

Controls on plot-scale growing season CO₂ and CH₄ fluxes in restored peatlands: Do they differ from unrestored and natural sites?

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SUMMARY

This study brings together plot-scale growing season fluxes of carbon dioxide (CO₂) and methane (CH₄) from six Canadian peatlands restored by the moss layer transfer technique (MLTT) and compares them with fluxes from adjacent unrestored and natural peatlands to determine: 1) if CO₂ and CH₄ fluxes return to natural-site levels and 2) whether the ecohydrological controls (e.g. water table, plant cover) on these fluxes are similar between treatments. We also examine differences between eastern (humid/maritime climate) and western (sub-humid climate) Canadian plots, and between restoration of former horticultural peat extraction sites and oil industry well-pads. Our results indicate that restored site fluxes of CO₂ and CH₄ are not significantly different between eastern and western Canada or between a restored well-pad and restored horticultural peat extraction sites. Restoration resulted in gross primary production rates similar to those at natural plots and significantly greater than those at unrestored plots. Ecosystem respiration was not significantly different at restored and unrestored plots, and was lower at both than at natural plots. Methane emission was significantly greater at restored plots than at unrestored plots, but remained significantly lower on average than at natural plots. Water table was a significant control on CH₄ flux across restored and natural plots. Vascular plant cover was significantly related to CO₂ uptake (gross photosynthesis) at restored and unrestored plots, but not at natural plots, while higher moss cover resulted in significantly greater net uptake of CO₂ at natural plots but not at restored and unrestored plots. Overall, MLTT restoration greatly alters CO₂ and CH₄ dynamics compared to unrestored areas but fluxes remain, on average, significantly different from those in natural peatlands, in both the magnitude of mean growing season fluxes and controls on variation in these fluxes among plots. Peatland restoration by MLTT results in reduced CO₂ emissions and higher CH₄ emissions; however, more year-round measurements in more restored peatlands over longer periods post-restoration are needed to improve greenhouse gas emission estimates for restored Canadian peatlands.

KEY WORDS: cutover peatland, emission factors, greenhouse gas, rewetting, well-pad restoration

INTRODUCTION

Peatlands represent a globally significant stock of soil carbon (C) estimated at around 600 Gt C (Page *et al.* 2011), with northern peatlands accounting for approximately 390–440 Gt C of this total (Page *et al.* 2011, Loisel *et al.* 2014). This C stock has resulted from a small imbalance, over millennia, between C uptake as gross primary production (GPP) and loss of C as ecosystem respiration (ER), methane (CH₄) emissions and fluvial C exports. Methane release from northern peatlands also represents a globally significant greenhouse gas (GHG) source (e.g. Bridgman *et al.* 2013), although research suggests that the balance of long-term C sequestration and

CH₄ emissions from northern peatlands has resulted in net atmospheric cooling over the Holocene (Frolking & Roulet 2007).

Many northern peatlands have been disturbed by human activities that include agriculture, forestry, and resource exploration and extraction. This disturbance often results in the release of soil C (e.g. Turetsky *et al.* 2002, Rooney *et al.* 2012). In Canada, peat is extracted mainly for horticultural use. An estimated 27,500 ha of peatland has been disturbed by horticultural peat extraction, which is currently active on 16,000 ha (Canadian Sphagnum Peat Moss Association, personal communication). Peat extraction involves clearing the site of vegetation and lowering the water table, which results in large and

persistent CO₂ emissions (Waddington *et al.* 2002), lower CH₄ flux from peat fields (Waddington & Day 2007) and the conversion of GHG sinks to sources. Restoration may reverse these changes; in Canada the explicit goals of peatland restoration are to return peatland species and hydrological conditions to a state that allows peat and C accumulation functions to recover in the long term (Rocheffort *et al.* 2003). These goals and two decades of research (e.g. Campeau & Rocheffort 1996, Price *et al.* 1998, Waddington *et al.* 2002, Cobbaert *et al.* 2004, González *et al.* 2014) have led to development of the moss layer transfer technique (MLTT) for peatland restoration. In this method, drainage ditches are blocked or completely filled and donor material is collected from an undisturbed area and spread on the extracted peatland, covered with straw mulch and often fertilised with rock phosphate (Rocheffort *et al.* 2003). Sites restored using MLTT have lower CO₂ emission rates (Waddington *et al.* 2010, Strack & Zuback 2013, Strack *et al.* 2014) and higher CH₄ emissions (Waddington & Day 2007, Strack *et al.* 2014) than unrestored sites, and may return to being growing season C sinks within ~5–10 years (e.g. Waddington *et al.* 2010, Strack *et al.* 2014).

Increasingly, peatlands in northern Canada (where they are a dominant land cover type, Vitt *et al.* 1998) are impacted by mining operations, e.g. minerals and oil sands extraction. When disturbance includes the removal of vegetation, the MLTT may again be useful for peatland restoration and the approach is currently being tested on a constructed peatland following open pit extraction of oil sands (Daly *et al.* 2012) and for the restoration of former well-pads used for oil extraction (Sobze *et al.* 2012).

For all of these applications it is essential that the GHG emissions or removals related to MLTT restoration are quantified in Canada's national inventory report to the United Nations Framework Convention on Climate Change (UNFCCC), as GHG exchanges on managed land. While the IPCC *Wetlands Supplement* (IPCC 2014) provided updated guidance on reporting of GHG emissions and removals from rewetted organic soils (Blain *et al.* 2014), it is unclear how fluxes following MLTT may differ from those associated with simply rewetting drained peatland. Moreover, a better understanding of fluxes from peatlands in Canada that have been restored using MLTT can be used to derive the Canada-specific emission factors needed for reporting at Tier 2 or Tier 3 levels. In this context it is important to consider not only GHG emissions, but also the controls on these emissions. To ensure the availability of activity data for use in constructing national scale inventories, these controls should be

relatively easy to measure across many sites or utilise data that can be obtained from independent sources. The uptake of CO₂ through photosynthesis is related to availability of light (e.g. Frolking *et al.* 1998), plant functional type and cover (e.g. Leppälä *et al.* 2008, Strack *et al.* 2014) and water table position (e.g. Sulman *et al.* 2010). Emissions of CO₂ *via* soil respiration are generally correlated to soil temperature (e.g. Lafleur *et al.* 2005) and water table position (e.g. Sulman *et al.* 2010), while plant cover may be important when plant respiration makes an important contribution to ecosystem respiration (e.g. Strack *et al.* 2014, Renou-Wilson *et al.* 2016). Water table is often the strongest predictor of CH₄ flux (e.g. Couwenberg & Fritz 2012, Wilson *et al.* 2016), although soil temperature (e.g. Treat *et al.* 2007) and the presence of species with aerenchyma, also referred to as “shunt” species (Couwenberg & Fritz 2012), may also be important controls. As hydrology and plant type at restored sites may differ from those at natural and unrestored peatlands (e.g. Poulin *et al.* 2013, McCarter & Price 2015), the relative importance of these controls on GHG fluxes may also differ. A better understanding of controls on GHG emissions can help inform restoration planning to minimise GHG emissions when climate change mitigation is a primary goal of the restoration project. A comparison of the relative importance of controls at unrestored, restored and natural sites will also help to evaluate the return of biogeochemical function post-restoration.

Therefore, the objective of this study was to compile plot-scale GHG flux data from Canadian peatlands restored using the MLTT method, in order to answer the following questions: 1) What are the mean growing season fluxes of CO₂ and CH₄ from MLTT restored peatlands and how do they compare with fluxes from adjacent unrestored and natural peatlands? 2) Do CO₂ and CH₄ fluxes from MLTT restored peatlands vary between eastern and western Canada, or by the type of disturbance prior to restoration (well-pad *versus* horticultural peat extraction)? 3) How are plant functional type (e.g. moss, graminoid, shrub) and total plant cover, mean water table position and mean surface soil temperature related to CO₂ and CH₄ fluxes and do these relationships vary between unrestored, restored and natural peatlands? We hypothesised that plots in MLTT restored peatlands would have similar fluxes to natural peatlands and greater CH₄ emissions and net CO₂ uptake than unrestored plots. Given the levels of vegetation recovery observed, we also hypothesised that fluxes would be similar in eastern and western Canada, and at well-pads and sites disturbed by horticultural peat extraction. Finally, we

hypothesised that vegetation cover would be a significant control on CO₂ flux and water table a significant control on CH₄ flux, with sensitivity to water table being similar at natural and restored plots but lower at unrestored peatlands (e.g. Blain *et al.* 2014).

STUDY SITES

Three study sites in Alberta and three in Québec, Canada were included in the present study. Horticultural peat had been extracted from five of these sites while the sixth was restored following partial removal of a mineral soil pad that had been placed for oil extraction. Details of each study site are given below. In each case the MLTT was used for restoration. To restore a peatland using MLTT the site is first prepared by levelling the peat surface. In some cases (often in Alberta), ditches are filled completely with peat while in other cases (often in Québec), the ditches are blocked but left open and may contain standing water. In the case of the well-pad, the mineral soil fill was removed completely or buried beneath the peat prior to moss reintroduction. Donor (moss layer) material is collected from the top 10 cm of a nearby peatland with moss dominant in the understorey and spread on the area to be restored, usually in a 1:10 ratio (1 ha donor area spread over 10 ha restored area). Although MLTT targets moss-dominated donor areas, vascular plant propagules are also transplanted as seeds and rhizomes collected with the moss. The donor material is covered with straw mulch to create a favourable microclimate for moss establishment. Rock phosphate fertiliser is often applied to promote the establishment of *Polytrichum strictum* and vascular plants that help stabilise the peat surface. Quinty & Rochefort (2003) recommend the application of straw at 3000 kg ha⁻¹ and rock phosphate at 150 kg ha⁻¹. Straw was applied at these rates at all study sites and details of fertilisation are given in the site descriptions.

Bois-des-Bel (BDB)

The 7.5 ha restored area (47.833 °N, 69.417 °W) had been left for ~20 years following the cessation of horticultural peat extraction, prior to restoration. As the first step of restoration, any vegetation that had recolonised during this time was removed from the surface and pushed into the ditches. The ditches were blocked but not infilled. Donor material was collected from a nearby ombrotrophic bog. Straw and fertiliser were applied at the recommended rates (see above). The unrestored peatland was part of the same extracted area and was separated from the restored

section by one peat field (30 m wide) left as a buffer. Vegetation was not removed from the unrestored area. The natural area was an open section of a sparsely treed ombrotrophic bog and part of the same peatland as the restored site but located ~2 km to the north-west. Sample plots (60 × 60 cm) in the natural area were distributed to capture the microtopography present in the bog. Data were collected at the restored and unrestored plots in Years 1–3 following restoration. The measurements were repeated in Year 10 and also included measurements at the natural site. In Year 15, fluxes were measured at the restored site and the data for unrestored peatland were collected at a peatland near Saint-Alexandre-de-Kamouraska (47.733 °N, 69.611 °W), where extraction ceased in 1999 - the year in which Bois-des-Bel was restored.

Bic-St.-Fabien (BSF)

At Bic-St.-Fabien (48.322° N, 68.833° W) manual block-cut peat extraction began in 1946 and was superseded by vacuum harvesting in recent decades (see also Mahmood & Strack 2011). Vacuum harvesting ceased in 2000, leaving only a shallow (0.4 to >1.1 m) residual peat layer on top of gyttja (Malloy & Price 2014). Because this resulted in more minerotrophic conditions at the surface, the goal at this site was to establish a fen ecosystem. Bunds were created along topographic contours to hold water on the site and in November 2009 donor material from a nearby moderately-rich fen was spread over ~2 ha and covered with straw mulch at a typical rate for MLTT. Measurements were made on four bare peat areas in summer 2009, prior to restoration, and represent unrestored values. Six additional C flux plots were established along a hydrological gradient in the MLTT area of the site in spring 2010, and measured for the first three years post-restoration. A natural moderately-rich fen immediately adjacent to the restored area was used as a natural site with triplicate plots placed on *Sphagnum*-dominated hummocks and triplicate plots in hollows dominated by *Drepanocladus* spp., *Trichophorum cespitosum* and other herbaceous species.

Pointe-Lebel (PLB)

Vacuum harvesting at the Pointe-Lebel peatland (49.133° N, 68.241° W) began in the 1970s. The natural portion of the bog is open with occasional low *Picea mariana* trees, ericaceous shrubs, and *Sphagnum rubellum* and *Sphagnum fuscum* as the dominant moss species (Cagampan & Waddington 2008). Twelve plots were distributed across the natural area to capture the full range of vegetation communities represented. The restored area was treated with the standard MLTT protocols and five

plots were measured in the first year post-restoration. Ditches were blocked but remained open (i.e. they were not completely infilled with peat) and were rarely full of water during the measurement period. Six plots were installed for flux measurement in the unrestored area, which was adjacent to the restored area and had no vegetation. At both the restored and unrestored sites, plots were distributed to capture the hydrological gradients present on the site.

Seba Beach (SEB)

At the ~30 ha restored section (53.458° N, 114.884° W) ditches were completely infilled but a perimeter ditch remained. Donor material was collected from a treed ombrotrophic bog within the same peatland complex. Straw mulch was spread within the study area immediately following donor material placement, but in the north-east portion of the site straw application was delayed until the following winter due to wet conditions. During this second straw spreading, straw was also added to the study plots and this probably resulted in higher rates of application than recommended by Quinty & Rochefort (2003). The restored site was not fertilised during the study period. A total of 18 plots, arranged systematically along the hydrological gradient, were measured at the restored site. The unrestored peatland, with six plots, was ~300 m from the restored area. Three plots, located in the main plant communities, were measured in the natural peatland. This was a treed ombrotrophic bog immediately adjacent to the area where the donor material was collected. Data were collected in the first and second years following restoration.

Wandering River (WRR)

The 10 ha restored peatland (55.293° N, 112.475° W) is located north of the town of Wandering River, Alberta (see also Strack *et al.* 2014). Ditches within the restored area were completely infilled, but the perimeter ditch remained open. Donor material was collected at an ombrotrophic bog within the same peatland complex and straw and fertiliser were applied according to Quinty & Rochefort (2003). Twelve plots were installed in a grid to capture the variation in water table position and plant cover across the restored site. Three plots were installed along the hydrological gradient at the unrestored peatland, which was immediately adjacent to the restored area but separated from it by a ditch. At the natural peatland, which was a treed ombrotrophic bog located approximately 9 km from the restored site, six plots were installed representing triplicate hummocks and hollows (Munir *et al.* 2014). Data were collected three years after restoration.

Peace River inversion pad (PRP)

The restored section is a 1.4 ha former well-pad that was constructed but never drilled, located in a treed moderately-rich fen north-east of Peace River, Alberta (56.397° N, 116.890° W). Restoration involved removal of the mineral soil fill and geotextile material that was placed to construct the well-pad, and inversion of the underlying peat (see Sobze *et al.* 2012 for details). Where the peat was shallow, some mineral soil fill was buried beneath the peat so that the surface was 10 cm lower than adjacent hollows. This altitude difference was chosen to allow for rebound of the peat, with the intention that the restored area should be level with nearby hollows afterwards. Thicker peat was simply inverted without burial of mineral soil. Once a flat bare peat surface had been created, donor material from neighbouring fens was placed on most of the restored area with some strips left as unvegetated controls. All plots used in this study were then covered with straw mulch, but not fertilised. A total of 39 plots were installed to represent all restoration activity (i.e. fill burial, complete fill removal) and donor site combinations (i.e. different fens). Since the entire well-pad was removed and inverted, there was no unrestored area at this site. Eighteen natural plots were located ~100 m from the well-pad in a surrounding fen. Measurements were made two years after restoration.

METHODS

All flux data included in this study represent mean growing season fluxes. For inclusion in the analysis, a frequency of at least monthly measurements over the period May to August resulting in a minimum of five flux measurements for a given study plot was required. In most cases (> 90 % of the dataset), values are averages of 8–12 measurements made over one growing season (May–late August/early September).

Carbon dioxide flux

Carbon dioxide exchange ($\text{g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$) was determined using the closed chamber method (e.g. Alm *et al.* 1997). The net ecosystem exchange (NEE) of CO₂ was determined with a clear acrylic chamber placed on a stainless steel collar (60 × 60 cm) permanently installed at each sampling plot. The chambers were 60 × 60 cm × 30 cm high except for some bare peat respiration measurements (BSF, WRR) and all measurements at BDB in the period 1999–2002, which used cylindrical chambers 20 cm in diameter and 20–40 cm tall placed on collars of the same diameter. A groove in the collar held the

chamber and was filled with water to create a seal. A battery-operated fan installed inside the collar circulated the headspace air throughout the measurement period, and the chamber was lifted from the collar between each pair of measurements to allow equilibration to ambient CO₂ concentration and temperature. The concentration of CO₂ (ppm) was determined inside the chamber at 15–30 second intervals for 2–5 minutes using a portable infrared gas analyser (IRGA; EGM, various models, PP Systems, Massachusetts, USA). Photon flux density of photosynthetically active radiation (PAR) was measured with a sensor connected to the IRGA. The linear change in CO₂ concentration over time was used to calculate NEE. Fluxes were rejected if the concentration change was not linear ($R^2 < 0.75$) unless the CO₂ concentration was stable (change was < 2 ppm) indicating NEE close to zero, in which case the flux was retained. Less than 1 % of the data were omitted. Ecosystem respiration (ER) was determined by darkening the chamber with an opaque shroud. Gross ecosystem photosynthesis (GEP) was calculated as the difference between NEE and ER. Maximum rates of GEP and NEE (GEP_{max}, NEE_{max}) were determined at each plot when photon flux density of PAR was greater than 1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ and photosynthesis should not be limited by available radiation (Bubier *et al.* 2003). We use the sign convention that positive values indicate a release of CO₂ from the ecosystem to the atmosphere.

Methane flux

Methane flux was determined at the same plots used for NEE measurements using opaque closed chambers (same volume as CO₂ chambers) equipped with battery-operated fans to circulate the air in the chamber headspace. Chambers were placed on the collars and 20 ml gas samples were collected 3–4 times over a period of 30–45 minutes after closure and stored in pre-evacuated vials (Exetainers, Labco Ltd., UK), or syringes in 1999–2002 at BDB. The concentration of CH₄ in the samples was determined on a Varian 3800 gas chromatograph (GC) equipped with a flame ionisation detector at 250 °C and helium as a carrier gas at 30 ml min⁻¹. Standards of known CH₄ concentration (50 ppm) were run every eight samples to check for drift. CH₄ flux ($\text{mg CH}_4 \text{m}^{-2} \text{d}^{-1}$) was determined from the linear change in concentration over time. When the change in concentration over time was within the precision of the GC (~ 0.5 ppm over the 35 minute sampling period, minimum detection limit $\sim 5 \text{ mg CH}_4 \text{m}^{-2} \text{d}^{-1}$), the flux was considered zero. Fluxes with erratic changes in concentration that suggest ebullition related to disturbance during chamber placement

were omitted, resulting in 5–10 % data loss depending on the site.

Environmental conditions

At most sites the position of the water table was determined manually in a groundwater well installed adjacent to the sample plot during each flux measurement. Soil temperature profiles at 5 cm intervals to a depth of 20 cm were measured adjacent to each plot using a thermocouple thermometer. The volume of the chamber was corrected by measuring the height of the ground surface relative to the top of the collar for at least 12 locations systematically distributed across the collar footprint. Vegetation cover within each plot was estimated visually in July or August. Species were grouped as mosses, forbs, graminoids, shrubs and trees and the cover of each plant functional type was estimated to the nearest 1 %.

Statistical analysis

The distribution of plots within each site was not consistent. In some cases, plots were placed systematically across the site while in others specific plant communities were targeted. However, in all cases, plots were distributed to account for the variation in plant cover and water table across the study site and thus the mean values of GHG flux account for this variation. For our analysis, each plot was kept as an individual measurement and we made no attempt to estimate site-specific flux based on the actual distribution of vegetation types across the site because these data were not available for all sites. Instead, the focus was on improving our understanding of the controls on the plot-scale fluxes to facilitate future estimation of fluxes across restored sites where flux data are unavailable. Therefore, the data comprise repeated measurements where fluxes were measured at multiple locations within a peatland, sometimes in several years. To address this, all data analysis was completed using linear mixed effects (LME) models in R (R Core Team 2013) using the package nlme (Pinheiro *et al.* 2014) with site as a random factor. All models were visually inspected for normality and homogeneity of residuals and the data were transformed or variance structures included in models where required (Zuur *et al.* 2009). Seasonal mean values of flux measured at each plot were used in all cases with statistical significance considered at the $\alpha = 0.05$ level.

In order to evaluate differences in fluxes of CO₂ and log(CH₄) between restored, unrestored and natural plots, LME was used with restoration state (i.e. restored, unrestored or natural) as a fixed factor and site as a random factor. When significant differences were present, Tukey pairwise

comparisons using the package *multcomp* (Hothorn *et al.* 2008) were completed. Statistics are reported considering type III errors and F-values generated using the *Anova* command in R.

To evaluate differences in fluxes between eastern and western Canada, LME was used with restoration state, location and their interaction as fixed factors and site as a random factor. If significant factors were found, Tukey pairwise comparisons were completed. If the interaction term was significant, a one-way Anova (with site as a random factor) with Tukey pairwise comparisons was completed with each restoration state-location combination as a group (i.e. restored/eastern Canada *versus* restored/western Canada *versus* unrestored/eastern Canada, *etc.*). A similar approach was used to evaluate differences between horticultural and well-pad plots with land use as a factor instead of location.

To investigate controls on fluxes and whether these varied between restored, unrestored and natural peatlands, each LME was constructed starting with a full model that considered water table position, moss cover, vascular plant cover, mean growing season soil temperature at 5 cm depth, restoration state and two-way interactions between each of these factors and restoration state as fixed factors and site as a random factor. Graminoid cover and graminoid-restoration state interaction (Couwenberg & Fritz 2012) were also added to the initial model for CH₄ flux. Non-significant factors were dropped one at a time from the model, starting with the least significant, until the final model was determined. In cases where the interaction term was significant, the individual factors were retained in the model even when they were non-significant. Evaluation of residuals from the models indicated mild heterogeneity in all cases. To address this, a fixed variance structure was implemented with different variances by site; this improved normality and homogeneity of residuals. We calculated the amount of variance described by each model as R^2_{GLMM} , as defined by Nakagawa & Schielzeth (2013), using the package *MuMIn* (Barton 2015).

RESULTS

After compiling data from all sites and years, 316 individual plot-year mean fluxes were included. Not all plots had data for all fluxes and environmental variables, so some plots were omitted from some analyses due to missing data. In general, restoration resulted in a significantly shallower water table (i.e. wetter conditions; Tukey contrasts, $z = 11.04$, $p < 0.001$) and a significant increase in vascular

vegetation and moss cover compared to unrestored plots (vascular, $z = 4.57$, $p < 0.001$; moss, $z = 8.48$, $p < 0.001$); however, restored plots remained on average significantly drier than natural plots ($z = 2.81$, $p = 0.013$), and had a significantly lower cover of mosses and shrubs but a higher cover of graminoids (Table 1; moss, $z = 9.604$, $p < 0.001$; shrub, $z = 2.338$, $p = 0.05$; graminoid, $z = 6.436$, $p < 0.001$). Soil temperature at 5 cm depth was significantly lower at the natural plots than at the restored ($z = 8.536$, $p < 0.001$) and unrestored ($z = 7.784$, $p < 0.001$) plots, which were similar (Table 1).

Mean carbon gas fluxes at restored peatland plots

Restoration under full light conditions (photosynthetically active photon flux density $> 1000 \mu\text{mol m}^{-2} \text{s}^{-1}$) resulted in greater rates of growing season GPP, higher ER and a switch in NEE from a loss of CO₂ to the atmosphere to a sink when compared to unrestored plots. Aside from ER, these changes were statistically significant (Figure 1). Compared to natural plots, restored plots had statistically similar GPP, lower ER, and NEE that was a greater sink. Methane flux was greater at restored plots than at unrestored plots (Figure 1), although not significantly different ($z = -2.057$, $p = 0.097$), and significantly lower than at natural plots ($z = 3.228$, $p = 0.004$).

There was no significant effect of location (eastern *versus* western Canada) or interaction of location with restoration status on ER (location: $F_{1,5} = 4.43$, $p = 0.09$, location \times restoration: $F_{2,298} = 2.53$, $p = 0.08$) or CH₄ flux (location: $F_{1,5} = 5.18$, $p = 0.07$, location \times restoration: $F_{2,248} = 2.22$, $p = 0.11$). For GPP there was a significant interaction between location and restoration status ($F_{2,297} = 6.51$, $p = 0.002$). The one-way Anova indicated that unrestored plots had significantly lower productivity than natural plots in eastern Canada, but this difference was not significant in western Canada; restored plots in both locations had significantly greater productivity (more negative GPP) than unrestored plots. There was also a significant location-restoration interaction for NEE ($F_{2,297} = 17.21$, $p < 0.001$) with restored plots having significantly greater uptake of CO₂ than unrestored plots in western Canada, while the difference was not significant in eastern Canada. As with GPP, differences in NEE between restored and unrestored plots were significant in both locations, with restored plots acting as sinks for CO₂ while unrestored plots were sources. Over all flux components, there were no significant differences specifically between restored plots in eastern Canada and western Canada based on Anova (Figure 2).

Table 1. Average (standard error) site characteristics.

Site*		# plots measured	Soil temp 5 cm (°C)	Water table (cm)	Vascular plant cover (%)	Shrub cover (%)	Graminoid cover (%)	Moss cover (%)
BDB	Natural	6	13.9 (0.7)	-15.4 (0.9)	22 (5)	13 (5)	2 (1)	90 (6)
	Restored (1–3 years)	6–11	16.3 (0.4)	-32.6 (1.7)	21 (8)	1 (1)	18 (9)	37 (9)
	Restored (10–15 years)	16–24	14.5 (0.3)	-25.6 (1.4)	32 (3)	16 (2)	12 (2)	70 (5)
	Unrestored	7–12	16.1 (0.2)	-51.0 (1.6)	18 (5)	20 (7)	2 (1)	9 (5)
BSF	Natural	6	14.4 (0.3)	-18.1 (5.6)	18 (5)	3 (1)	8 (3)	97 (3)
	Restored	6	16.1 (0.5)	-26.4 (2.3)	11 (5)	0 (0)	3 (2)	3 (2)
	Unrestored	4	18.8 (0.6)	-33.6 (2.6)	0 (0)	0 (0)	0 (0)	0 (0)
PLB	Natural	12	16.8 (0.5)	-23.1 (2.2)	46 (9)	38 (9)	2 (1)	92 (3)
	Restored	5	16.6 (0.5)	-36.9 (6.1)	n.d.	n.d.	n.d.	n.d.
	Unrestored	6	17.8 (0.5)	-50.7 (10.7)	0 (0)	0 (0)	0 (0)	0 (0)
WRR	Natural	6	13.6 (0.3)	-36.4 (3.7)	112 (11)	74 (4)	0 (0)	77 (7)
	Restored	12	16.9 (0.3)	-26.3 (5.3)	57 (7)	15 (3)	39 (6)	27 (9)
	Unrestored	3	15.1 (0.1)	-57.2 (20.4)	0 (0)	0 (0)	0 (0)	0 (0)
SEB	Natural	3	15.3 (1.2)	-28.9 (3.7)	32 (7)	24 (5)	6 (4)	78 (11)
	Restored	18	15.7 (0.3)	-27.3 (2.5)	14 (5)	n.d.	n.d.	n.d.
	Unrestored	6	17.3 (0.6)	-64.1 (4.5)	0 (0)	0 (0)	0 (0)	0 (0)
PRP	Natural	18	12.1 (0.5)	-9.2 (1.1)	39 (2)	17 (2)	2 (1)	55 (3)
	Restored	33	18.9 (0.4)	-19.1 (1.4)	46 (4)	7 (1)	34 (4)	22 (4)
mean [§]	Natural		14.1 (0.3) ^a	-19.2 (1.6) ^a	44 (4) ^c	27 (4) ^b	3 (1) ^a	77 (6) ^c
	Restored		16.6 (0.2) ^b	-25.0 (1.0) ^b	33 (2) ^b	9 (1) ^a	22 (2) ^b	38 (3) ^b
	Unrestored		16.7 (0.2) ^b	-52.1 (2.6) ^c	11 (3) ^a	7 (3) ^a	5 (2) ^a	3 (2) ^a

*Site locations are given in the text. BDB=Bois-des-Bel, BSF=Bic-St. Fabien, PLB=Pointe Lebel, WRR=Wandering River, SEB=Seba Beach, PRP = Peace River well-pad

[§]Different letters indicate significant differences between groups

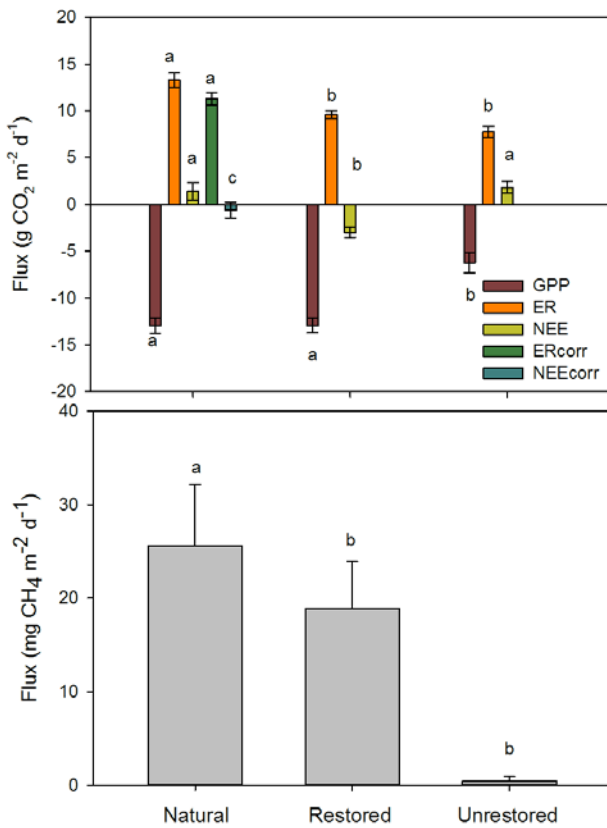


Figure 1. Top: Mean growing season gross primary production (GPP), ecosystem respiration (ER), net ecosystem CO₂ exchange (NEE); and bottom: methane (CH₄) flux (mg CH₄ m⁻² d⁻¹). GPP and NEE fluxes (g CO₂ m⁻² d⁻¹) when photon flux density of photosynthetically active radiation was greater than 1000 μmol m⁻² s⁻¹. Error bars are standard errors. Negative values represent uptake by the ecosystem. Values are significantly different based on Tukey pairwise comparisons if they have no letters in common; letters should be compared only within one flux component. ERcorr and NEEcorr at natural was calculated by subtracting 3.25 g CO₂ m⁻² d⁻¹ from ER values measured at treed sites (BSF, PRP, WRR) to remove the contribution of tree root respiration (see Discussion for details). Letters above these bars can be compared with respective ER and NEE values at restored and unrestored. Statistical tests for difference in CH₄ flux between treatments were based on log transformed data (see Methods), but non-transformed data are presented here.

There was no significant difference between the well-pad restored plots and the horticultural restored plots for any carbon gas flux (Figure 2; GPP: $F_{1,4}=0.49$, $p=0.52$; ER: $F_{1,4}=1.62$, $p=0.27$; NEE: $F_{1,4}=0.34$, $p=0.59$; logCH₄: $F_{1,4}=2.55$, $p=0.19$). Based on this, and the limited effect of location, all

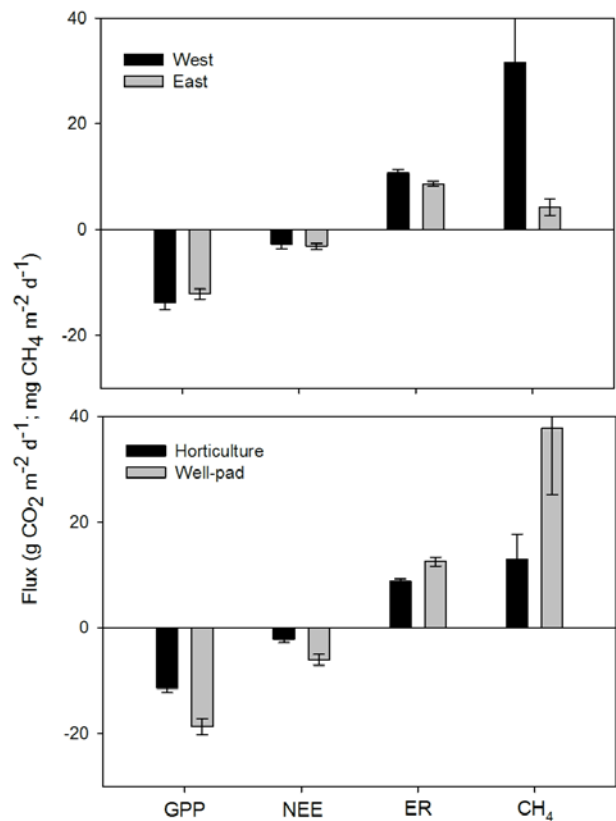


Figure 2. Comparison of fluxes of carbon dioxide (CO₂; g CO₂ m⁻² d⁻¹) (GPP=gross primary production, NEE=net ecosystem exchange, ER=ecosystem respiration) and methane (CH₄; mg CH₄ m⁻² d⁻¹) at peatlands restored using the moss layer transfer technique in eastern and western Canada (top) and peatlands formerly used for horticultural peat extraction and well-pads (bottom). Error bars give standard error. Negative values indicate uptake by the ecosystem.

restored plots were grouped together as “restored” in the analysis of controls on fluxes.

Controls on carbon gas fluxes

Variables included in the final models for each C flux component are given in Table 2. Variation in GPP was significantly related to restoration status, vascular plant cover and the interaction between restoration and vascular plant cover. In general, greater vascular plant cover resulted in greater productivity, but the slope of the relationship differed significantly between natural plots and both restored and unrestored plots, which were similar (Figure 3A).

Vascular plant cover, restoration status and the interaction between these variables significantly described the variation in ER. Across all plots, higher vascular plant cover resulted in higher ER, although this was only significant at restored and unrestored

Table 2. Statistical results of linear mixed effects models^a.

Flux component	Effect	F	p	R ² _{GLMM} ^b
GPP	Vascular	F _{1, 228} = 155.8	<0.0001	0.78
	Restoration	F _{2, 228} = 30.3	<0.0001	
	Vascular × restoration	F _{2, 228} = 36.0	<0.0001	
	Intercept	F _{1, 228} = 21.8	<0.001	
ER	Vascular	F _{1, 229} = 43.1	<0.0001	0.28
	Restoration	F _{2, 229} = 19.9	<0.0001	
	Vascular × restoration	F _{2, 229} = 9.7	<0.0001	
	Intercept	F _{1, 229} = 10.7	0.0013	
NEE	Vascular	F _{1, 178} = 83.4	<0.0001	0.76
	Moss	F _{1, 178} = 2.7	0.10	
	Water table	F _{1, 178} = 2.1	0.14	
	Restoration	F _{2, 178} = 8.6	0.0003	
	Vascular × restoration	F _{2, 178} = 9.1	0.0002	
	Moss × restoration	F _{2, 178} = 6.7	0.0015	
	Water table × restoration	F _{2, 178} = 4.6	0.011	
Intercept	F _{1, 178} = 0.4	0.52		
CH ₄	Water table	F _{1, 243} = 29.9	<0.0001	0.35
	Restoration	F _{2, 243} = 2.9	0.055	
	Water table × restoration	F _{2, 243} = 4.0	0.020	
	Intercept	F _{1, 243} = 169.3	<0.0001	

^aAll models have a random factor of site to account for repeated measurements made at each site. Details of models and final model selection are given in Methods.

^bWe report the marginal R²_{GLMM} accounting for variance explained by fixed factors only.

plots and not at natural plots (Figure 3B), resulting in the significant interaction term.

Variation in NEE was significantly described by vascular plant cover and restoration status (Figure 3C). There were also significant interactions between restoration status and vascular plant cover, moss cover and water table position. In general, as vascular plant cover increased, plots moved from acting as sources of CO₂ to sinks. However, this trend was only significant for restored and unrestored plots, not natural plots. In contrast, natural plots tended to act as greater sinks as moss cover increased, while there was no significant relationship between moss

cover and NEE for restored or unrestored plots (Figure 3D). Water table position was significantly correlated to NEE at restored plots but not at natural and unrestored plots (Figure 4).

Methane flux was significantly related to water table position and to an interaction between water table position and restoration state. Overall, shallower water table position resulted in higher CH₄ flux. The water table - flux relationship was significant and had a similar slope at natural and restored plots (Figure 4); the dry conditions across unrestored plots resulted in no significant correlation between water table and CH₄ flux.

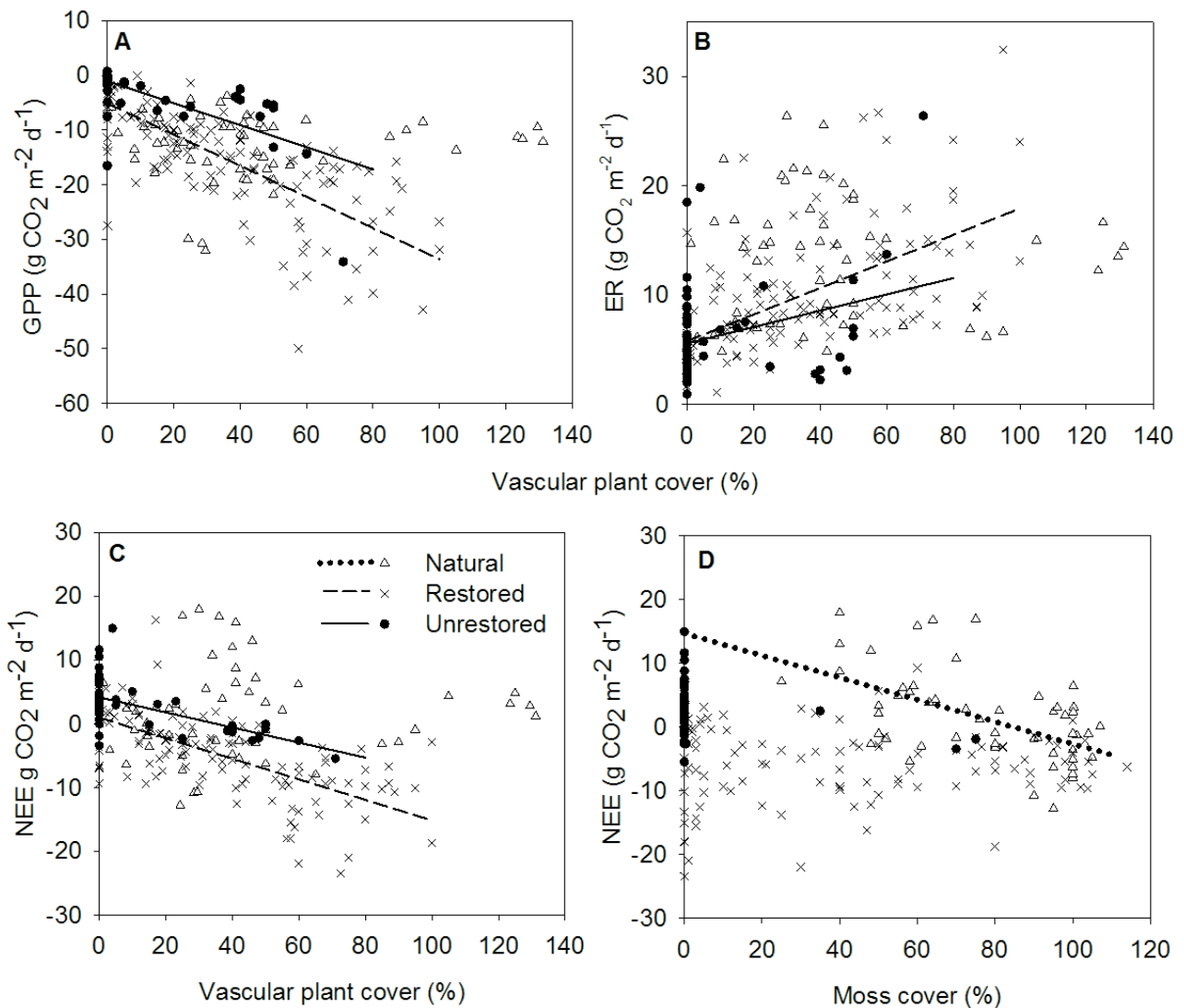


Figure 3. A) Gross primary production (GPP; g CO₂ m⁻² d⁻¹), B) ecosystem respiration (ER; g CO₂ m⁻² d⁻¹), C) net ecosystem exchange (NEE; g CO₂ m⁻² d⁻¹) versus vascular plant cover and D) NEE versus moss cover. GPP and NEE fluxes measured when photon flux density of photosynthetically active radiation was greater than 1000 μmol m⁻² s⁻¹. Negative values indicate uptake of CO₂ by the ecosystem. Regression lines are plotted for each restoration class when statistically significant. Regression equations are: A) unrestored: $GPP = -0.20(\text{vascular plant cover}) - 1.06$; restored: $GPP = -0.28(\text{vascular plant cover}) - 5.13$, B) unrestored: $ER = 0.075(\text{vascular plant cover}) + 5.61$; restored: $ER = 0.12(\text{vascular plant cover}) + 5.84$, C) unrestored: $NEE = -0.12(\text{vascular plant cover}) + 4.17$; restored: $NEE = -0.16(\text{vascular plant cover}) + 0.97$, D) natural: $NEE = -0.17(\text{moss cover}) + 14.7$.

DISCUSSION

In contrast to the results reported in the *Wetlands Supplement* (IPCC 2014), CO₂ and CH₄ fluxes from restored plots were not always statistically similar to those from natural plots (Figure 1); however, restoration consistently altered fluxes compared to unrestored plots. Restored plots had similar GPP to natural plots, but ER remained similar to unrestored plots. Although rewetting during restoration is likely to have reduced peat oxidation, ER can remain high

due to increasing plant respiration as the site is recolonised post-restoration (Strack & Zuback 2013, Strack *et al.* 2014, Figure 2) and due to the contribution of straw decomposition to CO₂ emissions (Waddington *et al.* 2003). ER from natural plots was significantly greater than from restored or unrestored plots and, on average, natural plots were a source of CO₂ to the atmosphere while restored plots were sinks. Both the high ER and net CO₂ source at natural plots is probably a result of using plot-scale measurements that capture only the ground level

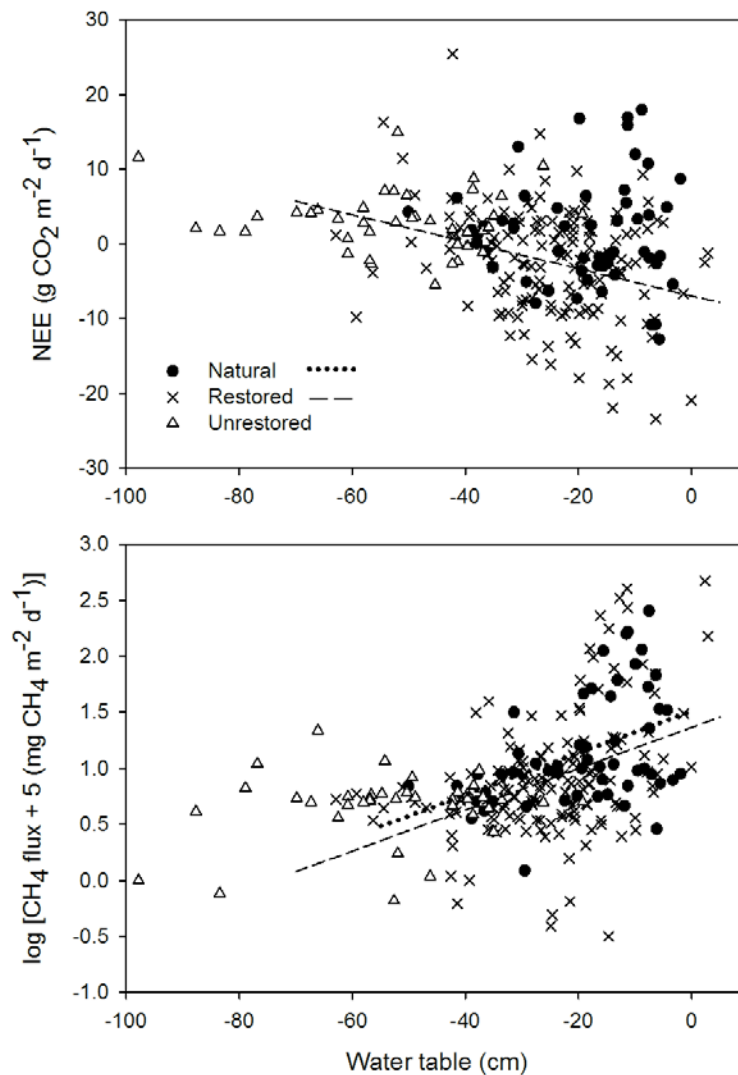


Figure 4. Net ecosystem exchange of carbon dioxide (CO₂; NEE; top) and methane (CH₄) flux (bottom) versus water table (WT) position. NEE fluxes (g CO₂ m⁻² d⁻¹) were measured when photon flux density of photosynthetically active radiation was greater than 1000 μmol m⁻² s⁻¹. Negative values indicate uptake of CO₂ by the ecosystem. Regression lines are plotted for each restoration class when statistically significant. Regression equations are: top) restored: $NEE = -0.18(WT) - 6.91$, bottom) natural: $\log(CH_4 + 5) = 0.019 + 1.51$; restored: $\log(CH_4 + 5) = 0.018 + 1.37$.

fluxes. Since three of the six sites were treed, these plot-scale fluxes include tree root respiration but omit GPP of the overstorey trees and thus underestimate C uptake by the ecosystem as a whole. To illustrate this effect, we subtracted the mean tree root respiration estimated at the natural site at WRR (3.25 g CO₂ m⁻² d⁻¹; Munir *et al.* 2014) from the treed natural peatland (BSF, WRR, PRP) ER and NEE fluxes (Figure 1). This reduced mean natural site ER and NEE to 11.3 g CO₂ m⁻² d⁻¹ and -0.6 g CO₂ m⁻² d⁻¹ respectively and is likely to better represent CO₂ exchange attributable to the understorey. Using these corrected NEE values, restored plots were still significantly greater sinks of CO₂ than natural plots.

Clearly, this correction still ignores NPP of the overstorey, which makes a significant contribution to C exchange in treed peatlands (e.g. Wieder *et al.* 2009, Munir *et al.* 2015), illustrating one of the complications of using chambers to determine GHG exchange. Trees are slow to recolonise restored sites (e.g. Pouliot *et al.* 2011) and it is likely to take decades for the overstorey component of the vegetation to recover (e.g. Wieder *et al.* 2009).

Average CH₄ emissions remained significantly lower at the restored plots than at the natural plots (Figure 1), although this is at least partially explained by the lower average water table position (Table 1) of the former and the dominant water table control on

CH₄ emissions (Figure 4). Lower CH₄ flux post-restoration has also been associated with the time taken for the microbial community, particularly archaea, to re-establish at restored sites (e.g. Juottonen *et al.* 2012). Moreover, as the goal of the present study was not to estimate site-specific annual emissions, we did not spatially weight fluxes to account for the area covered by each plot type on site. The substantial emission of CH₄ from remnant drainage ditches in drained and restored peatlands has been well documented (Waddington & Day 2007, Schrier-Uijl *et al.* 2011, Strack & Zuback 2013), and it is likely that accounting for the actual extent of these features following restoration would increase the estimated CH₄ flux at restored sites where ditches remain unfilled (e.g. Waddington & Day 2007, Strack & Zuback 2013, Cooper *et al.* 2014).

In addition to differences in mean fluxes between natural and restored plots, the controls on these fluxes often diverged between the site types. For example, vascular plant cover was the dominant driver of CO₂ exchange at restored and unrestored plots but was not statistically significant at natural plots. In contrast, moss cover significantly accounted for variation in NEE at natural plots but not at unrestored and restored plots. This difference is at least partially explained by the dominance of vascular plants over mosses at restored plots, particularly in the first few years post-restoration (Table 1). Similarly, Leppälä *et al.* (2008) reported that the replacement of sedges and herbs, which have high photosynthetic efficiency, by shrubs and *Sphagnum* mosses in later stages of peatland succession resulted in a reduction of seasonal variation in CO₂ exchange. This reflects the shifting importance of the role of mosses in CO₂ exchange during peatland succession, which may also occur over time following restoration (Table 1). Several studies have noted the peat forming potential of vascular plants in spontaneously revegetated (Graf & Rochefort 2009, Mahmood 2011) and restored peatlands (Andersen *et al.* 2013). While sedge peat is common in some fens (e.g. Zoltai *et al.* 2000), cores from many North American peatlands indicate a dominance of bryophyte remains in the peat (Vitt 2000). Our results indicate a shift from mosses at natural plots to vascular plants at restored plots as the main driver for net CO₂ uptake. The time needed for a shift to bryophyte dominance post-restoration and the implications of persistent vascular plant dominance for long-term peat accumulation at restored sites remains unclear.

There was generally greater variation in CO₂ and CH₄ fluxes at restored plots than at either unrestored or natural plots and this is likely to be linked to the larger variance in plant cover and water table position

at the former. Additionally, this variance could represent the changing conditions at restored peatlands with time since restoration. Although rewetting occurs quite rapidly once ditches are blocked, it takes several growing seasons for plant cover to establish (e.g. Waddington *et al.* 2010, Poulin *et al.* 2013) and community composition may continue to evolve over decades (Pouliot *et al.* 2011). This is likely to impact on GHG fluxes; however, given the limited available data, with only BDB having flux measurements carried out for more than three years post-restoration, the temporal trajectory of fluxes in restored Canadian peatlands cannot be described broadly. Looking at sites that had GHG fluxes measured in more than one year (BDB, BSF, SEB) it seems clear that GPP increases over time as plants become established, but then levels off over a decade timescale (considering only BDB; data not shown). There is also a clear shift from graminoid dominance in the early years post-restoration at BDB to greater importance of shrubs and mosses after ten years (Table 1). This may have implications for not only GPP but also ER and NEE rates, given the lower decomposability of *Sphagnum* compared to vascular plants (e.g. Graf & Rochefort 2009); and for CH₄ flux given the role that sedges play in transporting CH₄ to the atmosphere (e.g. Couwenberg & Fritz 2012). However, since data at this timescale are available for BDB only, we are unable to determine whether this trajectory is generally applicable or dependent on site-specific conditions. More GHG flux data from more sites at longer times post-restoration is required to address this question.

Many studies have reported factors controlling peatland GHG fluxes, which include water table position (e.g. Couwenberg & Fritz 2012), plant cover and type (e.g. Riutta *et al.* 2007), temperature (e.g. Lafleur *et al.* 2005), growing season length (e.g. Roulet *et al.* 2007), microbial community composition (e.g. Godin *et al.* 2012), nutrient availability (e.g. Lund *et al.* 2009), and pore water and peat chemistry (e.g. Basiliko *et al.* 2007). All of these factors are probably also important in determining restored peatland GHG fluxes. However, when attempting to develop useful estimates of GHG emissions for reporting at national level, it is only practical to consider controls that can be measured, or where data are available, at regional to national scales. For this reason we have focused the analysis here on soil temperature (measurable with inexpensive on-site sensors or estimated from meteorological data), plant cover (measurable with optical remote sensing or field level vegetation surveys) and water table position. The latter was found to be a significant control on plot-scale NEE

and CH₄ flux (Table 2, Figure 4), but is probably the most problematic to estimate at broad scales. Mapping of wet areas using LiDAR may be useful for determining water table position (Murphy *et al.* 2011), but has not been tested in managed peatlands. Water table can also be measured locally using relatively inexpensive water level recorders, but these values will not represent the spatial variation in water table position across the site unless combined with spatially distributed altitude data. Given the log-linear relationship between CH₄ flux and water table position, a mean water table estimate for a given site is likely to underestimate actual CH₄ flux (Becker *et al.* 2008, Baird *et al.* 2009). In any case, the results of the present study suggest that the development of methods to provide reliable water table estimates in restored peatlands will greatly improve GHG flux estimations.

The development of national inventories also involves decisions on how to disaggregate sites. In Canada there have been concerns that restoration efforts may lead to different results in eastern and western Canada due to the more continental climate in the west (Strack *et al.* 2014). We found very few differences in fluxes between plots in eastern and western Canada and no significant difference when restored eastern Canadian peatlands were compared to western Canadian peatlands. Based on these findings, a national value for GHG flux from restored peatland is likely to be appropriate, with improved estimates resulting when information on plant cover and water table position is considered. However, it is possible that differences between the regions in climate, hydrochemistry and species established post-restoration combine to produce similar mean GHG fluxes in the first few years. In this case, the response of the restored sites to disturbance and the temporal trajectory of recovery could vary and further research is required to evaluate this.

We also compared GHG fluxes between sites restored following horticultural peat extraction and a former well-pad site, and we found no significant difference. Our results suggest that, in some cases, emission factors developed from restored horticultural peat mines may be broadly applicable to restored peatlands in general. On the other hand, we have data from only one well-pad site two years post-restoration and the trajectory of the site over time remains unclear. Buried mineral soil could alter local chemistry with yet unmeasured consequences for GHG fluxes. Moreover, restoration of more highly disturbed industrial sites, such as the areas near Fort McMurray (Alberta) where surface mining of oil sands has been carried out, can result in extensive changes in hydrophysical and chemical properties of

peat (Nwaishi *et al.* 2015), and contamination with oil sands process water may limit plant establishment and productivity (Pouliot *et al.* 2012). As peatland construction under these conditions is a new endeavour (Daly *et al.* 2012, Pollard *et al.* 2012), more research is needed to develop emission factors for these sites.

Nitrous oxide (N₂O) is another GHG that is potentially emitted from managed peatlands (e.g. Maljanen *et al.* 2010). However, there are very few published values of N₂O emissions from unrestored or restored peatlands (Maljanen *et al.* 2010, Järveoja *et al.* 2016) or from natural peatlands in Canada (Wray & Bayley 2007). Even globally, estimates of N₂O emissions from active and restored peat extraction sites are scarce, although drainage has been shown to increase N₂O emissions in some cases (Maljanen *et al.* 2010, Drösler *et al.* 2014) with reduced fluxes at rewetted sites (Wilson *et al.* 2013, Wilson *et al.* 2016). Measurements are needed to develop a N₂O emission factor for restored Canadian peatlands, although the low nitrogen content at most sites suggests the flux is also likely to be low (e.g. Strack *et al.* 2014).

We have focused the present analysis on plot-scale values of CO₂ and CH₄ fluxes, as this is the scale at which most measurements have been made in Canada. This scale also allows an investigation of the controls on fluxes, which often vary at metre to sub-metre scales. In contrast, since these plot-scale measurements are discrete in time and often made only during the growing season, empirical modelling must be used to develop seasonal emission totals, with estimates of non-growing season fluxes incorporated to arrive at the annual estimates needed to develop emission factors. Using this approach, growing season estimates of -30 to 102 g C m⁻² for CO₂ exchange at MLTT restored Canadian peatlands have been reported in the literature (Waddington *et al.* 2010, Strack & Zuback 2013, Strack *et al.* 2014). Growing season CH₄ emissions have been estimated as 0.8 to 3.7 g CH₄-C m⁻² (Waddington & Day 2007, Strack & Zuback 2013, Strack *et al.* 2014). Eddy covariance measurements can provide a continuous ecosystem-scale estimate of CO₂ and CH₄ exchange, with an annual value if the equipment is operated throughout the winter period. The only reported flux determined by eddy covariance on a restored Canadian peatland is from Petrone *et al.* (2001), with a measured source of 478 g CO₂-C m⁻² over the growing season (May 17–October 11) measured at BDB in the first year post-restoration where decomposition straw mulch contributed an estimated 80–140 g CO₂-C m⁻² to total emissions (Waddington *et al.* 2003). If it is assumed that restored sites will

eventually have fluxes similar to natural peatlands (e.g. IPCC 2014), eddy covariance data from natural sites may also be useful. For example, Roulet *et al.* (2007) reported mean (standard deviation) annual fluxes over six years as -40.2 (40.5) and 3.7 (0.5) g C m⁻² for CO₂ and CH₄ respectively in a temperate shrubby bog in Québec. Syed *et al.* (2006) reported CO₂ exchange of -144 g C m⁻² for a treed moderately-rich fen in Alberta. At the same site, emissions of CH₄ between mid-May and mid-September released 2.4 g C m⁻² (Long *et al.* 2010). Net annual CO₂ has also been measured at several Canadian boreal bogs with values in the range of -28 to -126 g C m⁻² (Humphreys *et al.* 2014, Strachan *et al.* 2016). Further eddy covariance measurements of both CO₂ and CH₄ fluxes on restored and unrestored peatlands in eastern and western Canada are ongoing and these data will be critical in the development of future emission factors for peatland restoration.

CONCLUSIONS

Based on plot-scale fluxes from six restored peatlands across Canada, restoration *via* the moss layer transfer technique increases GPP, has little effect on ER, results in a sink of CO₂ under full light conditions and increases CH₄ flux compared to unrestored plots. Restored plots on average had similar GPP, lower ER, acted as greater sinks of CO₂ (as NEE) and had lower CH₄ emissions than natural plots. Vascular plant cover largely explained the variation in CO₂ exchange at restored and unrestored plots, while moss cover was significantly correlated to greater CO₂ uptake at natural plots. Water table explained the variation in CH₄ emissions. Since mean fluxes were not weighted to account for the actual distribution of water table and plant cover at each site or within each restoration class, this mean value is unlikely to accurately represent the actual flux from any given restored area. However, this improved understanding of controls on CO₂ and CH₄ fluxes at these sites provides insight into which data (e.g. plant cover, water table position) are required to more accurately estimate fluxes at ecosystem and regional scales.

Plot-scale fluxes of CO₂ and CH₄ from restored plots were not statistically significantly different between eastern and western Canada, or between a restored well-pad and peatlands formerly extracted for horticultural peat. This suggests that nationwide emission factors/estimation methods will be appropriate for Canada as long as the variations in controlling factors are considered in the flux estimation. Moreover, additional physicochemical

and biological constraints on C gas fluxes from highly disturbed areas (e.g. opencast mines) should be further investigated before applying emission factors derived from restored horticultural peat extraction sites to restored peatlands in general.

Overall, there are still limited data available on CO₂ and CH₄ fluxes from restored peatlands, with little to no data on year-round ecosystem-scale fluxes. Data from more than ten years post-restoration is limited to only one study site. More measured fluxes from more sites over longer time periods post-restoration are required to improve GHG flux estimates from restored peatlands and our understanding of how these fluxes change over space and time.

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REFERENCES

- Alm, J., Talanov, A., Saarnio, S., Silvola, J., Ikkonen, E., Aaltonen, H., Nykänen, H. & Martikainen, P.J. (1997) Reconstruction of the carbon balance for microsites in a boreal oligotrophic pine fen, Finland. *Oecologia*, 110, 423–431.
- Andersen, R., Pouliot, R. & Rochefort, L. (2013) Above-ground net primary production from vascular plants shifts the balance towards organic matter accumulation in restored *Sphagnum* bogs. *Wetlands*, 33, 811–821.
- Baird, A.J., Belyea, L.R. & Morris, P.J. (2009) Upscaling of peatland-atmosphere fluxes of methane: small-scale heterogeneity in process rates and the pitfalls of “bucket-and-slab” models. In: Baird, A.J., Belyea, L.R., Comas, X., Reeve, A.S. & Slater, L.D. (eds.) *Carbon Cycling in Northern Peatlands*, Geophysical Monograph 184, American Geophysical Union, Washington, DC, 37–53.
- Barton, K. (2015) *MuMin: Multi-Model Inference*. R

- package version 1.13.4. Online at: <http://CRAN.R-project.org/package=MumIn>
- Basiliko, N., Blodau, C., Roehm, C., Bengtson, P. & Moore, T.R. (2007) Regulation of decomposition and methane dynamics across natural, commercially mined, and restored northern peatlands. *Ecosystems*, 10, 1148–1165.
- Becker, T., Kutzbach, L., Forbrich, I., Schneider, J., Jager, D., Thees, B. & Wilmking, M. (2008) Do we miss the hot spots? - The use of very high resolution aerial photographs to quantify carbon fluxes in peatlands. *Biogeosciences*, 5, 1387–1393.
- Blain, D., Murdiyarso, D., Couwenberg, J., Nagata, O., Renou-Wilson, F., Sirin, A., Strack, M., Tuittila, E.-S., Wilson, D., Evans, C.D., Fukuda, M. & Parish, F. (2014) Rewetted organic soils. In: Hiraishi, T., Krug, T., Tanabe, K., Srivastava, N., Baasansuren, J., Fukuda, M. & Troxler, T. (eds.) *2013 Supplement to the 2006 Inter-Governmental Panel on Climate Change Guidelines for National Greenhouse Gas Inventories: Wetlands*, IPCC, Switzerland, 3.1–3.42.
- Bridgham, S.D., Cadillo-Quiroz, H., Keller, J.K. & Zhuang, Q. (2013) Methane emissions from wetlands: biogeochemical, microbial, and modeling perspectives from local to global scales. *Global Change Biology*, 19, 1325–1346.
- Bubier, J.L., Bhatia, G., Moore, T.R., Roulet, N.T. & Lafleur, P.M. (2003) Spatial and temporal variability in growing-season net ecosystem carbon dioxide exchange at a large peatland in Ontario, Canada. *Ecosystems*, 6, 353–367.
- Cagampan, J.P. & Waddington, J.M. (2008) Net ecosystem CO₂ exchange of a cutover peatland rehabilitated with a transplanted acrotelm. *Écoscience*, 15, 258–267.
- Campeau, S. & Rochefort, L. (1996) *Sphagnum* regeneration on bare peat surfaces: field and greenhouse experiments. *Journal of Applied Ecology*, 33, 599–608.
- Cobbaert, D., Rochefort, L. & Price, J.S. (2004) Experimental restoration of a fen plant community after peat mining. *Applied Vegetation Science*, 7, 209–220.
- Cooper, M.D.A., Evans, C.D., Zielinski, P., Levy, P.E., Gray, A., Peacock, M., Norris, D., Fenner, N. & Freeman, C. (2014) Infilled ditches are hotspots of landscape methane flux following peatland re-wetting. *Ecosystems*, 17, 1227–1241.
- Couwenberg, J. & Fritz, C. (2012) Towards developing IPCC methane ‘emission factors’ for peatlands (organic soils). *Mires and Peat*, 10(03), 1–17.
- Daly, C., Price, J.S., Rezanezhad, F., Pouliot, R., Rochefort, L. & Graf, M. (2012) Initiatives in oil sand reclamation: Considerations for building a fen peatland in a post-mined oil sands landscape. In: Vitt, D. & Bhatti, J.S. (eds.) *Restoration and Reclamation of Boreal Ecosystems - Attaining Sustainable Development*, Cambridge University Press, 179–201.
- Drösler, M., Verchot, L.V., Freibauer, A., Pan, G., Evans, C.D., Bourbonniere, R.A., Alm, J.P., Page, S., Agus, F., Hergoualc’h, K., Couwenberg, J., Jauhiainen, J., Sabiham, S., Wang, C., Srivastava, N., Bourgeau-Chavez, L., Hooijer, A., Minkinen, K., French, N., Strand, T., Sirin, A., Mickler, R., Tansey, K. & Larkin, N. (2014) Drained inland organic soils. In: Hiraishi, T., Krug, T., Tanabe, K., Srivastava, N., Baasansuren, J., Fukuda, M. & Troxler, T. (eds.) *2013 Supplement to the 2006 IPCC Guidelines for National Greenhouse Gas Inventories: Wetlands*, IPCC, Switzerland, 2.1–2.79.
- Frolking, S.E., Bubier, J.L., Moore, T.R., Ball, T., Bellisario, L.M., Bhardwaj, A., Carroll, P., Crill, P.M., Lafleur, P.M., McCaughey, J.H., Roulet, N.T., Suyker, A.E., Verma, S.B., Waddington, J.M. & Whiting, G.J. (1998) Relationship between ecosystem productivity and photosynthetically active radiation for northern peatlands. *Global Biogeochemical Cycles*, 12, 115–126.
- Frolking, S. & Roulet, N.T. (2007) Holocene radiative forcing impact of northern peatland carbon accumulation and methane emissions. *Global Change Biology*, 13, 1079–1088.
- Godin, A., McLaughlin, J.W., Webster, K.L., Packalen, M. & Basiliko, N. (2012) Methane and methanogen community dynamics across a boreal peatland nutrient gradient. *Soil Biology and Biochemistry*, 48, 96–105.
- González, E., Rochefort, L., Boudreau, S. & Poulin, M. (2014) Combining indicator species and key environmental and management factors to predict restoration success of degraded ecosystems. *Ecological Indicators*, 46, 156–166.
- Graf, M. & Rochefort, L. (2009) Examining the peat-accumulating potential of fen vegetation in the context of fen restoration of harvested peatlands. *Écoscience*, 16, 158–166.
- Hothorn, T., Bretz, F. & Westfall, P. (2008) Simultaneous inference in general parametric models. *Biometrical Journal*, 50, 346–363.
- Humphreys, E.R., Charron, C., Brown, M. & Jones, R. (2014) Two bogs in the Canadian Hudson Bay Lowlands and a temperate bog reveal similar annual net ecosystem exchange of CO₂. *Arctic, Antarctic and Alpine Research*, 46, 103–113.

- IPCC (2014) *2013 Supplement to the 2006 Intergovernmental Panel on Climate Change Guidelines for National Greenhouse Gas Inventories: Wetlands*. Hiraishi, T., Krug, T., Tanabe, K., Srivastava, N., Baasansuren, J., Fukuda, M. & Troxler, T.G. (eds.), IPCC, Switzerland. Online at: <http://www.ipcc-nggip.iges.or.jp/public/wetlands/index.html>
- Järveoja, J., Peichl, M., Maddison, M., Soosaar, K., Vellak, K., Karofeld, E., Teemusk, A. & Mander, Ü. (2016) Impact of water table level on annual carbon and greenhouse gas balances of a restored peat extraction area. *Biogeosciences*, 13(9), 2637–2651.
- Juottonen, H., Hynninen, A., Nieminen, M., Tuomivirta, T.T., Tuittila, E.-S., Nousiainen, H., Kell, D.K., Yrjälä, K., Tervahauta, A. & Fritze, H. (2012) Methane-cycling microbial communities and methane emission in natural and restored peatlands. *Applied and Environmental Microbiology*, 78, 6386–6389.
- Lafleur, P.M., Moore, T.R., Roulet, N.T. & Frolking, S. (2005) Ecosystem respiration in a cool temperate bog depends on peat temperature but not water table. *Ecosystems*, 8, 619–629.
- Leppälä, M., Kukko-Oja, K., Laine, J. & Tuittila, E.-S. (2008) Seasonal dynamics of CO₂ exchange during primary succession of boreal mires as controlled by phenology of plants. *Écoscience*, 15, 460–471.
- Loisel, J., Yu, Z., Beilman, D.W., Camill, P., Alm, J., Amesbury, M.J., Anderson, D., Andersson, S., Bochicchio, C., Barber, K., Belyea, L.R., Bunbury, J., Chambers, F.M., Charman, D.J., de Vleeschouwer, F., Failkiewicz-Kozziel, B., Finkelstein, S.A., Galka, M., Garneau, M., Hammarlund, D., Hinchcliffe, W., Holmquist, J., Hughes, P., Jones, M.C., Klein, E.C., Kokfelt, U., Korhola, A., Kuhry, P., Lamarre, A., Lamentowicz, M., Large, D., Lavoie, M., MacDonald, G., Magnan, G., Mäkilä, M., Mallon, G., Mathijssen, P., Mauquoy, D., McCarroll, J., Moore, T.R., Nichols, J., O'Reilly, B., Oksanen, P., Packalen, M., Peteet, D., Richard, P.J.H., Robinson, S., Ronkainen, T., Rundgren, M., Sannel, A.B.K., Tarnocai, C., Thom, T., Tuittila, E.-S., Turetsky, M., Väiliranta, M., van der Linden, M., van Geel, B., van Bellen, S., Vitt, D., Zhao, Y. & Zhou, W. (2014) A database and synthesis of northern peatland soil properties and Holocene carbon and nitrogen accumulation. *The Holocene*, 24, 1028–1042.
- Long, K.D., Flanagan, L.B. & Cai, T. (2010) Diurnal and seasonal variation in methane emissions in a northern Canadian peatland measured by eddy covariance. *Global Change Biology*, 16, 2420–2435.
- Lund, M., Christensen, T.R., Mastepanov, M., Lindroth, A. & Ström, L. (2009) Effects of N and P fertilization on the greenhouse gas exchange in northern peatlands with contrasting N deposition rates. *Biogeosciences*, 6, 2135–2144.
- Mahmood, M.S. (2011) *Carbon Dynamics of Recolonized Cutover Minerotrophic Peatland: Implications for Restoration*. MSc thesis, University of Calgary, Calgary, Alberta, Canada, 147 pp. Online at: http://www.gret-perg.ulaval.ca/uploads/tx_centrecherche/Mahmood_MSc_Thesis2011_02.pdf
- Mahmood, M.S. & Strack, M. (2011) Methane dynamics of recolonized cutover minerotrophic peatland: Implications for restoration. *Ecological Engineering*, 37, 1859–1868.
- Maljanen, M., Sigurdsson, B.D., Guðmundsson, J., Óskarsson, H., Huttunen, J.T. & Martikainen, P.J. (2010) Greenhouse gas balances of managed peatlands in the Nordic countries - present knowledge and gaps. *Biogeosciences*, 7, 2711–2738.
- Malloy, S. & Price, J.S. (2014) Fen restoration on a bog harvested down to sedge peat: A hydrological assessment. *Ecological Engineering*, 64, 151–160.
- McCarter, C.M. & Price, J.S. (2015) The hydrology of the Bois-des-Bel peatland restoration: hydrophysical properties limiting connectivity between *Sphagnum* and remnant vacuum harvested peat deposit. *Ecohydrology*, 8, 173–187.
- Munir, T.M., Perkins, M., Kaing, E. & Strack, M. (2015) Carbon dioxide flux and net primary production of a boreal treed bog: Responses to warming and water-table-lowering simulations of climate change. *Biogeosciences*, 12, 1091–1111.
- Munir, T.M., Xu, B., Perkins, M. & Strack, M. (2014) Responses of carbon dioxide flux and plant biomass to water table drawdown in a treed peatland in northern Alberta: a climate change perspective. *Biogeosciences*, 11, 807–820.
- Murphy, P.N.C., Ogilvie, J., Meng, F.-R., White, B., Bhatti, J.S. & Arp, P.A. (2011) Modelling and mapping topographic variations in forest soils at high resolution: A case study. *Ecological Modelling*, 222, 2314–2332.
- Nakagawa, S. & Schielzeth, H. (2013) A general and simple method for obtaining R² from generalized linear mixed-effects models. *Methods in Ecology and Evolution*, 4, 133–142.
- Nwaishi, F., Petrone, R.M., Price, J.S., Ketcheson, S.J., Slawson, R. & Andersen, R. (2015) Impacts of donor-peat management practices on the functional characteristics of a constructed fen.

- Ecological Engineering*, 81, 471–480.
- Page, S.E., Rieley, J.O. & Banks, C.J. (2011) Global and regional importance of the tropical peatland carbon pool. *Global Change Biology*, 17, 798–818.
- Petrone, R.M., Waddington, J.M. & Price, J.S. (2001) Ecosystem scale evapotranspiration and net CO₂ exchange from a restored peatland. *Hydrological Processes*, 15, 2839–2845.
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. & R Core Team (2014) nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-118. Online at: <http://CRAN.R-project.org/package=nlme>
- Pollard, J., McKenna, G.T., Fair, J., Daly, C., Wytrykush, C. & Clark, J. (2012) Design aspects of two fen wetlands constructed for reclamation research in the Athabasca oil sands. In: Fourie, A.B. & Tibbett, M. (eds.) *Mine Closure 2012*, Australian Centre for Geomechanics, Perth, Australia, 815–830.
- Poulin, M., Andersen, R. & Rochefort, L. (2013) A new approach for tracking vegetation change after restoration: A case study with peatlands. *Restoration Ecology*, 21, 363–371.
- Pouliot, R., Rochefort, L. & Graf, M.D. (2012) Impacts of oil sands process water on fen plants: Implications for plant selection in required reclamation projects. *Environmental Pollution*, 167, 132–137.
- Pouliot, R., Rochefort, L. & Karofeld, E. (2011) Initiation of microtopography in re-vegetated cutover peatlands: evolution of plant species composition. *Applied Vegetation Science*, 15, 369–382.
- Price, J., Rochefort, L. & Quinty, F. (1998) Energy and moisture considerations on cutover peatlands: surface microtopography, mulch cover and *Sphagnum* regeneration. *Ecological Engineering*, 10, 293–312.
- Quinty, F. & Rochefort, L. (2003) *Peatland Restoration Guide: Second Edition*. Canadian Sphagnum Peat Moss Association & New Brunswick Department of Natural Resources and Energy, Québec, Canada, 106 pp.
- R Core Team (2013) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Online at: <http://www.R-project.org/>
- Renou-Wilson, F., Müller, C., Moser, G. & Wilson, D. (2016) To graze or not to graze? Four years GHG balances and vegetation composition from a drained and a rewetted organic soil under grassland. *Agriculture, Ecosystem and the Environment*, 222, 156–170.
- Riutta, T., Laine, J. & Tuittila, E.-S. (2007) Sensitivity of CO₂ exchange of fen ecosystem components to water level variation. *Ecosystems*, 10, 718–733.
- Rochefort, L., Quinty, F., Campeau, S., Johnson, K. & Malterer, T. (2003) North American approach to the restoration of *Sphagnum* dominated peatlands. *Wetlands Ecology and Management*, 11, 3–20.
- Rooney, R.C., Bayley, S.E. & Schindler, D.W. (2012) Oil sands mining and reclamation cause massive loss of peatland and stored carbon. *Proceedings of the National Academy of Sciences of the United States of America*, 109, 4933–4937.
- Roulet, N.T., Lafleur, P.M., Richard, P.J.H., Moore, T.R., Humphreys, E.R. & Bubier, J. (2007) Contemporary carbon balance and late Holocene carbon accumulation in a northern peatland. *Global Change Biology*, 13, 397–411.
- Schrier-Uijl, A.P., Veraart, A.J., Leffelaar, P.A., Berendse, F. & Veenendaal, E.M. (2011) Release of CO₂ and CH₄ from lakes and drainage ditches in temperate wetlands. *Biogeochemistry*, 102, 265–279.
- Sobze, J.-M., Gauthier, M.-E. & Thomas, R. (2012) *Peatland Restoration – Harvest and Transfer of Donor Material*. Technical Note, November 2012, Northern Alberta Institute of Technology, Edmonton, Alberta, Canada. Online at: http://www.nait.ca/docs/1_Donor_Site_Harvesting_and_Moss_Transfer.pdf
- Strachan, I.B., Pelletier, L. & Bonneville, M.-C. (2016) Inter-annual variability in water table depth controls net ecosystem carbon dioxide exchange in a boreal bog. *Biogeochemistry*, 127, 99–111.
- Strack, M., Keith, A.M. & Xu, B. (2014) Growing season carbon dioxide and methane exchange at a restored peatland on the Western Boreal Plain. *Ecological Engineering*, 64, 231–239.
- Strack, M. & Zuback, Y.C.A. (2013) Annual carbon balance of a peatland 10 yr following restoration. *Biogeosciences*, 10, 2885–2896.
- Sulman, B.N., Desai, A.R., Saliendra, N.Z., Lafleur, P.M., Flanagan, L.B., Sonnentag, O., Mackay, D.S., Barr, A.G. & van der Kamp, G. (2010) CO₂ fluxes at northern fens and bogs have opposite responses to inter-annual fluctuations in water table. *Geophysical Research Letters*, 37, L19702, doi: 10.1029/2010GL044018.
- Syed, K.H., Flanagan, L.B., Carlson, P.J., Glenn, A.J. & van Gaalen, K.E. (2006) Environmental control of net ecosystem CO₂ exchange in a treed moderately rich fen in northern Alberta. *Agricultural and Forest Meteorology*, 140, 97–114.

- Treat, C.C., Bubier, J.L., Varner, R.K. & Crill, P.M. (2007) Timescale dependence of environmental and plant-mediated controls on CH₄ flux in a temperate fen. *Journal of Geophysical Research*, 112, G01014, doi: 10.1029/2006JG000210.
- Turetsky, M., Wieder, K., Halsey, L. & Vitt, D. (2002) Current disturbance and the diminishing peatland carbon sink. *Geophysical Research Letters*, 29, 1526, doi: 10.1029/2001GL014000.
- Vitt, D.H. (2000) Peatlands: Ecosystems dominated by bryophytes. In: Shaw, A.J. & Goffinet, B. (eds.) *Bryophyte Biology*, Cambridge University Press, Cambridge, UK, 312–343.
- Vitt, D.H., Halsey, L.A., Thormann, M.N. & Martin, T. (1998) *Peatland Inventory of Alberta Phase 1: Overview of Peatland Resources in the Natural Regions and Subregions of the Province*. Alberta Peat Task Force, Edmonton. Published by the NCE-SFMN, University of Alberta, Edmonton, AB., 117 pp.
- Waddington, J.M. & Day, S.M. (2007) Methane emissions from a peatland following restoration. *Journal of Geophysical Research - Biogeosciences*, 112, G03018, doi: 10.1029/2007JG000400.
- Waddington, J.M., Greenwood, M.J., Petrone, R.M. & Price, J.S. (2003) Mulch decomposition impedes recovery of net carbon sink function in a restored peatland. *Ecological Engineering*, 20(3), 199–210.
- Waddington, J.M., Strack, M. & Greenwood, M.J. (2010) Towards restoring the net carbon sink function of degraded peatlands: Short-term response in CO₂ exchange to ecosystem-scale restoration. *Journal of Geophysical Research - Biogeosciences*, 115, G01008, doi: 10.1029/2009JG001090.
- Waddington, J.M., Warner, K.D. & Kennedy, G.W. (2002) Cutover peatlands: A persistent source of atmospheric CO₂. *Global Biogeochemical Cycles*, 16, 1002, doi: 10.1029/2001GB001398.
- Wieder, R.K., Scott, K.D., Kamminga, K., Vile, M.A., Vitt, D.H., Bone, T., Xu, B., Benscoter, B.W. & Bhatti, J.S. (2009) Postfire carbon balance in boreal bogs of Alberta, Canada. *Global Change Biology*, 15, 63–81.
- Wilson, D., Blain, D., Couwenberg, J., Evans, C.D., Murdiyarto, D., Page, S., Renou-Wilson, F., Rieley, J., Sirin, A., Strack, M. & Tuittila, E.-S. (2016) Greenhouse gas emission factors associated with rewetting of organic soils. *Mires and Peat*, 17(04), 1–28.
- Wilson, D., Farrell, C.A., Müller, C., Hepp, S. & Renou-Wilson, F. (2013) Rewetted industrial cutaway peatlands in western Ireland: prime location for climate change mitigation? *Mires and Peat*, 11(01), 1–22.
- Wray, H.E. & Bayley, S.E. (2007) Denitrification rates in marsh fringes and fens in two boreal peatlands in Alberta, Canada. *Wetlands*, 27(4), 1036–1045.
- Zoltai, S.C., Siltanen, R.M. & Johnson, J.D. (2000) *A Wetland Data Base for the Western Boreal, Subarctic, and Arctic Regions of Canada*. Information Report NOR-X-368, Natural Resources Canada, Canadian Forest Service, Northern Forestry Centre, Edmonton, Alberta, 30 pp. Online at: http://www.cfs.nrcan.gc.ca/bookstore_pdfs/12183.pdf, accessed 11 Jun 2016.
- Zuur, A.G., Ieno, E.N., Walker, N.J., Saveliev, A.A. & Smith, G.M. (2009) *Mixed Effect Models and Extensions in Ecology with R*. Springer-Verlag, New York, xxii + 574 pp.

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