NEE}_{\text{LAND}}$ in September, October, and December were more positive than $\text{NEE}_{\text{WET}}$ 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 $\text{GPP}_{\text{WET}}$ and $\text{ER}_{\text{WET}}$ being significantly smaller than $\text{GPP}_{\text{LAND}}$ and $\text{ER}_{\text{LAND}}$ 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 $\text{GPP}_{\text{WET}}$ being 1.8 μmol m$^{-2}$ s$^{-1}$ smaller than medians of $\text{GPP}_{\text{LAND}}$ and
monthly medians of \( \text{ER}_{\text{WET}} \) being 1.6 \( \mu \text{mol m}^{-2} \text{s}^{-1} \) smaller than medians of \( \text{ER}_{\text{LAND}} \). In 2016, the largest differences in monthly medians of GPP and ER were observed in July with 1.5 \( \mu \text{mol m}^{-2} \text{s}^{-1} \) and 1.3 \( \mu \text{mol m}^{-2} \text{s}^{-1} \), 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 \( \Sigma \text{NEE}_{\text{LAND}} \) and \( \Sigma \text{NEE}_{\text{WET}} \) (\( \Sigma \text{NEE}, \ g \text{ C-CO}_2 \text{ m}^{-2}; \ 1 \text{ August 2015 to 31 July 2016} \)) 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, \( \Sigma \text{NEE}_{\text{LAND}} \) was more positive (65.1 g C-CO\(_2\) m\(^{-2}\)) than \( \Sigma \text{NEE}_{\text{WET}} \) (39.3 g C-CO\(_2\) m\(^{-2}\)). The following larger landscape net CO\(_2\) uptake between May and July 2016 reduced the annual \( \Sigma \text{NEE} \) 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 \( \Sigma \text{NEE}_{\text{LAND}} \) and \( \Sigma \text{NEE}_{\text{WET}} \), the \( \Sigma \text{GPP}_{\text{LAND}} \) of 532 g C-CO\(_2\) m\(^{-2}\) was larger than the \( \Sigma \text{GPP}_{\text{WET}} \) of 378 g C-CO\(_2\) m\(^{-2}\). Similarly, the \( \Sigma \text{ER}_{\text{LAND}} \) (512 g C-CO\(_2\) m\(^{-2}\)) exceeded the \( \Sigma \text{ER}_{\text{WET}} \) (355 g C-CO\(_2\) m\(^{-2}\), data not shown).
Meteorological controls of potential NEE, GPP, and ER

While both GPP\textsubscript{LAND} and ER\textsubscript{LAND} increased consistently with T\textsubscript{a}, the largest mean daily net CO\textsubscript{2} uptake (NEE\textsubscript{LAND}) was observed at mean daily T\textsubscript{a} of approximately 15 °C (Tab. 1 & Fig. 5). Daily mean NEE\textsubscript{POT} was −0 \, \mu\text{mol} \, \text{m}^{-2} \, \text{s}^{-1} for mean daily T\textsubscript{a} < 2 °C, became increasingly more negative at warmer T\textsubscript{a} reaching a minimum of −2 \, \mu\text{mol} \, \text{m}^{-2} \, \text{s}^{-1} at about 15 °C, before it became again slightly less negative for warmer T\textsubscript{a} (Fig. 5a). Currently, mean daily T\textsubscript{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 21\textsuperscript{st} century for the RCP 8.5 scenario (median of 4.8 °C; 2091-2100). Under the current climate, 15 % of daily T\textsubscript{a} exceed the optimum NEE\textsubscript{POT} temperature of 15 °C. The fraction of days with daily T\textsubscript{a} above this threshold is projected to rise to 30 % (RCP8.5) by the end of the 21\textsuperscript{st} century.

Both T\textsubscript{a} and SW\textsubscript{in} limit GPP\textsubscript{POT} (Fig. 5 b - d). Maximum mean daily GPP\textsubscript{LAND} of ~6 \, \mu\text{mol} \, \text{m}^{-2} \, \text{s}^{-1} was observed when mean daily T\textsubscript{a} and T\textsubscript{a, week} were warmer than 15 °C and mean daily SW\textsubscript{in} was larger than ~200 W m\textsuperscript{-2}. Mean daily ER\textsubscript{LAND} rapidly increased with T\textsubscript{a} above the freezing point reaching a maximum ER\textsubscript{LAND} of ~5 \, \mu\text{mol} \, \text{m}^{-2} \, \text{s}^{-1} at T\textsubscript{a} warmer than 20 °C. The T\textsubscript{a}-based Q\textsubscript{10}-model explained 75 % of the variance in daily ER\textsubscript{LAND} (root-mean-square error (RMSE): 0.8 \, \mu\text{mol} \, \text{m}^{-2} \, \text{s}^{-1}; for model parameters see Fig. 6 & Tab. S1). The combined T\textsubscript{a}-SW\textsubscript{in} model of GPP\textsubscript{LAND} explained 88 % of the variance in daily GPP\textsubscript{LAND} (RMSE: 0.7 \, \mu\text{mol} \, \text{m}^{-2} \, \text{s}^{-1}; for model parameters see Tab. S1). Modeled NEE\textsubscript{MOD} - the difference between GPP\textsubscript{MOD} and ER\textsubscript{MOD} - explained 45 % of the variance in mean daily NEE\textsubscript{LAND} (RMSE: 0.7 \, \mu\text{mol} \, \text{m}^{-2} \, \text{s}^{-1}).
Temperature- and light-limitation of $\text{GPP}_{\text{POT}}$

During the measurement period, $\text{GPP}_{\text{POT}}$ was mainly temperature-limited in late winter (until early May) with cold $T_a$ suppressing GPP despite high $\text{SW}_{\text{in}}$ (Fig. 5 d & Fig. 7 a). With warming $T_a$ in June 2016, the fraction of days when $\text{GPP}_{\text{POT}}$ was $T_a$-limited dropped to 33 % compared to 94 % in May 2016 (Fig. 7a). In July 2016, $\text{GPP}_{\text{POT}}$ was co-limited by $T_a$ and $\text{SW}_{\text{in}}$ 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 $\text{SW}_{\text{in}}$ 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 $\text{GPP}_{\text{POT}}$ between April and October. The largest reduction in the fraction of days with $T_a$-limited $\text{GPP}_{\text{POT}}$ 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 $\text{GPP}_{\text{POT}}$ is projected for June (+24 % [RCP 4.5] and +40 % [RCP 8.5]). Increases in the fraction of days with $\text{SW}_{\text{in}}$-limited $\text{GPP}_{\text{POT}}$ are most pronounced in September with 14 % (RCP 4.5) and 37 % (RCP 8.5). Between March and July, projected increases in days with $\text{SW}_{\text{in}}$-limited $\text{GPP}_{\text{POT}}$ are smaller than 10 % (RCP 4.5 and RCP 8.5).
Projected changes in GPP$\text{MOD}$, ER$\text{MOD}$, and NEE$\text{MOD}$

By the end of the 21st century, the projected changes in $T_a$ and $SW_{in}$ enhance GPP$\text{MOD}$ with maximum increases in May (Fig. 8). For the RCP 8.5 scenario, the projected increase in annual GPP$\text{MOD}$ is about twice as large as for the RCP 4.5 scenario. However, the increase in annual ER$\text{MOD}$ 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$\text{MOD}$, monthly ER$\text{MOD}$ is expected to increase most strongly in August and July. The differences in the timing of increases in GPP$\text{MOD}$ and ER$\text{MOD}$ result in a more negative NEE$\text{MOD}$ early in the summer and less negative NEE$\text{MOD}$ in July - the warmest summer month. Annual NEE$\text{MOD}$ switches its sign from $-9\pm39$ g C-CO$_2$ m$^{-2}$ ($\pm95\%$ CI; 2006-2015) to $+16\pm42$ g C-CO$_2$ m$^{-2}$ (2091-2100) for the RCP 4.5 scenario and becomes a significant net CO$_2$ source with $+94\pm54$ g C-CO$_2$ m$^{-2}$ (2091-2100) for the RCP 8.5 scenario. Similar annual NEE$\text{MOD}$ for the wetland (i.e., NEE$\text{MOD}$ derived from GPP$\text{WET}$ and ER$\text{WET}$) was modeled with projected annual NEE$\text{MOD}$ (2091-2100) of $-9\pm27$ g C-CO$_2$ m$^{-2}$ and $+60\pm31$ 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$\text{MOD}$, 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$_\text{LAND}$ differed more from NEE$_\text{WET}$ with increasing wetland

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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. 1c). 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).

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In contrast to $\Sigma GPP$ and $\Sigma ER$, annual $\Sigma NEE_{\text{LAND}}$ and $\Sigma NEE_{\text{WET}}$ 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 $\Sigma NEE$. The long-term negative $\Sigma NEE$ (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

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bogs \[ n = 52 \]; data from Treat et al., 2016) to landscapes with low C stocks would result in large net CO\textsubscript{2} emissions. Our results suggest that the magnitude of these emissions will strongly depend on future anthropogenic CO\textsubscript{2} emission pathways (Fig. 8).

**Comparison with Earth system models and CO\textsubscript{2} flux inversion modeling**

A comparison with five end-of-21\textsuperscript{st}-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\textsubscript{2} uptake (7 to 36 g C-CO\textsubscript{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\textsubscript{2} sink to a net CO\textsubscript{2} source. Similar to our study, all ESMs project the largest monthly increase in net CO\textsubscript{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\textsubscript{2} uptake later in summer.

For the period 2006 to 2015, all five ESMs indicate a mean net CO\textsubscript{2} sink for the southern Taiga Plains region with differences of less than 20 g C-CO\textsubscript{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\textsubscript{2} m\(^{-2}\) at Scotty Creek, global CO\textsubscript{2} flux inversions (1° x 1° resolution, CarbonTracker, 2016) suggest a mean annual NEE (2006 – 2015) of -39±52 g C-CO\textsubscript{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\textsubscript{2} uptake in

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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 CO₂ fertilization effect on GPP (Girardin et al., 2016). For Sphagnum spp. and vascular bog species, only small or negative CO₂ 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 CO₂ enrichment experiments, the thermal optimum of light-saturated net CO₂ 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 CO₂ uptake was found to decrease for the warmest treatments (+8 °C) (Way & Sage, 2008; Kroner & Way, 2016). A better constraint of the impacts of CO₂ fertilization and thermal acclimation on the productivity of boreal plant species is therefore needed to fully understand the response of boreal forest-wetland landscape CO₂ 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 21$^{\text{st}}$ 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 21$^{\text{st}}$ 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-21$^{st}$-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-21$^{st}$-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 CO₂ exchange (NEE\textsubscript{LAND}), gross primary productivity (GPP\textsubscript{LAND}), and ecosystem respiration (ER\textsubscript{LAND}) at landscape-level (± one standard deviation) for 5 °C-daily air temperature (T\textsubscript{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\textsubscript{a} within the bins at Fort Simpson between 2006 and 2015 (data from: Environment Canada, 2016; http://climate.weather.gc.ca/climate_data/).

<table>
<thead>
<tr>
<th>T\textsubscript{a} (°C)</th>
<th>NEE\textsubscript{LAND} ± std μmol m\textsuperscript{-2} s\textsuperscript{-1}</th>
<th>GPP\textsubscript{LAND} ± std μmol m\textsuperscript{-2} s\textsuperscript{-1}</th>
<th>ER\textsubscript{LAND} ± std μmol m\textsuperscript{-2} s\textsuperscript{-1}</th>
<th>n</th>
<th>days %</th>
</tr>
</thead>
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<tr>
<td>≤-2.5 °C</td>
<td>+0.28±0.22</td>
<td>0.04±0.11</td>
<td>0.33±0.17</td>
<td>169</td>
<td>45.6</td>
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<tr>
<td>-2.5 °C &lt; T\textsubscript{a} ≤ 2.5 °C</td>
<td>+0.28±0.27</td>
<td>0.21±0.19</td>
<td>0.49±0.22</td>
<td>53</td>
<td>8.5</td>
</tr>
<tr>
<td>2.5 °C &lt; T\textsubscript{a} ≤ 7.5 °C</td>
<td>+0.16±0.56</td>
<td>0.72±0.68</td>
<td>0.88±0.62</td>
<td>52</td>
<td>9.1</td>
</tr>
<tr>
<td>7.5 °C &lt; T\textsubscript{a} ≤ 12.5 °C</td>
<td>-0.45±0.65</td>
<td>2.26±1.32</td>
<td>1.81±1.03</td>
<td>63</td>
<td>10.5</td>
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<tr>
<td>12.5 °C &lt; T\textsubscript{a} ≤ 17.5 °C</td>
<td>-0.67±0.85</td>
<td>3.74±1.40</td>
<td>3.08±1.06</td>
<td>90</td>
<td>15.2</td>
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<tr>
<td>17.5 °C &lt; T\textsubscript{a} ≤ 22.5 °C</td>
<td>-0.80±0.58</td>
<td>4.35±1.32</td>
<td>3.55±1.07</td>
<td>86</td>
<td>9.8</td>
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<tr>
<td>T\textsubscript{a} &gt; 22.5 °C</td>
<td>-0.59±0.52</td>
<td>5.15±0.59</td>
<td>4.56±0.74</td>
<td>12</td>
<td>1.3</td>
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</tbody>
</table>

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\textsubscript{LAND}) and wetland-scale (NEE\textsubscript{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\textsubscript{WET}). The solid blue and yellow lines show the total least squares regressions for low (FP\textsubscript{WET} < 50 %) and high FP\textsubscript{WET} (FP\textsubscript{WET} ≥ 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 25\textsuperscript{th} and 75\textsuperscript{th} 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\textsubscript{LAND} & ΣNEE\textsubscript{WET}, solid lines). Grey shaded areas indicating 95 % confidence

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intervals of $\Sigma$NEE 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 ($\text{NEE}_{\text{LAND}}$). Closed circles show measured $\text{NEE}_{\text{LAND}}$ 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 10th and 90th percentiles. Mean daily gross primary productivity derived from $\text{NEE}_{\text{LAND}}$ ($\text{GPP}_{\text{LAND}}$) 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 ($\text{SW}_{\text{in}}$). (d) $\text{GPP}_{\text{LAND}}$ against $\text{SW}_{\text{in}}$. Color-coding shows $T_a$.

**Fig. 6:** Mean daily ecosystem respiration at the landscape tower ($\text{ER}_{\text{LAND}}$) 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 ($\text{GPP}_{\text{POT}}$) is limited by (a) air temperature ($T_a$), (c) incoming shortwave radiation ($\text{SW}_{\text{in}}$), or (b) co-limited by both variables. The dashed line shows $\text{GPP}_{\text{POT}}$-limitation for $T_a$ and $\text{SW}_{\text{in}}$ measured at Scotty Creek between August 2015 and July 2016. Solid lines indicate ensemble mean $\text{GPP}_{\text{POT}}$-limitation for the recent and projected modeled $T_a$ and $\text{SW}_{\text{in}}$ from six combinations of four regional and three global climate models.

**Fig. 8:** Projections (2091-2100) of monthly modeled gross primary productivity ($\text{GPP}_{\text{MOD}}$), ecosystem respiration ($\text{ER}_{\text{MOD}}$), and net ecosystem carbon dioxide exchange ($\text{NEE}_{\text{MOD}}$) 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) $\text{GPP}_{\text{MOD}}$, $\text{ER}_{\text{MOD}}$, and $\text{NEE}_{\text{MOD}}$. 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-21st-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 ($\pm$10% difference in mean annual precipitation and $\pm$0.5 °C of mean annual air temperature). Red circles indicate locations where, additionally, differences in annual incoming shortwave radiation ($\text{SW}_{\text{in}}$) are $\pm$30%. Grey shaded area is the current extent of the boreal zone (data from Brandt, 2009).
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