

**Carbon cycling at a post-extraction restored peatland:
Small-scale processes to global climate impacts**

Kelly A. Nugent

Department of Natural Resource Sciences
McGill University, Montreal

November 15, 2019

A thesis submitted to McGill University
in partial fulfillment of the requirements of the degree of
Doctor of Philosophy

© Kelly Nugent, 2019

ABSTRACT

Peatlands store large amounts of organic carbon (C) and are an important component of the global climate system. Climate and peatland land surfaces are closely coupled through land-atmosphere exchanges of greenhouse gases (GHG), such as carbon dioxide (CO₂) and methane (CH₄). When undisturbed, peatlands exert a long-term (millennia) negative radiative GHG forcing (i.e. climate cooling) through CO₂ removal from the atmosphere, and a short-term (decades) positive forcing (i.e. climate warming) with the addition of CH₄ to the atmosphere. Degradation from peatland drainage and extraction, however, results in mineralization of stored peat, releasing large amounts of CO₂ while generally reducing CH₄ to minimal levels. Rewetting and actively restoring native vegetation is now a restoration approach used to reduce CO₂ emissions from degraded peatlands. However, the timeframe needed for restoration to re-establish the C sink function of an undisturbed peatland remains poorly constrained due to a lack of multi-year measurements. In this thesis, I analyze three years of eddy covariance flux measurements from a post-extraction restored peatland in eastern Quebec, Canada that was restored 14 years prior. I link these measurements with flux footprint modelling, satellite remote sensing data, stable isotope fractionation data and pore water concentrations to characterize how belowground C cycling and fluxes are impacted by restoration. I combine a series of flux towers at post-extraction unrestored and restored peatlands in eastern and western Canada with an atmospheric perturbation model to further reveal how after-use management is affecting the global climate.

The post-extraction restored peatland was a C sink of $78 \pm 17 \text{ g C m}^{-2} \text{ yr}^{-1}$ within fourteen years of restoration, due to strong CO₂ uptake and small CH₄ emission and dissolved organic carbon export. Low growing season inter-annual variability in net ecosystem exchange of CO₂ (NEE) was linked to constancy of the early spring water table position, controlled by the blocked drainage ditches and water storage structures. Methane emission was small except when *Typha latifolia*-invaded drainage ditches were in the tower footprint; but, this effect at the ecosystem level was small as ditches represent a minor fraction of the site. A comparison with an undisturbed reference peatland (Mer Bleue) revealed annual NEE at the restored peatland was most similar to wetter, more productive years at the reference peatland. A mapping of post-extraction (1980 onwards) canopy structure changes, using the enhanced vegetation index (EVI), showed broad comparability between the restored peatland and surrounding intact peatland within five years of

restoration. The EVI results suggest that the developing vegetation in general had a normal response to environmental factors and was not experiencing any enduring stress from the underlying cutover peat.

While the processes behind the surface net CO₂ flux appear successfully recovered, approximately two thirds of the restored peatland was a minimal source of CH₄, suggesting a lag in the recovery of belowground C cycling processes. Carbon turnover in the cutover peat beneath the new *Sphagnum* layer was slow and appeared to occur only with *E. vaginatum* substrate input and plant-mediated transport. The C isotopic fractionation factor for CH₄ and CO₂ in the restored field pore water exhibited a dominance of acetoclastic methane production, even deeper in the cutover peat profile. In contrast, isotopic fractionation in the former drainage ditches showed a balance of acetoclastic and hydrogenotrophic methanogenesis deeper in the profile, indicating that some bulk peat C turnover was occurring. Over time (decades), C turnover of the new peat is expected to limit the impacts of the cutover peat on the surface CH₄ flux.

Flux measurements at unrestored sites in eastern and western Canada reveal that not restoring post-extraction peatlands leads to decades of CO₂ addition to the atmosphere, with low CH₄ emission. The after-use decision to not restore results in a positive radiative forcing seven times more powerful than the negative forcing achieved by active restoration after 500 years. Prompt active restoration achieves a neutral climate impact (excluding C losses in the removed peat) about 155 years earlier than restoration after a 20-year delay. In contrast, IPCC Tier 1 emission factors based on a wide range of rewetting activities display a continually positive radiative forcing, even with prompt rewetting.

Research in this thesis is timely as interest in using peatland restoration as a climate mitigation strategy is increasing. This work shows that re-establishing key peatland species and integrating structures to increase water retention are effective at re-establishing the net C sink rate to that of an undisturbed peatland within a decade and a half. The legacy of cutover peat in reducing CH₄ production and thus emission helps increase C accumulation in the short-term while also reducing the climate warming impact of the restored site during the transition to a C sink. An after-use plan that includes prompt active restoration is most effective at reducing the climate impact of a post-extraction site and is key to utilizing peatland restoration as a climate change mitigation strategy.

RESUMÉ

Les tourbières stockent de grandes quantités de carbone (C) organique et constituent une composante importante du système climatique de la planète. Le climat et les surfaces de tourbières sont étroitement liés par des échanges de gaz à effet de serre (GES). Lorsqu'elles ne sont pas perturbées, les tourbières exercent un refroidissement du climat à long terme (millénaire) en éliminant le CO₂ de l'atmosphère et provoquent un réchauffement climatique (décennies) avec un ajout de CH₄ dans l'atmosphère. Cependant, la dégradation causée par le drainage et l'extraction des tourbières entraîne la minéralisation de la tourbe, libérant de grandes quantités de CO₂ tout en réduisant généralement le CH₄ à des niveaux minimaux. La réhumidification et la restauration active de la végétation indigène sont désormais une approche de restauration utilisée pour réduire les émissions de CO₂ provenant des tourbières dégradées. Or, le délai nécessaire à la restauration visant à rétablir la fonction de puits de C d'une tourbière non perturbée demeure mal défini en raison du manque de mesures pluriannuelles. Dans le cadre de cette thèse, j'analyse trois années de mesures des flux turbulents dans une tourbière restaurée après l'extraction dans l'est du Québec au Canada (restaurée 14 ans auparavant). J'associe ces mesures à la modélisation d'empreintes de flux, à des données de télédétection satellite, à des données de fractionnement d'isotopes stables et à des concentrations d'eaux interstitielles afin de caractériser l'impact de la restauration sur les échanges de cyclage du C souterrain et de flux. Je combine une série de tours de flux turbulents dans des tourbières restaurées et non restaurées après l'extraction, dans l'est et l'ouest du Canada, avec un modèle de perturbation atmosphérique afin de mieux saisir l'impact de la gestion après utilisation sur le climat mondial.

La tourbière restaurée présentait un puits de C de $78 \pm 17 \text{ g C m}^{-2} \text{ an}^{-1}$ à moins de 14 ans de restauration, en raison de la forte absorption de CO₂, de la faible émission de CH₄ et de l'exportation de carbone organique dissous dans l'eau. Une faible variabilité interannuelle de l'échange écosystémique net de CO₂ (ÉÉN) était liée à la constance de la position de la table d'eau au printemps et contrôlée par l'obstruction des fossés de drainage et les structures de stockage d'eau. Les émissions de CH₄ étaient faibles, sauf lorsque les fossés de drainage envahis par la *Typha latifolia* se trouvaient dans l'empreinte de la tour. Néanmoins, cet effet était faible sur le plan l'écosystème, car les fossés ne représentent qu'une petite fraction du site. Une comparaison avec une tourbière non perturbée (Mer Bleue) a révélé que le ÉÉN annuel sur le site de la tourbière

restaurée était plus similaire à des années plus humides et plus productives de la tourbière de la Mer Bleue. Une représentation des changements de structure de la canopée après l'extraction (à partir de 1980) à l'aide de l'indice de végétation amélioré (IVA), a démontré une large comparabilité entre la tourbière restaurée et la tourbière intacte environnante après cinq ans de restauration. Les résultats IVA tendent à démontrer que le développement de la végétation en général a réagi normalement aux facteurs environnementaux et n'a subi aucune contrainte persistante provenant de la tourbe coupée sous-jacente.

Alors que les processus derrière le flux net de CO₂ semblent avoir été récupérés avec succès, environ les deux tiers de la tourbière restaurée constituaient une source minime de CH₄, ce qui laisse présager un retard dans la récupération des processus de cyclage du C souterrain. Le renouvellement du C dans la tourbe, sous la nouvelle couche de *sphaigne* était faible et semblait se produire uniquement avec l'entrée du substrat d'*E. vaginatum* et le transport à médiation par les plantes. Le facteur de fractionnement isotopique du C pour le CH₄ et le CO₂ dans l'eau de porosité de champ restaurée a démontré une prédominance dans la production de méthane acétoclastique et même plus profonde dans le profil de tourbe coupée. Par contre, le fractionnement isotopique dans les anciens fossés de drainage a démontré un équilibre entre la méthanogénèse acétoclastique et hydrogénotrophe plus en profondeur dans le profil, indiquant qu'un certain renouvellement de C de la tourbe en masse se produisait. Au fil du temps (en décennies), on s'attend à ce que le renouvellement du C de la nouvelle tourbe limite les impacts de la tourbe coupée sur le flux de surface CH₄.

Les mesures de flux effectuées sur des sites non restaurés de l'est et de l'ouest du Canada révèlent que le fait de ne pas restaurer les tourbières après l'extraction entraîne des décennies d'ajout de CO₂ dans l'atmosphère, avec de faibles émissions de CH₄. La décision « après utilisation » de ne pas restaurer a pour résultat un forçage radiatif positif sept fois plus puissant que le forçage négatif obtenu par une restauration active après 500 ans. Une restauration active rapide permet d'avoir un impact neutre sur le climat (à l'exception des pertes de C dans la tourbe retirée) environ 155 ans plus tôt que la restauration après une période de 20 ans. En revanche, les facteurs d'émission de niveau 1 du GIEC, fondés sur un large éventail d'activités de remouillage, provoquent un forçage radiatif positif continu, même avec un remouillage rapide.

Dans cette thèse, la recherche tombe à point nommé, car l'intérêt pour l'utilisation de la restauration des tourbières comme stratégie d'atténuation des changements climatiques

s'accroît. Ce travail démontre que le rétablissement de végétation tourbeuse et l'intégration de structures visant à augmenter la rétention d'eau sont efficaces pour rétablir le taux net de puits de C à celui d'une tourbière non perturbée au cours d'une décennie et demie. L'héritage de la tourbe coupée visant à réduire la production de CH₄ et par le fait même les émissions contribue à augmenter l'accumulation de C à court terme tout en réduisant l'impact sur le réchauffement climatique sur le site restauré au cours de la transition vers un puits de C. Un plan « après utilisation » comprenant une restauration active rapide demeure le moyen le plus efficace de réduire l'impact climatique d'un site après l'extraction. De plus, ce plan est clé pour l'utilisation de la restauration des tourbières comme stratégie d'atténuation des changements climatiques.

TABLE OF CONTENTS

ABSTRACT.....	i
RESUMÉ	iii
TABLE OF CONTENTS.....	vi
LIST OF FIGURES	ix
LIST OF TABLES.....	xi
LIST OF APPENDICES.....	xii
PREFACE.....	xiii
Acknowledgements.....	xiii
Contribution of authors	xiv
Original contributions	xv
CHAPTER 1: INTRODUCTION	1
CHAPTER 2: LITERATURE REVIEW	5
2.1 Peatland description.....	5
2.2 Carbon dioxide production and flux mechanisms and drivers.....	6
2.3 Methane production and flux mechanisms and drivers.....	10
2.4 Aquatic carbon flux mechanisms and drivers	13
2.5 Methodological approaches to compute the NECB	15
2.5.1 Eddy covariance flux measurements	16
2.5.2 Closed chamber flux measurements.....	17
2.5.3 Deriving DOC export.....	18
2.6 Computing radiative forcing of climate	18
2.7 Key methods to investigate belowground C cycling.....	22
2.7.1 Stable isotope analysis background and methods.....	22
2.7.2 Organic acid analysis	24
CHAPTER 3: MULTI-YEAR NET ECOSYSTEM CARBON BALANCE OF A RESTORED PEATLAND REVEALS A RETURN TO CARBON SINK	25
Bridging statement to Chapter 3	25
3.1 Abstract.....	25
3.2 Introduction.....	26
3.3 Materials and methods	29
3.3.1 Site description.....	29

3.3.2 Eddy covariance measurements, data processing and ancillary measurements	31
3.3.3 Spatial and temporal controls of F_{CH_4} and spectral decomposition	34
3.3.4 NEE partitioning	35
3.3.5 Vegetation survey	35
3.3.6 Enhanced vegetation index	36
3.4 Results	36
3.4.1 Vegetation characteristics	36
3.4.2 Meteorological conditions	38
3.4.3 Net ecosystem exchange of CO_2	41
3.4.4 Ecosystem methane flux	44
3.4.5 Dissolved organic carbon flux	46
3.4.6 Net ecosystem carbon balance	46
3.4.7 Reference peatland carbon balance	46
3.4.8 Canopy structure changes: Abandonment to present	46
3.4.9 Site inter-comparisons	48
3.5 Discussion	48
CHAPTER 4: CUTOVER PEAT LIMITS METHANE PRODUCTION CAUSING LOW EMISSION AT A RESTORED PEATLAND	53
Bridging statement to Chapter 4	53
4.1 Abstract	53
4.2 Introduction	55
4.3 Methods	58
4.3.1 Site description	58
4.3.2 Flux measurements	58
4.3.3 Pore water sample collection and analyses	61
4.3.4 Statistical analysis	63
4.3.5 Greenness index	63
4.4 Results	64
4.4.1 Surface fluxes	64
4.4.2 Pore water carbon concentration	67
4.4.3 Acetate concentration	70
4.4.4 Carbon isotopic composition of dCH_4 and DIC	73
4.5 Discussion	74

4.5.1 <i>Surface carbon exchange</i>	74
4.5.2 <i>Belowground carbon cycling</i>	76
4.5.3 <i>CH₄ production pathways and oxidation</i>	78
4.6 Conclusion	79
CHAPTER 5: PROMPT ACTIVE RESTORATION OF PEATLANDS SUBSTANTIALLY REDUCES CLIMATE IMPACT.....	81
Bridging statement to Chapter 5	81
5.1 Abstract.....	81
5.2 Introduction.....	81
5.3 Methods.....	84
5.3.1 <i>Data sources</i>	84
5.3.2 <i>Modelling radiative forcing</i>	85
5.4 Results.....	88
5.4.1 <i>Chronosequence establishment</i>	88
5.4.2 <i>Comparison with IPCC Tier 1 emission factors</i>	90
5.4.3 <i>Climate impact of peatland restoration</i>	91
5.5 Discussion.....	94
CHAPTER 6: SYNTHESIS, CONCLUSIONS AND FUTURE DIRECTIONS	96
6.1 Chapter syntheses.....	96
6.2 Conclusions and broad context	98
6.3 Directions for future research	100
BIBLIOGRAPHY	101

LIST OF FIGURES

Figure 2.1: Comparison of annual net ecosystem exchange (NEE) of CO ₂ at post-extraction rewetted and restored peatlands	8
Figure 2.2: Diagram depicting the atmospheric perturbation model	20
Figure 3.1: Locations of the undisturbed reference peatland (REF) and the restored peatland (RES) in eastern Canada	30
Figure 3.2: Daily (a) air temperature (T_a ; °C), (b) photosynthetic photon flux density (PPFD; $\mu\text{mol m}^{-2} \text{s}^{-1}$), and (c) cumulative precipitation (ΣPPT ; mm) for individual months 14, 15 and 16 years post-restoration at the restored peatland.....	39
Figure 3.3: Daily (a) air temperature (T_a ; mean, min; °C), (b) photosynthetic photon flux density (PPFD; $\mu\text{mol m}^{-2} \text{s}^{-1}$) and (c) gap-filled net ecosystem exchange (NEE; $\text{g C m}^{-2} \text{d}^{-1}$)	40
Figure 3.4: Daily values of methane flux (F_{CH_4} ; $\text{mg C m}^{-2} \text{d}^{-1}$), soil temperature (T_s ; °C) and water table depth (WTD; cm) between 1 May and 31 October at the restored peatland (a) 14, (b) 15 and (c) 16 years post-restoration.....	42
Figure 3.5: Daily gross primary productivity (GPP; $\text{g C m}^{-2} \text{d}^{-1}$), ecosystem respiration (ER; $\text{g C m}^{-2} \text{d}^{-1}$) and net ecosystem exchange (NEE; $\text{g C m}^{-2} \text{d}^{-1}$) for individual months during the 14 th , 15 th and 16 th year post-restoration at the restored peatland	43
Figure 3.6: (a) Water table exceedance curves over the growing season in the 3 study years at the restored Bois-des-Bel peatland (RES; lines) compared to the reference Mer Bleue peatland (REF; grey shaded range)	44
Figure 3.7: Comparison of median summer (day of year 151 to 243) enhanced vegetation index (EVI) from 1984 to present at the restored (RES) and undisturbed (NAT) sections of the Bois-des-Bel peatland complex.....	47
Figure 3.8: Mean (\pm SD) annual net ecosystem exchange of CO ₂ (NEE; $\text{g C m}^{-2} \text{yr}^{-1}$) at peatland sites with multiple year eddy covariance CO ₂ datasets	48
Figure 4.1: Site map of the post-extraction restored peatland Bois-des-Bel in Québec, Canada.	59
Figure 4.2: Mean (\pm SD) instantaneous net ecosystem exchange of CO ₂ (NEE, in $\mu\text{mol m}^{-2} \text{s}^{-1}$) when photosynthetically active radiation (PAR) is greater than 1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ in: (a) former drainage ditch plots (<i>T. latifolia</i> and Bare ditch), and, (b) restored peat field plots (<i>E. vaginatum</i> and <i>Sphagnum</i>).....	65
Figure 4.3: Mean (\pm SD) concentration of (a) dissolved CH ₄ , (b) dissolved inorganic carbon (DIC), and, (c) dissolved organic carbon (DOC) at 0.2 m (root zone) and 0.8 m (cutover peat) below the surface of the restored peatland and reference peatland over the study period.....	69
Figure 4.4: Pore water acetate concentration (μM) in the former drainage ditches (top panel) and restored peat fields (bottom panel)	72
Figure 4.5: Cross-plot showing stable isotope carbon composition (¹³ C) of DIC ($\delta^{13}\text{C-CO}_2$) and dissolved CH ₄ ($\delta^{13}\text{C-CH}_4$) in pore water	73

Figure 5.1: Ten site years of annual cumulative net CO ₂ flux (NEE) at Canadian post-extraction peatlands	89
Figure 5.2: Instantaneous net (CO ₂ + CH ₄) radiative forcing of post-extraction peatlands	93
Figure I.1: The spectral signature of the CH ₄ flux footprint is expected to vary at a higher frequency (<i>e.g.</i> hours) in relation to rapid changes in footprint composition, with instantaneous effects on flux measurements.....	132
Figure II.1: Instantaneous net radiative forcing of a post-extraction unrestored peatland using IPCC Tier 1 emission factors with (light blue line) and without (dark blue line) N ₂ O emission included.....	140

LIST OF TABLES

Table 2.1: Mean annual net ecosystem CO ₂ exchange (NEE), in g CO ₂ -C m ⁻² yr ⁻¹ , at post-extraction unrestored and rewetted/restored peatlands compared to long-term records at undisturbed northern peatlands	9
Table 2.2: Atmospheric perturbation model flux fraction (f_i) and lifetime (τ_i) parameters (see Figure 2.1 and Equations 2.3 and 2.4)	22
Table 3.1: Percent vegetation cover and ditch cover (FC_{ditch}) for three 30° direction bins for the area of the mean growing season 80% probability tower flux footprint.....	37
Table 3.2: Average (\pm SD) growing season (1 May to 31 October, inclusive) methane flux (F_{CH_4}), air temperature (T_a), soil temperature (T_s), water table depth (WTD) and cumulative precipitation (ΣPPT) at the restored peatland 14, 15 and 16 years post-restoration.....	41
Table 3.3: Cumulative (\pm 95% CI) growing season fluxes and annual balance (\pm SD) of the restored peatland in g C m ⁻² yr ⁻¹	44
Table 3.4: Multiple linear models using daily values to examine potential drivers of methane flux at the restored peatland, RES. Statistics were applied to the entire study period dataset, growing season only (GS), and Spring combined with GS.....	45
Table 4.1: Mean (SE) fluxes of carbon at the surface-air interface during the early (May & June), mid (July & August) and late (September–November) season	66
Table 4.2: Mean (SE) concentration at 0.2 m and 0.8 m depth in June–August of dissolved organic carbon (DOC), dissolved CH ₄ (dCH ₄), dissolved inorganic carbon (DIC), acetate in pore water and root exudates, as well as mean stable isotope composition ($\delta^{13}\text{C}$) of CH ₄ and apparent fractionation factor for carbon (α)	71
Table 5.1: Canadian post-extraction peatland C fluxes compared to IPCC Tier 1 emission factors	87
Table 5.2: Atmospheric perturbation model scenario inputs	88
Table I.1: Eddy covariance-derived seasonal CH ₄ emissions from undisturbed or semi-undisturbed northern peatlands	133
Table II.1: Main characteristics of the study sites	135
Table II.2: Site-specific measurement techniques and instrumentation for CO ₂ , CH ₄ and DOC fluxes.....	136
Table II.3: Site-specific gap-filling methods for CO ₂ and CH ₄	137
Table II.4: Annual CO ₂ , CH ₄ and DOC fluxes at the study sites.....	138
Table II.5: Comparing modelled instantaneous net radiative forcing (RF) to applying the global warming potential (GWP metric).....	142
Table II.6: The relative climate benefit of peatland restoration actions at 20 years.....	143

LIST OF APPENDICES

Appendix I: Chapter 3..... 132
Appendix II: Chapter 5 134

PREFACE

Acknowledgements

The work presented in this thesis was supported by a Collaborative Research and Development grant to Dr. Ian B. Strachan, Dr. Maria Strack, Dr. Nigel T. Roulet and Dr. Line Rochefort from the Natural Sciences and Engineering Research Council of Canada (NSERC) in partnership with the Canadian Sphagnum Peat Moss Association. I was also supported by a doctoral fellowship from the Fonds de recherche Québec: Nature et technologies, the McGill Graduate Excellence program and a GREAT travel grant from the Department of Natural Resource Sciences at McGill University. Landsat Spectral Indices products were courtesy of the U.S. Geological Survey Earth Resources Observation and Science Center. The satellite image used to classify the main site was courtesy of the Digital Globe Foundation.

I am grateful to my PhD supervisor, Ian Strachan, for his guidance, support, open-door policy and humor. His trust and respect of my abilities allowed me to challenge myself and grow as a scientist and individual. I would like to also thank my co-supervisor, Maria Strack, for her open-Skype policy, which always led to turning points in my work. Maria is an inspiring researcher and deserves a Guinness World Record for the quickest manuscript turnarounds! Many thanks also to the final member of my committee, Nigel Roulet, for his valuable input, good discussions (work and life) and for introducing me to a broader research network.

I am grateful to everybody that has worked with me at the Bois-des-Bel peatland. Your help in the field has made this thesis possible. In particular, Luc Pelletier and Manual Helbig helped with collecting and processing a lot of the field data for this thesis. As well, Tracy Rankin, a good friend who has been on many field trips with me, provided invaluable support in data collection, sampling processing and statistical analyses. Finally, thank you to all the Peatmeeters who gave me an excuse to go to the downtown campus and were a wonderful support and learning group.

I am deeply grateful to my mother, Donna, and step-father, Kendall, for their support and love throughout my multiple degrees and beyond. My brother, Scott, who's been in the same PhD boat and made it to the other side- I appreciated our Matlab vents! As well, my in-law family who are among my biggest fans and brag about my work to their friends, even when they're not fully sure what its about. Most importantly, thank you Rich, for your comprehension of the importance

of this work to me, and for your support and love that has enabled me (us) to have Vera, finish my PhD and start a job, with much overlap. Cheers to the great adventures to come!

Contribution of authors

This thesis contains three results chapters (Chapters 3 to 5) that are written as manuscripts in a format suitable for publication in scientific journals. For Chapters 3 and 4, I developed the research questions and research design, collected the data, did the majority of analysis, interpreted the results, and wrote the manuscripts as lead author. For Chapter 5, I did all of the above steps except that study design was co-conceived by my supervisor and co-supervisor, and data collection at three of the four post-extraction peatland research stations was completed by two MSc graduates in my lab, Scott Macdonald and Tracy Rankin as well as a postdoctoral researcher, Manuel Helbig. My work builds on their findings and analyzes the data in an original manner.

Co-author contributions: My PhD supervisor Ian B. Strachan and co-supervisor Maria Strack along with my PhD committee member Nigel T. Roulet provided advice on the development of my research questions, research planning and data analysis and have read and provided detailed comments on my manuscripts. My supervisor Ian Strachan had an essential role in the planning and operation of the four field research stations set up in post-extraction peatlands. Dr. Elyn Humphreys and Nigel Roulet provided additional data for the Mer Bleue reference peatland. Elyn Humphreys is not a co-author on any of the manuscripts, however, her contribution has been gratefully recognized in the acknowledgement sections of the manuscripts when submitted to journals. The roles of other co-authors are described below:

Manuscript I (Chapter 3): Nugent K. A., Strachan, I. B., Strack, M., Roulet, N. T. & Rochefort, L. (2018). Multi-year net ecosystem carbon balance of a restored peatland reveals a return to carbon sink. *Global Change Biology*, 24, 5751-5768. LR provided vegetation composition data, interpretation of results and detailed comments on the manuscript.

Manuscript II (Chapter 4): Nugent K. A., Strachan, I. B., Strack, M., Roulet, N. T., Ström, L. & Chanton, J. P. Cutover peat limits methane production causing low emission at a restored peatland. *In preparation*. LS provided advice on field acetate sampling, directed me in analyzing the acetate samples and provided detailed comments on the manuscript. JPC provided advice on stable isotope sampling, conducted the sample analysis and provided detailed comments on the manuscript.

Manuscript III (Chapter 5): Nugent K. A., Strachan, I. B., Roulet, N. T., Strack, M., Frohling, S. & Helbig, M. Prompt active restoration of peatlands substantially reduces climate impact. *Accepted to Environmental Research Letters*. Article reference: ERL-107336.R1. SF and NTR designed the atmospheric perturbation model. SF provided detailed suggestions for model simulations and interpretations of results and detailed comments on the manuscript. MH performed primary analysis on the eddy covariance data at two of the research sites and provided detailed comments on the manuscript.

Original contributions

This body of research constitutes the first effort to measure continuous CO₂ and CH₄ fluxes across a series of peatlands of different post-extraction and restoration ages. The empirical measurements provide a foundation to quantify the climate impact of peatland restoration, in order to determine if restoration for long-term C management can be an effective climate change mitigation strategy. The topic is timely as industries, governments and societies are searching for cost- and time-effective strategies to reduce or offset greenhouse gas emissions. The results of Chapters 3 and 5 are informative for restoration practitioners outside of the horticultural peat moss industry and for future policy decisions on wise-use of peatlands. This thesis also contains an in-depth study of belowground C cycling at the older post-extraction restored peatland that uses a multi-disciplinary experimental design not previously done in a single study. The results of Chapter 4 advance our knowledge on the legacy of industrial activity on peatland C accumulation after restoration.

CHAPTER 1

INTRODUCTION

Peatlands play a significant role in the global carbon (C) cycle through sequestering carbon dioxide (CO₂), emitting methane (CH₄) and being a net export of dissolved carbon toward downstream ecosystems (Billett et al., 2004; Nilsson et al., 2008; Roulet et al., 2007; Waddington and Roulet 2000). As a result of their large extent (4,622,500 km²), peatlands constitute a major global storage of C and represent the largest terrestrial C stock by storing ~644 Gt C (Dargie et al., 2017; Page et al., 2011; Yu, 2012). However, more than 50% of total wetland area, including peatlands, has been lost since 1700 CE due to land use change (Davidson, 2014). Approximately 15% of remaining peatland area is drained – particularly in the temperate zone and (sub)tropics – for a variety of industries including horticulture, agriculture, forestry and grazing (Buckmaster et al., 2014). Soil mineralization in drained peatlands is estimated to be responsible for almost 6% of the total global anthropogenic greenhouse gas (GHG) emissions (Buckmaster et al., 2014).

In Canada, *Sphagnum* moss-dominated peatlands have been subject to mechanized peat extraction for more than half a century, either through mechanical block cutting or more recently through extensive vacuum-harvesting (Rocheffort et al., 2003). Approximately 34,000 hectares (ha) of Canadian peatlands have been disturbed for horticultural peat moss extraction, supporting an industry valued at \$337 million (CSPMA, 2014). For comparison, Germany and Ireland have industrially extracted roughly 30,000 ha and 50,000 ha, respectively (Beyer and Höper, 2015; Wilson et al., 2015). When a peatland is drained and its stored C exposed, the internal GHG dynamics that result in net C uptake are fundamentally altered. Because of draining, CH₄ emissions are reduced to minimal levels, except from the drainage ditches, which can be localized large sources (Sundh et al., 2000; Waddington and Day, 2007). The compressed, mineralizing surface left after extraction inhibits spontaneous vegetation recovery, resulting in extracted sites releasing large amounts of CO₂ (Waddington and McNeil, 2002). Peat oxidation in post-extraction peatlands represents a persistent source of CO₂ to the atmosphere without intervention (Aslan-Sungur et al., 2016; Rankin et al., 2018).

The recognition that degraded peatlands bear a significant cost to society through loss of multiple ecological services, including climate regulation, has resulted in significant money being invested in peatland restoration projects around the world (Andersen et al., 2017). Over 25 years

of research on peatland restoration in North America has determined that an active ecological restoration approach has the best recovery outcome (Chimner et al., 2017). Active restoration in post-extraction *Sphagnum* peatlands involves re-introducing *Sphagnum* species and re-establishing a suitable hydrologic regime with ditch infilling and profiling (Graf and Rochefort, 2016). The goal of active restoration is to re-establish a C sink in the short-term (decades), with the hope of re-initializing long-term peat accumulation (Rochefort et al., 2003). The horticultural peat moss industry in Canada aims to be a sustainable practices leader by ensuring restoration of post-extraction sites is in accordance with government compliance and consumer expectations (CSPMA, 2014). Future action at the industry and government level is linked to scientific research determining whether restoration actions can return C accumulation at a post-extraction peatland in a timely manner.

Studies that have examined C fluxes in restored or rewetted peatlands with periodic (i.e. non-continuous) chamber measurements over multiple years have often reported large variation in the C balance that makes determining the achievement of the management actions difficult (Renou-Wilson et al., 2018; Swenson et al., 2019; Vanselow-Algan et al., 2015; Wilson et al., 2016). Meanwhile, studies in undisturbed *Sphagnum* peatlands indicate there is considerable temporal variability in greenhouse gas (GHG) exchange between years and that long-term ecosystem-scale records are required to produce a robust estimate of C sequestration (e.g. Roulet et al., 2007). Multi-year continuous ecosystem exchange of CO₂ and CH₄ measured by eddy covariance with simultaneous accounting of aquatic C losses is arguably the most robust approach to quantify the net ecosystem C balance (NECB) of a system. As of yet, no published studies exist in post-extraction peatlands that have determined a multi-year NECB that meets these criteria.

Re-establishing soil C sequestration by peatland restoration could be a benefit to climate. However, the success of peatland restoration for long-term C management through its impact on the radiative forcing of climate is unknown. Addressing the question in a scientifically robust manner requires quantifying the climate impact of a restored peatland over time relative to not restoring. A common approach with post-extraction peatland studies has been to use non-continuous flux measurements with a global warming potential (GWP) metric applied (e.g. Renou-Wilson et al., 2016; 2018; Swenson et al., 2019; Wilson et al., 2013; Wilson et al., 2016). Among other issues with this method, the GWP is only capable of comparing the relative climate impact of GHGs over a fixed time frame and thus does not directly address the research question. A more

informative approach would be to dynamically model the atmospheric perturbation of the dominant peatland GHG exchanges on time integrations more appropriate for continuous ecosystem exchanges (Neubauer and Megonigal, 2015). This approach would allow a direct comparison of the effects of temporally changing rates of GHG exchange at post-extraction unrestored and restored sites, providing a more appropriate way of assessing restoration as a climate change mitigation strategy.

In this thesis, I aim to provide a better understanding of the impact of active restoration on post-extraction peatland C cycling to evaluate the success of peatland restoration for long-term C management. My specific research objectives are to:

- (1) Establish the multi-year NECB of a post-extraction peatland restored 14 years prior;
- (2) Investigate belowground C cycling processes to improve understanding of CH₄ emissions at post-extraction restored peatlands;
- (3) Quantify the climate impact of peatland restoration actions using an atmospheric perturbation model with a space-for-time series of measurements at Canadian post-extraction peatlands.

This thesis comprises six chapters including this introductory chapter. Chapter 2 presents a review of literature on peatland structure and function, carbon biogeochemistry, peatland restoration and key measurement techniques. The literature review will present knowledge on undisturbed peatland C cycling in order to set a framework for comparing existing knowledge on post-extraction peatlands and new knowledge gained in this thesis. The research results are organized into three Chapters (3-5) which have been published, submitted or are being prepared for submission to peer-reviewed journals. In Chapter 3, the first manuscript presents the multi-year NECB of a restored post-extraction peatland (Objective 1). This includes comparing seasonal patterns in water storage and net ecosystem exchange of CO₂ (NEE) at the restored peatland to an undisturbed Canadian peatland with a long-term eddy covariance record. The second manuscript, Chapter 4, presents the effects of cutover peat in limiting CH₄ production, causing low emission at the restored peatland (Objective 2). The carbon isotopic fractionation factor is used to show differences in methanogenesis pathways occurring in the former drainage ditches and restored peat fields while comparison with the surrounding undisturbed peatland reveals differences in decomposition and surface-atmosphere C exchange. The final manuscript, Chapter 5, uses

measurements of C fluxes across a chronosequence of post-extraction unrestored and restored peatlands in Canada to investigate the climate impact of peatland restoration (Objective 3). An atmospheric perturbation model is used to compute the instantaneous radiative forcing associated with active restoration compared to average rewetting actions and to not restoring. The thesis concludes in Chapter 6 with a summary of my main findings and proposed future research.

CHAPTER 2

LITERATURE REVIEW

2.1 Peatland description

A peatland is defined as an ecosystem that has accumulated incompletely decomposed plant material of more than 30 cm thickness (Glaser, 1987). Long-term C storage in peatlands results from C accumulation rates exceeding decomposition of organic material (Moore et al., 1998). This is primarily related to organic matter decomposition rates, which in northern peatlands (latitude 40° to 70°N), arise from cool temperatures, waterlogging and soil organic matter properties that limit microbial respiration (Moore and Basiliko, 2006). Northern peatlands can be broadly classified into two categories, bog and fen, based on vegetation composition, nutrient status and hydrology (Clymo, 1984). Ombrogenic bogs receive water and nutrients mainly from precipitation, and are typically dominated by *Sphagnum* mosses (Glaser, 1987). In contrast, minerogenic fens receive water and nutrients through lateral flow and tend to have a higher portion of herbaceous vascular plant cover; differences in base cation presence and pH due to differences in water supply further subdivide fens into rich, intermediate and poor (Glaser, 1987; Wheeler and Proctor, 2000).

Peatlands often form as complexes that incorporate the different peatland types and can cover up to thousands of square kilometres of terrain, for example the Hudson Bay Lowland in Canada. Within a peatland, plants will assemble based on microscale differences in hydrology, resulting in well documented hummock-hollow vegetation associations (e.g. Blodau 2002; Rochefort et al., 1990). Vertically, peat profiles consist of a saturated zone depleted in oxygen (O₂), where organic matter (peat) is decomposed anaerobically, and an overlying oxic zone consisting of vegetation, fresh litter and collapsed layers, which may be seasonally saturated (Clymo, 1984). It is estimated that approximately 98.5% of the total peatland C pool resides in the litter and peat whereas ~1.5% is within the vegetation itself (Gorham, 1991). Due to the decomposition resistance of *Sphagnum* litter (Dorrepaal et al., 2005; Limpens and Berendse, 2003; Rydin and Jeglum, 2006), bogs, and to a lesser extent poor fens, form peat more readily than other peatland types (Hájek et al., 2011). Properties such as air and water-holding capacity have resulted in *Sphagnum* peatlands being targeted for extraction for horticultural use.

Peatlands play an important role in the global C cycle. While their annual uptake of C is small relative to many other ecosystems, the limited release back to the atmosphere has created a major C reservoir (Holden, 2005). Peatlands are estimated to be the largest terrestrial C stock, storing ~644 Gt C (Dargie et al., 2017; Page et al., 2011; Yu et al., 2010), with northern peatlands estimated to contain ~500 Gt C (Scharlemann et al., 2014; Yu, 2012). For context, atmospheric CO₂ levels reached 402.8 ± 0.1 ppm in 2016, equivalent to ~862 Gt C (Dlugokencky and Tanis, 2017). Thus, peatlands hold roughly 77% of the amount of C contained in the atmosphere, while occupying ~3% of the world's land surface (Yu et al., 2010). The importance of peatlands to the global C cycle, especially in the context of anthropogenic climate change and disturbances, has prompted scientific research into the controls and dynamics of C gas exchange in undisturbed peatlands, and their response to disturbances.

2.2 Carbon dioxide production and flux mechanisms and drivers

Carbon cycling in undisturbed peatlands is a function of primary production and microbial decomposition processes. Atmospheric CO₂ is taken up through the cell walls of non-vascular plants, *i.e.* mosses, or through the pores (stomata) on the leaves of vascular plants (Lafleur, 2009). Carbon dioxide is then used in the photosynthesis process with water and sunlight to produce raw materials for growth, with O₂ being a by-product (Lafleur, 2009). Some CO₂ is respired by plant leaves, stem and roots predominantly as a by-product of converting raw materials to energy (mitochondrial respiration) but also as a result of inefficiencies in the photosynthetic process (photorespiration) (Kamal and Varma, 2008; Lafleur, 2009). Further CO₂ is released from the ecosystem when plant litter is consumed by microbes during the process of organic C mineralization (Blodau, 2002). Carbon mineralization is a slow process in peatlands as O₂, required for the process, is limited by high water content and water table position (Limpens et al., 2008). The difference between gross primary productivity (GPP) through photosynthesis and ecosystem respiration [ER = autotrophic respiration (AR) + heterotrophic respiration (HR)] is the net amount of CO₂ taken up or released by the ecosystem and is commonly known as the net ecosystem exchange (NEE).

Surface-atmosphere CO₂ exchange processes are controlled by environmental (e.g. plant species and physiology, substrate quality and microbial communities) and meteorological (e.g. light, air temperature and water availability and demand) factors (Lafleur, 2009). GPP is mainly controlled by the interaction of light, air temperature, and atmospheric water demand (e.g. Dunn

et al., 2007; Illeris et al., 2004; Lindroth et al. 2007; Lund et al., 2010; Novick et al., 2016), while vegetation type and soil moisture and nutrient availability determine the response of the ecosystem to the meteorological forcings (e.g. Christensen et al., 2003; McVeigh et al., 2014; Ward et al., 2013). ER is driven mainly by soil temperature and soil moisture, with spatial differences in autotrophic respiration controlled by vegetation type, and heterotrophic respiration by substrate quality (e.g. Bubier et al., 2003; Chapman and Thurlow, 1996; Lafleur et al., 2005; Lindroth et al., 2007; Lund et al., 2010; Pelletier et al., 2011; Silvola et al., 1996; Yavitt et al., 1997). The effect of the water table position on ER appears to differ with microtopography and between peatland sites, suggesting a strong effect of local conditions on microbial response to changes in water storage (Dimitrov et al., 2010). Factors such as moisture and temperature can have confounding effects on the components of NEE. For example, warming temperatures can stimulate both GPP and ER resulting in little net effect on NEE (e.g. Sulman et al., 2010). However extreme conditions such as drought brought on by high temperature and/or low rainfall has been found to shift the balance between GPP and ER, causing reduced net CO₂ uptake on a seasonal basis (e.g. Alm et al., 1999, Aurela et al., 2007, Peichl et al., 2014).

At extracted peatlands, the lack of GPP after vegetation is removed, and increased HR with drainage, results in often large net CO₂ loss from the system (e.g. McNeil and Waddington, 2003; Rankin et al., 2018; Tuittila et al., 1999; Waddington et al., 2010). The vacuum-harvesting technique used for peat extraction in Canada can result in much higher emissions compared to other techniques utilized in European countries, due to the degree of disturbance and possibly the shallower, more labile peat C exposed (Wilson et al., 2015). The range of emissions measured in post-extraction peatlands is 75–517 g CO₂-C m⁻² yr⁻¹, compared to an average uptake of 5 to 114 g CO₂-C m⁻² yr⁻¹ in undisturbed northern peatlands (Table 2.1). Mean annual NEE at rewetted or restored post-extraction peatlands varies considerably, from -119 to 470 g CO₂-C m⁻² yr⁻¹, in part due to the timing of measurements relative to restoration (Figure 1.1).

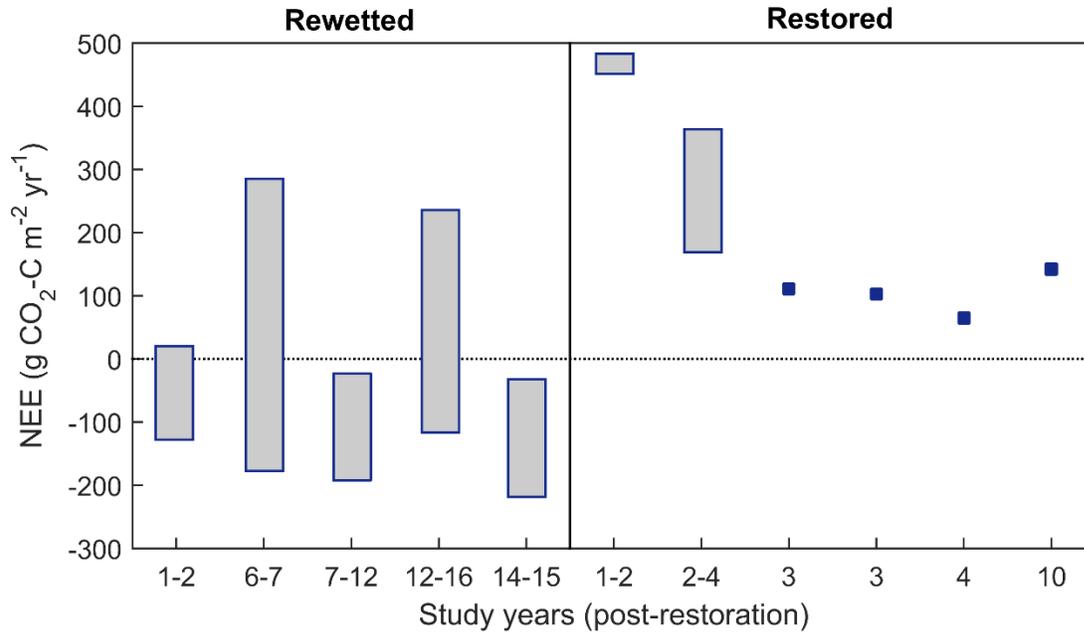


Figure 2.1 – Comparison of annual net ecosystem exchange (NEE) of CO₂ at post-extraction rewetted and restored peatlands. Grey bars show the range of annual NEE measured at a site with multiple years of measurements. Blue squares are sites with a single year of measurements. The study period is along the x-axis Rewetted peatland literature: D’Acunha et al. (2019), Lee et al. (2017), Renou-Wilson et al. (2019), Swenson et al. (2019), Wilson et al. (2016). Restored peatland literature: Järveoja et al. (2016), MacDonald (2017), Petrone et al. (2003), Strack and Zuback (2013).

In comparison, a meta-analysis by the Intergovernmental Panel on Climate Change (IPCC) for temperate-poor rewetted organic soils, *i.e.* temperate *Sphagnum* peatlands, determined a mean (95% CI) flux of -23 (-64 – 18) g CO₂-C m⁻² yr⁻¹ (IPCC, 2014). Due to the low amount of published fluxes from post-extraction rewetted/restored peatlands, undisturbed peatland flux data was needed to supplement the IPCC emission factor (IPCC, 2014). Critically, this default emission factor assumes a CO₂ sink is achieved immediately upon restoration, which is unrealistic (Figure 1.1).

Table 2.1 – Mean annual net ecosystem CO₂ exchange (NEE), in g CO₂-C m⁻² yr⁻¹, at post-extraction unrestored and rewetted/restored peatlands compared to long-term records at undisturbed northern peatlands. Negative values indicate net CO₂ uptake from the atmosphere to the ecosystem. Measurement method is either CH (closed chamber) or EC (eddy covariance).

Class	Mean NEE	SD	Years	Method	Reference
Unrestored (5 sites)	285		1	CH	Salm <i>et al.</i> (2012)
Unrestored (6 sites)	154		1	CH	Sundh <i>et al.</i> (2000)
Unrestored	75	25	3	CH	Tuittila <i>et al.</i> (2000)
Unrestored	517		1	CH	Strack and Zuback (2013)
Unrestored	384	241	3	EC	Aslan-Sungur <i>et al.</i> (2016)
Unrestored	226	75	2	EC	Rankin <i>et al.</i> (2018)
Rewetted (1 year prior)	-49	68	2	CH	Renou-Wilson <i>et al.</i> (2019)
Rewetted (6 years prior)	64	220	2	CH	Swenson <i>et al.</i> (2019)
Rewetted (7 years prior)	-104	80	5	CH	Wilson <i>et al.</i> (2016)
Rewetted (12 years prior)	66	168	4	CH	Renou-Wilson <i>et al.</i> (2019)
Rewetted (14 years prior)	-119	86	2	EC	D'Acunha <i>et al.</i> (2019)
Restored (1 year prior)	470 (670)*	7	2	EC	Petrone <i>et al.</i> (2003)
Restored (2 years prior)	272	89	3	EC	Macdonald (2017)
Restored (3 years prior)	111		1	CH	Järveoja <i>et al.</i> (2016)
Restored (3 years prior)	103		1	CH	Järveoja <i>et al.</i> (2016)
Restored (4 years prior)	65		1	EC	Macdonald (2017)
Restored (10 years prior)	142		1	CH	Strack and Zuback (2013)
Temperate	-73	40	17	EC	Roulet, N. T. personal communication
Temperate	-36	7	3	EC	Olson <i>et al.</i> (2013)
Temperate	-5	28	4	EC	Lund <i>et al.</i> (2012)
Temperate	-64	34	11	EC	Helfter <i>et al.</i> (2015)
Temperate-maritime	-56	19	9	EC	McVeigh <i>et al.</i> (2014)
Temperate-maritime	-114	10	6	EC	Levy and Gray (2015)
Boreal	-20	18	4	EC	Lund <i>et al.</i> (2015)
Boreal	-58	21	12	EC	Peichl <i>et al.</i> (2014)
Boreal	-76	40	5	EC	Strachan <i>et al.</i> (2016)
Subarctic	-90	6	8	EC	Christensen <i>et al.</i> (2012)

* Annual NEE is an estimate.

The trajectory of annual NEE after restoration toward net CO₂ uptake is conditional on the starting conditions, which may be highly site-specific. Aside from differences in climate zones and nutrient status, the degree of disturbance, expressed by the vegetation composition present before restoration, and the restoration approach used are likely to have a significant influence on GHG dynamics post-restoration. Rewetting may be sufficient to return a CO₂ sink in domestic hand-cut

peatlands where vegetation was already present (e.g. Renou-Wilson et al., 2019), but successful ecological re-establishment can be patchy at rewetted industrial cutover sites (Renou-Wilson et al., 2019; Swenson et al., 2019; Wilson et al., 2007; 2016). At one studied site, rewetting did not aid in the return of typical ombrogenic bog flora, and resulted in a 4-year mean CO₂ source over a decade after rewetting (Renou-Wilson et al., 2019). Incomplete vegetation re-establishment at another rewetted site caused the site to switch from an annual CO₂ sink to source under slightly drier conditions, 7-12 years after rewetting (Wilson et al., 2016). The depth that the water table is restored to (at or below the surface), and subsequent vegetation changes, appear to be defining factors in the restoration trajectory of rewetted sites (Renou-Wilson et al., 2019; Wilson et al., 2016). Even active ecological restoration, where the moss layer transfer technique (MLTT) is used to apply *Sphagnum* diaspores homogeneously across a site, can nonetheless result in heterogeneous vegetation emergence (MacDonald, 2017). Thus far, the return to an annual CO₂ sink has not been measured at an actively restored post-extraction site (Figure 1.1), with the oldest site evaluated being 10 years post-restoration (MacDonald, 2017; Järveoja et al., 2016; Petrone et al., 2003; Strack and Zuback, 2013; Waddington et al., 2010). It remains unclear when, or even if, restored peatlands could show a magnitude of net CO₂ uptake similar to undisturbed peatlands.

2.3 Methane production and flux mechanisms and drivers

Methane flux at the peatland surface is strongly associated with biogeochemical processes and controls that are involved in belowground decomposition of organic matter into its terminal end-products, CO₂ and CH₄ (Limpens et al., 2008). Primary production provides reduced compounds which, with the accumulation of litter and peat, creates a redox gradient to the atmosphere (Limpens et al., 2008). Oxygen transfer is downward, however due to diffusion constraints, O₂ concentration depletes rapidly below the water table, with the lower layers of peat remaining permanently anoxic (Blodau et al., 2004). Oxidative capacity is also stored in oxidants, such as nitrate, sulfate and ferric iron, allowing anaerobic decomposition to occur (Limpens et al., 2008; Artz, 2009). Decomposition under anaerobic conditions occurs in three steps: hydrolysis, fermentation and lastly methanogenesis. For methanogenesis to occur, the environment redox potential must be less than -330mV, corresponding to a depletion of oxidants (Kamal and Varma, 2008; Lai, 2009).

Methanogenesis primarily occurs through two pathways in peatlands: (i) the reduction of CO₂ with hydrogen (H₂) (hydrogenotrophic methanogenesis); and, (ii) acetate fermentation into

CO₂ and CH₄ (acetoclastic methanogenesis) (Chanton, 2005). With both pathways, the stable isotope carbon composition (¹³C) of organic matter is fractionated to form more enriched δ¹³C-CO₂ and more depleted δ¹³C-CH₄. (Corbett et al., 2013a). The degree of fractionation is dependent on the pathway, with less of a difference between CO₂ and CH₄ with acetate fermentation than with H₂/CO₂ reduction (Chasar et al., 2000a). Carbon isotopic fractionation evidence has been instrumental in determining that *Sphagnum* peatlands tend to favor methanogenesis from H₂/CO₂ reduction (Chanton et al., 1995, 2005; Chasar et al., 2000a, b; Kelly et al., 1992; Lansdown et al., 1992; Popp et al., 1999). Acetoclastic methanogenesis, meanwhile, has been shown to occur in substrates surrounding vascular plants, particularly sedges (e.g. Ström et al. 2003; 2005; 2012). The plant root system is a source of a wide range of labile carbon compounds, such as organic acids, amino acids and carbohydrates, which provide easily available substrate for microbial decomposition (Joabsson et al., 1999; Proctor and He, 2017). Root release of acetate and precursors to acetate can stimulate CH₄ production in the soil (Joabsson et al., 1999; Ström and Christensen, 2007; Ström et al., 2003; 2005; 2012). However, acetate concentrations found in the pore water have been found to correspond to only a few hours of CH₄ flux, suggesting the need for a continuous input to maintain acetate fermentation (Ström et al., 2012). The link between root exudates and acetate fermentation may be one explanation for why primary productivity, which plays a role in supplying labile C, has been found to correlate with CH₄ release (e.g. Bubier et al., 1995; Moore et al., 2011; Whiting and Chanton, 1993).

In addition to production, the net efflux of CH₄ is controlled by the degree of consumption during transport through the peat profile to the surface (Whalen, 2005). Methane transport occurs by way of diffusion through the peat column pore spaces, mass transport by bubbling (ebullition) and plant-mediated transport. Because CH₄ has low solubility in water (23–40 mg/L at 20°C), concentration build-up results in CH₄ escaping through the sediment to the atmosphere by either diffusion or ebullition (Abdalla et al., 2016). Once CH₄ enters the oxic zone, a large portion can be oxidized to CO₂ by methanotrophic bacteria (Whalen, 2005). Highest methanotroph activity usually coincides with the zone of average water table, due to the oxic-anoxic boundary providing an optimal ratio of CH₄ to O₂ (Lai, 2009). As well, methanotrophic oxidation can occur in the rhizosphere, due to O₂ redistribution through the plant root system (Whalen, 2005). Vascular plants have developed specialized aerenchymatous tissues to transport O₂ into otherwise anaerobic layers, but, CH₄ can also be released to the atmosphere by this pathway (Joabsson et al., 1999).

Several peatland studies have reported vascular plants, in particular *Eriophorum* spp., enhancing the ecosystem CH₄ flux by allowing CH₄ to bypass the oxidation zone (e.g. Greenup et al., 2000; Joabsson and Christensen, 2001; Marinier et al., 2004; Moore et al., 2011; Ström et al., 2005; Tuittila et al., 2000). Herbaceous plants such as *Typha* spp. are also known to be conduits for release (Laanbroek, 2010); in a Canadian cool-temperate marsh, *Typha angustifolia* were found to release as CH₄ more than half of the CO₂ removed from the atmosphere, on an annual basis (Strachan et al., 2015).

At the ecosystem level, water table and temperature are dominant controls on CH₄ flux (Turetsky et al., 2014). An exponential dependence of CH₄ emission on peat temperature has been well documented in both bogs and fens (Jackowicz-Korczyński et al., 2010; Kim et al., 1998; Marushchak et al., 2016; Rinne et al., 2007; 2018). However, no simple dependence of CH₄ flux on water table has been observed, likely in part due to the overriding effect of vascular transport (Brown et al., 2014; Jackowicz-Korczyński et al., 2010; Rinne et al., 2007). Water table position, nonetheless, is a key factor for CH₄ production and oxidation as it determines the location of the redox boundary between oxic and anoxic (Bellisario et al., 1999). Accordingly, draining peatlands has been reported to result in increasing soil temperatures and oxidation rates and reduced CH₄ emissions (Abdalla et al., 2016). Drainage ditches can become localized anaerobic zones with similar or even increased CH₄ emissions relative to undisturbed peat (Huttunen et al., 2003; Minkkinen et al., 1997; Rankin et al., 2018; Schrier-Uijl et al., 2010; Strack and Zuback, 2013; Sundh et al., 2000; Waddington and Day, 2007). In a meta-analysis of CH₄ emissions from northern peatlands that have been drained for forestry, cropping, grazing and extraction, Abdalla et al. (2016) found that drainage reduced CH₄ emissions by 84%, resulting in a mean flux of 3.7 g C-CH₄ m⁻² year⁻¹ compared to 12 ± 21 g C-CH₄ m⁻² year⁻¹ in undisturbed peatlands. Emissions in post-extraction peatlands appear even lower, ranging from 0 to 2.7 g CH₄-C m⁻² yr⁻¹ (Alm et al., 2007; Järveoja et al., 2016; Maljanen et al., 2010; Strack and Zuback, 2013; Sundh et al., 2000; Waddington and Day, 2007). Restoration that raises the water table to below the surface has been found to increase CH₄ emissions relative to post-extraction values while often remaining lower than pre-disturbance (Beyer and Höper, 2015; Järveoja et al., 2016; Komulainen et al., 1998; Tuittila et al., 2000; Waddington and Day, 2007; Strack and Zuback, 2013; Strack et al., 2016; Wilson et al., 2009). A study of Canadian block-cut peatlands found a drastic reduction in CO₂ and CH₄ production in extracted and abandoned peat compared to undisturbed peat (Basiliko et

al., 2007). Aerobic and anaerobic decomposition of peat was found to be constrained by organic matter quality (phosphorus and C chemistry), and by the size of the microbial biomass capable of being supported by the limited resources (Basiliko et al., 2007). In a study addressing CH₄ cycling in forestry-drained peatlands, Juottonen *et al.* (2012) found poor establishment of methanogens a decade after restoration and hypothesized that prolonged drying made reduce peat quality, affecting development of methanogenic community populations post-restoration. The authors conclude that the unresponsiveness of methanogens to restoration rather than enhanced CH₄ oxidation was likely behind the observed low CH₄ emission (Juottonen et al., 2012). Assessing the availability of labile C compounds and the pathways of methanogenesis in restored peatlands would help to resolve this issue.

2.4 Aquatic carbon flux mechanisms and drivers

Carbon can be exported from peatlands through water movement, in particulate, dissolved (DOC, HCO₃⁻ and CO₃²⁻) and gaseous (free CO₂ and CH₄) forms (Dawson et al., 2002). DOC is the C fraction that passes through a 0.45 µm filter whereas particulate organic C (POC) is between 0.45 and 1.0 µm (Dawson et al., 2002). The release of dissolved C in peat soils represents a balance between production, adsorption, desorption and microbial use (Moore and Dalva, 2001). Although aquatic C losses are smaller than other C cycle processes such as photosynthesis and respiration, nonetheless they can account for steady losses of C from peatlands (Öquist et al., 2009). For peatlands close to net C equilibrium, aquatic losses may be decisive in whether the ecosystem is a net source or sink annually. DOC export is generally the largest of the aquatic C fluxes (1 to 50 g C m⁻² yr⁻¹) and as such has been reported most frequently in peatland C budgets (Christensen et al., 2012; Helfter et al., 2015; Koehler et al. 2011; Levy and Gray, 2015; Nilsson et al., 2008; Roulet et al. 2007, Worrall et al. 2009). Losses of DOC to downstream ecosystems have significant effects on productivity, biogeochemical cycles and attenuation of visible and UV radiation, impacting water chemistry and quality (Pastor et al., 2003). From a landscape perspective, any change in peatland DOC flux (F_{DOC}) can result in significant redistribution of regional terrestrial C (Limpens et al. 2008; Pastor et al., 2003). POC export and degassing of CO₂ and CH₄ are less well quantified in C budgets by comparison (e.g. Dinsmore et al., 2010; Nilsson et al., 2008). POC has been found to be large only in severely eroding peatlands, while degassing requires open water areas, such as stream networks, and as such is generally smallest of the C fluxes in undisturbed peatlands (Limpens et al., 2008).

DOC export rates are a function of controls on DOC production and consumption and water storage and flow through the peatland (Pastor et al., 2003; Price et al., 2005). The quality of DOC released with decomposition will depend on the substrate type, surrounding physical and chemical characteristics of the soil where DOC is being produced and consumed as well as the environment temperature (Kalbitz et al., 2000). Warmer summer temperatures drive DOC production more than DOC consumption (Freeman et al., 2001, Moore and Dalva, 2001), while higher DOC concentration midsummer is also associated with peak plant productivity (Strack et al., 2015). The nature of hydrologic events will also impact the DOC quality due to differences in mobility of the humic, hydrophobic and hydrophilic fractions (Strack et al., 2011). DOC concentration within the peat profile typically follows a pattern of higher concentrations during low flow periods, as dissolved C will accumulate in the peat pore structure until flushed out (Holden 2005). However F_{DOC} is expected to be larger under high discharge events, i.e. storm events, as F_{DOC} is calculated from discharge which is controlled by rainfall (Clark et al., 2007). Ombrogenic bogs tend to have flashy hydrological regimes, with high peak flows and discontinuous summer flow (Holden, 2005). Therefore snowmelt is expected to compose a large portion of the annual DOC export in areas with significant snow accumulation (Dyson et al., 2011). Water table position is a key control through changing the production zone (Koehler et al., 2009) as well as by controlling the amount of peatland area contributing to baseline F_{DOC} (Fraser et al., 2001).

Annual DOC export in undisturbed peatlands is fairly well quantified, ranging from 5 to 36 g C m⁻² yr⁻¹ in temperate sites according to a review by Evans *et al.* (2016). Only a few studies have quantified DOC export at post-extraction peatlands: to the best of my knowledge, three studies at rewetted sites, in Canada, Wales and Ireland, and re-occurring assessments at the active restoration site, Bois-des-Bel, in Canada. At the Irish and Canadian rewetted sites, DOC flux was found to be 10.4 and 15.6 g C m⁻² yr⁻¹, respectively (D'Acunha et al., 2019; Swenson et al., 2019). In contrast, DOC flux estimates at a rewetted blanket bog in Wales were < 6.4 g C m⁻² yr⁻¹, while POC estimates were much higher than available published estimates (Wilson et al., 2011). Blanket bog topography and the orientation of the drains can have a large effect in drainage channel erosion in these peatlands, presenting a unique challenge for reducing fluxes with rewetting (Wilson et al., 2011). At Bois-des-Bel, peat extraction resulted in an increase in DOC pore water concentration and runoff, resulting in higher DOC export when unrestored (Waddington et al., 2008). Within the

first few years following active restoration, DOC export was reduced by approximately one half, mainly due to reduced runoff (Waddington et al., 2008). A follow-up study at 10 years post-restoration found that DOC export remained similar to at three years post-restoration, $\sim 9 \text{ g C m}^{-2} \text{ yr}^{-1}$ with snowmelt included (Strack and Zuback, 2013). Vegetation growth and community changes and improved hydrological conditions with restoration were not found to significantly affect the quality of exported DOC, which remained similar to an unrestored section of the peatland complex (Strack et al., 2016). Understanding the trajectory of DOC dynamics with time following peatland restoration requires further study as these sites continue to develop.

2.5 Methodological approaches to compute the NECB

While a multi-year NECB that accounts for the CO_2 , CH_4 and DOC components has been computed for a few northern undisturbed peatlands (Christensen et al., 2012; Helfter et al., 2015; Levy and Gray, 2015; Roulet et al., 2007), many long-term assessments have focussed on NEE of CO_2 solely (Aurela et al., 2004; Helfter et al., 2015; Lund et al., 2012; 2015; McVeigh et al., 2014; Peichl et al., 2014; Strachan et al., 2016), or in combination with CH_4 (Koehler et al., 2011; Olson et al., 2013). Here, I define a multi-year study as having three or more consecutive years of measurements. The standard method used by these studies to measure NEE is the eddy covariance technique, which measures ecosystem-scale fluxes directly and continuously (see Section 2.5.1). Due to technological constraints until recently, the ecosystem CH_4 flux has more often been derived by up-scaling vegetation community fluxes measured with closed or auto-chambers (see Section 2.5.2). A few recent studies have published two or more years of CH_4 fluxes using eddy covariance (Brown et al., 2014; Drollinger et al., 2019; Fortuniak et al., 2017; Hanis et al., 2013; Jackowicz-Korczyński et al., 2010; Li et al., 2016; Neumann et al., 2019; Parmentier et al., 2011; Tagesson et al., 2012; Wang et al., 2018), however developing an NECB has not been a focus. Helfter *et al.* (2015) used literature values for NEE, CH_4 and aquatic C losses to determine an up-to-date NECB for the main long-term undisturbed peatland sites (Auchencorth Moss, Mer Bleue, Degerö Stormyr, Glencar and Stordalen). The authors noted a fairly narrow C sink range, of -17 to $-34 \text{ g C m}^{-2} \text{ yr}^{-1}$, when all flux pathways were accounted for (Helfter et al., 2015).

A multi-year evaluation of the NECB at a post-extraction peatland does not exist in the literature. Moreover, multi-year $\text{CO}_2 + \text{CH}_4$ flux studies appear limited to the Republic of Ireland. Renou-Wilson *et al.* (2019) report a 4-year mean release of $66 \pm 168 \text{ g CO}_2\text{-C m}^{-2} \text{ yr}^{-1}$ and $5.0 \pm 2.2 \text{ g CH}_4\text{-C m}^{-2} \text{ yr}^{-1}$ at a industrially extracted rewetted (12 years prior) site, when emissions from

a shallow lake were excluded. The same study included two years of data at a domestic cutover rewetted (1 year prior) site, where average NEE was $-49 \pm 68 \text{ g CO}_2\text{-C m}^{-2} \text{ yr}^{-1}$ and emitted CH_4 was $20 \pm 5 \text{ g CH}_4\text{-C m}^{-2} \text{ yr}^{-1}$ (Renou-Wilson et al., 2019). A second industrial cutover Irish site that was rewetted seven years prior had a 5-year mean balance of $-104 \pm 80 \text{ g CO}_2\text{-C m}^{-2} \text{ yr}^{-1}$ and $9 \pm 2 \text{ g CH}_4\text{-C m}^{-2} \text{ yr}^{-1}$ (Wilson et al., 2016). The large standard deviation on the reported numbers at the three rewetted sites is likely a combination of several factors: inter-annual weather variability, vegetation succession and propagated errors caused by up-scaling chamber fluxes. Measuring ecosystem-scale fluxes directly with the eddy covariance technique reduces the uncertainty in the annual flux estimates, which facilitates investigating the effects of the other two factors. Using eddy covariance, Rankin *et al.* (2018) found that an unrestored peatland in Canada emitted 173 and 259 $\text{g CO}_2\text{-C m}^{-2} \text{ yr}^{-1}$ at 14- and 15-years post-extraction, which the authors linked to wetter spring conditions driving a brief period of net CO_2 uptake in the first study year. The rewetted Burns Bog near Vancouver, Canada is currently the only post-extraction rewetted peatland with a published eddy covariance-based NECB, but, based on a single year of data (D'Acunha et al., 2019). The authors discuss their results relative to CO_2 and CH_4 fluxes published separately (Lee et al., 2017), noting large differences in the magnitude of the surface-atmosphere C sink between the consecutive years (-45 vs $-160 \text{ g C m}^{-2} \text{ yr}^{-1}$), again linked to weather differences (D'Acunha et al., 2019). Clearly there is a need for long-term ecosystem-scale GHG and NECB monitoring in post-extraction peatlands, to account for the potentially large inter-annual variability experienced because of succession and weather variability.

2.5.1 Eddy covariance flux measurements

The eddy covariance technique is one of the most accurate, direct and defensible approaches to determine trace gas exchange rates (Burba, 2005). The technique is based on the principle that air parcels, moving upward and downward due to turbulent atmospheric motion, transport energy and matter between the land surface and the atmosphere. The turbulent flux densities (more commonly known as fluxes) of energy and matter can be derived using the eddy covariance technique by measuring the covariance of high-frequency fluctuations of vertical wind speed and air temperature, H_2O , CH_4 or CO_2 concentration, or molar density (Baldocchi, 2003; 2014). Sonic anemometers are commonly used to derive high frequency vertical wind velocity and air temperature from speed-of-sound measurements. High-frequency gas densities are measured with infrared $\text{CO}_2/\text{H}_2\text{O}$ gas analyzers and, more recently, laser-based CH_4 gas analyzers. The

installation of these instruments on towers allows direct flux measurement over a large upwind surface ($\approx 10^4\text{--}10^5 \text{ m}^2$) with minimal disturbance to the ecosystem (Scanlon and Kiely, 2003). Typical measurement rates are 10 Hz (every 0.1 seconds), with the computed fluxes averaging the 10 Hz covariances over a 30-minute interval. Eddy covariance measurements are currently made using open- or closed-path gas analyzer systems. Open-path systems require less power than closed-path systems which makes them optimal for measuring in remote areas where adequate power supply is a major constraint. However, obstruction of the analyzer optical path during adverse weather conditions necessitates data rejection, while sensitivity to air temperature and humidity fluctuations can result in large uncertainties (Amiro, 2010). Equipment malfunction and absence of turbulent conditions also lend to data loss, which requires complex gap-filling strategies to have a complete annual dataset (e.g. Aubinet et al., 2012). Nonetheless, the eddy covariance technique is a valuable method to achieve long-term, high temporal resolution measurements of ecosystem-scale surface-atmosphere GHG exchange.

2.5.2 Closed chamber flux measurements

Closed chamber measurements have been used extensively in peatlands to study small-scale peatland CO_2 and CH_4 dynamics (e.g. Bubier et al., 1995; 2003; 2005; Moore and Knowles, 1989; Moore et al., 2002; Pelletier et al., 2007; Ruita et al., 2007; Strack et al., 2016; Sundh et al., 2000). Compared to eddy covariance, this method has much lower associated costs and it measures fluxes at a scale ($\sim 1 \text{ m}^2$) that enables targeting individual features within an ecosystem. Gas exchange measurements are generally carried out on permanently installed collars and made with a transparent or opaque polycarbonate chamber. Advancements in portable analyzers now allow simultaneous measurements of H_2O , CH_4 and CO_2 concentration at 1 Hz. To calculate an ecosystem level flux from chamber measurements requires high-precision mapping of the ecosystem. Even so, the spatial extrapolation and temporal interpolation required with upscaling chamber measurements can result in large errors (Bubier et al., 1999). Automated chambers provide greater temporal coverage, but their use is restricted by high cost and infrastructure requirements for installation and operation (Lai et al., 2012). The use of chambers can result in some artefacts and biases in the flux measurements (Lai et al., 2012). However, disturbances during the chamber deployment period or a decrease in diffusive concentration gradient over time can now be monitored directly with the latest analyzers, minimizing post-processing data loss.

Closed chambers provide a valuable method to investigate variations in fluxes in space and time, and associated controls (e.g. Bubier et al., 1995).

2.5.3 Deriving DOC export

The flux of DOC draining from a study area can be estimated based on an equation for the water balance in combination with DOC concentration data, as:

$$F_{DOC} = (PPT - ET - \Delta S) * [DOC] \quad (2.1)$$

where PPT is precipitation (mm), ET is evapotranspiration (mm) estimated from the water vapour flux measured with eddy covariance, ΔS is the change in storage (mm) obtained with water table position measurements and [DOC] is the concentration of DOC in water samples (mg L^{-1}). Alternatively, at sites where drainage channels direct to a single outflow, F_{DOC} can be determined directly by measuring discharge at a weir outflow and regressing against continuous water level measurements to estimate discharge continuously. In the case of no significant relationship being found between discharge and [DOC], Method-5 in Walling and Webb (1985) can be used to determine the flux:

$$F_{DOC} = \left\{ \left[\frac{K \sum_{i=1}^n (C_i Q_i)}{\sum_{i=1}^n Q_i} \right] Q_r \right\} / A \quad (2.2)$$

where K (d season^{-1}) is a correction factor to convert from a daily to seasonal time step, C_i (g L^{-1}) is the instantaneous [DOC], Q_i (L d^{-1}) is the instantaneous discharge, Q_r (L d^{-1}) is the mean discharge over the sampling period and A (m^2) is the total drainage area of the site.

2.6 Computing radiative forcing of climate

The persistent uptake and maintenance of sequestered atmospheric CO_2 over millennia has led to a long-term negative atmospheric radiative GHG forcing (Frolking et al., 2006; Frolking and Roulet, 2007). Radiative forcing of a peatland is the difference between the CH_4 fluxes, and the atmospheric CO_2 sequestered since peatland formation (millennia) taking into account recent perturbations (decades) (Frolking et al., 2006). The GWP metric is commonly used by the scientific community to compare the relative climate impact of CO_2 , CH_4 and other GHGs with different atmospheric lifetimes and radiative efficiencies. GHG emissions to, or removals from, the atmosphere are converted to an equivalency in metric tonnes of CO_2 ($\text{CO}_2\text{-eq}$). The sign of the $\text{CO}_2\text{-eq}$ determines whether the system has a net warming or cooling effect on the climate.

Peatlands, excluding those disturbed, have been classified as net GHG sources over a 20-year time horizon, net GHG sinks over a 500-year horizon and source or sink depending on peatland location (tropics vs. northern) over a 100-year horizon (Crill et al., 2000; Friberg et al., 2003; Roulet, 2000; Whiting and Chanton, 2001). A major shortcoming of the GWP metric is that it treats emissions as single pulses, which is not representative of the continuous and temporally varying exchanges occurring between ecosystems and the atmosphere (Neubauer and Megonigal, 2015). For example, when the GWP was compared with a sustained-flux approach, their application yielded the possibility of opposing interpretations of the radiative forcing of an ecosystem (Neubauer and Megonigal, 2015). An alternative method is dynamic modeling, which uses time integrations more appropriate for continuous ecosystem-atmosphere exchanges and does not have a time-fixed outcome (Neubauer and Megonigal, 2015). A simple atmospheric perturbation model forced by time series flux estimates has been used in previous studies to assess climate change and human-induced peatland disturbance impacts on the radiative forcing of climate (e.g. Dommain et al., 2018; Helbig et al., 2017; Laine et al. 1996, Neubauer, 2014). The strength of this method lies in its ability to quantify the role of ecosystems as regulators of climate, by determining change in global atmospheric burden over time (Neubauer and Megonigal, 2015). Nevertheless, both the GWP metric and the atmospheric perturbation model treats the exchanges as a perturbation in atmospheric concentrations assuming that the exchange and concentration were in equilibrium prior to the perturbation, which is never truly the case.

The atmospheric perturbation model uses a simple impulse-response representation of atmospheric perturbations to compute the radiative forcing impact over time of net CO₂ and CH₄ (and N₂O) fluxes (Neubauer and Megonigal, 2015). The residence time of C as it cycles through several Earth system reservoirs is very different. The model approximates the Earth system response to a GHG flux perturbation by representing the rest of the Earth system as a set of non-interacting linear exchanges of different lifetimes (Figure 2.2).

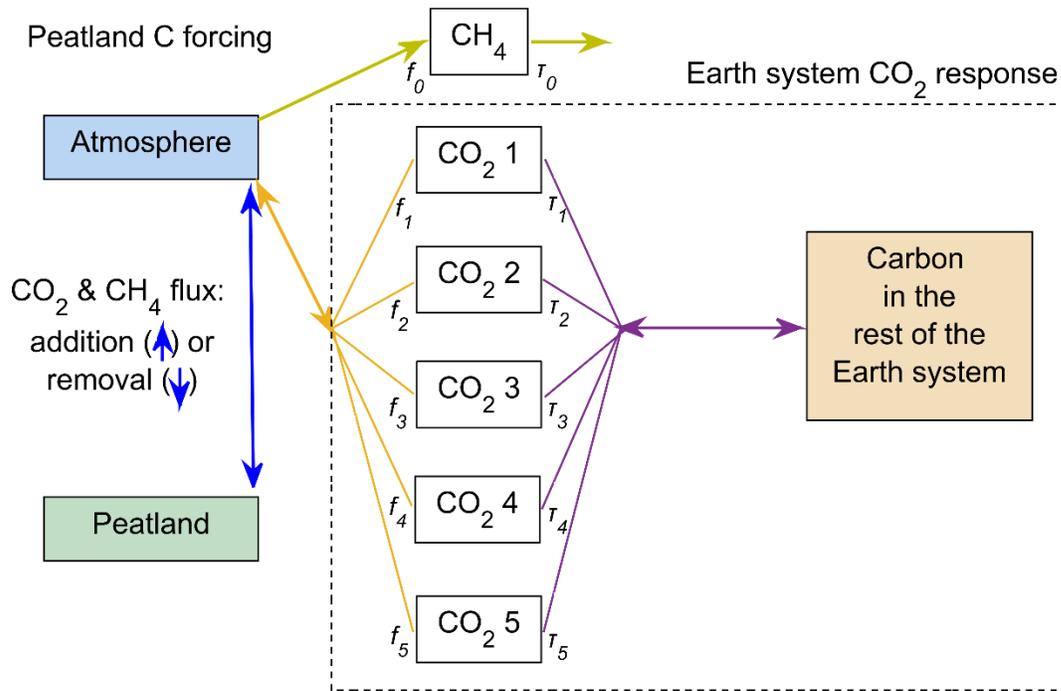


Figure 2.2 – Diagram depicting the atmospheric perturbation model. The atmospheric CH₄ perturbation (Equation 2.2) is represented by a single reservoir with a first-order decay rate (τ_0), where f_0 is equal to 1 (Table 2.2). The atmospheric CO₂ perturbation (Equation 2.1) is represented by five non-interacting reservoirs (CO₂ i) with first-order perturbation lifetimes (τ_i). When a peatland is taking up atmospheric CO₂, the CO₂ is fractionally removed from the five reservoirs (f_i). The rest of the Earth system delivers CO₂ to those five reservoirs, causing them to approach or reach a negative steady-state value for constant peatland uptake at their characteristic lifetimes (τ_i). Reservoirs CO₂ 4 and 5 have lifetimes on the order of millennia, thus their slow replenishment enables a long-term negative radiative forcing for a C-accumulating peatland. In a degrading peatland, CO₂ emission is added to the five atmospheric reservoirs at proportions (f_i), and the rest of the Earth system eventually removes CO₂ from these reservoirs causing them to approach or reach a positive steady-state value at their characteristic lifetimes (τ_i). Adapted from Dommain et al. (2018).

The lifetime of a CO₂ perturbation in the atmosphere can be represented by five lifetimes representing atmospheric removal by key reservoirs (e.g. Joos et al., 1996; 2013). A constant or time-varying net CO₂ flux (addition and removal), $\Phi_{\text{CO}_2}(t')$, since an arbitrary start time, $t = 0$, produces a perturbation to the atmospheric CO₂ burden at any time t that is given by:

$$CO_2(t) = \sum_{i=1}^5 \left(f_i \cdot \int_0^t \Phi_{CO_2}(t') e^{\frac{(t'-t)}{\tau_{CO_2}}} dt' \right) \quad (2.3)$$

where f_i is the fractional multiplier for the net CO₂ flux into reservoir i , and τ_i is the adjustment or residence time of the reservoir i . The parameterization of Equation 2.3 (see Table 2.2) was developed by fitting the model response to the carbon cycle dynamics of 15 Earth System Models (Joos et al., 2013), but with a modification to include an additional slow-response pool (CO₂ 4 in Figure 1.2) with a 7,000-year lifetime, representing ocean-sediment interactions within the carbon cycle (Dommain et al., 2018). The remaining long-term pool (CO₂ 5 in Figure 1.2), which is related to the weathering-burial component of the carbon cycle, is given a lifetime of 200,000 years (Archer et al., 1997; 1998).

The behavior of an input of CH₄ to the atmosphere, $\Phi_{CH_4}(t')$, is represented by a single reservoir, as:

$$CH_4(t) = \int_0^t \Phi_{CH_4}(t') e^{\frac{(t'-t)}{\tau_{CH_4}}} dt' \quad (2.4)$$

that loses CH₄ by a first-order process, with a constant lifetime of 12.4 years (Myhre et al., 2013). The integral in equations 2.3 and 2.4 is approximated with an annual time step discretization. The radiative forcing (RF, W m⁻²) of greenhouse gas i (CO₂ and CH₄) is calculated as:

$$RF_i = \xi_i A_i r_i \quad (2.5)$$

where ξ_i is a multiplier for indirect effects on ozone concentrations and stratospheric H₂O [CH₄ = 1.65, Myhre *et al.* (2013); CO₂ = 1], A_i is the radiative efficiency of greenhouse gas i (1.27 x 10⁻¹³ W m⁻² kg⁻¹ for CH₄ and 1.7517 x 10⁻¹⁵ W m⁻² kg⁻¹ for CO₂), and r_i is the current time atmospheric concentration perturbation of the respective greenhouse gas i due to all previous emissions/removals since a reference year. Note that CH₄ is the greenhouse gas for $i = 0$ and CO₂ is $i = 1-5$ (Figure 1.2). Methane oxidation in the atmosphere is not counted as an input to atmospheric CO₂, following the convention of IPCC for radiative forcing calculations (Myhre et al., 2013).

Table 2.2 – Atmospheric perturbation model flux fraction (f_i) and lifetime (τ_i) parameters (see Figure 2.1 and Equations 2.3 and 2.4)

Reservoir	f_i	τ_i (yr)
CH ₄	1.0	12.4 ^a
CO ₂ 1	0.2763 ^b	4.304 ^b
CO ₂ 2	0.3824 ^b	36.54 ^b
CO ₂ 3	0.224 ^b	394.4 ^b
CO ₂ 4	0.1473 ^c	7,000 ^c
CO ₂ 5	0.0700 ^c	200,000 ^c

^aMyhre *et al.* (2013).

^bMean model from Joos *et al.* (2013).

^cModified from Joos *et al.* (2013): CO₂ 4 reservoir added and CO₂ 5 pool flux fraction reduced from 0.2173 to 0.0700 and lifetime reduced from effectively infinite to 200,000 years (Archer *et al.*, 1997; 1998).

2.7 Methods to investigate belowground C cycling

2.7.1 Stable isotope analysis background and methods

Methanogenesis has been shown to be the dominant terminal decomposition pathway in undisturbed peatland systems (Chaser *et al.*, 2000a, b; Corbett *et al.*, 2013a, b; Romanowicz *et al.*, 1995). As organic matter is re-mineralized in peatlands, high molecular weight (HMW) molecules are broken down into low molecular weight molecules, followed by methanogenesis breaking down the smallest C sugars into CO₂ and CH₄ (Whiticar, 1999). Carbon dioxide is also a by-product of HMW fermentation, aerobic oxidation of organic matter, anaerobic breakdown with alternative electron acceptors (e.g. sulfate) (Keller and Bridgham, 2007), and perhaps anaerobic oxidation of organic matter using organic electron acceptors such as humics (Lovley *et al.*, 1996). Consequently, the mixture of CO₂ molecules from fermentation, etc. and methanogenesis is reflected in the isotope ratio of ¹³C/¹²C. Since none of the other processes fractionate C isotopes, CO₂ produced by these pathways will give a $\delta^{13}\text{C-CO}_2$ signature identical to the organic matter it came from ($\sim -26\text{‰}$) (Corbett *et al.*, 2013b). CO₂ produced by methanogenesis, however, will produce an enriched $\delta^{13}\text{C-CO}_2$ signature relative to the parent organic material that balances the depleted CH₄ that was also produced.

In peatlands, methanogenesis primarily occurs by either acetate fermentation (acetoclastic methanogenesis) or H₂/CO₂ reduction (hydrogenotrophic methanogenesis) (Chanton, 2005). During acetate fermentation, acetate is broken down into CH₄ and CO₂, with the carbon of the methyl group in the acetate going to CH₄ (Chanton et al., 2005; Whiticar et al., 1986), written as:



H₂/CO₂ reduction is a two-step process, with two organic molecules being broken down into two CO₂ molecules, followed by one of the CO₂ molecules being reduced to CH₄ (Chanton et al., 2005). The net overall equation for H₂/CO₂ reduction is:



The CH₄ isotopic signature for H₂/CO₂ reduction is between -60 and -100‰ whereas acetate fermentation gives a δ¹³C-CH₄ signature of -50 to -65‰ (Whiticar, 1999). The fractionation factor associated with methanogenesis can provide evidence of the pathways of methanogenesis occurring in a system, using the following equation (Whiticar et al., 1986):

$$\alpha = \frac{\delta^{13}C-DIC+1000}{\delta^{13}C-CH_4+1000} \quad (2.8)$$

In general, values of α > 1.065 and α < 1.055 are characteristic of environments dominated by H₂/CO₂ reduction and acetate fermentation, respectively (Whiticar et al., 1986; Whiticar, 1999).

A gas chromatograph-combustion interfaced-isotope ratio mass spectrometer can be used to conduct a stable isotope analysis of δ¹³C-DIC (DIC = ΣCO₂) and δ¹³C-CH₄ contained in pore water samples. Gas is extracted from the pore water into the headspace of sealed vials by the addition of first helium, to bring the vials up to atmospheric pressure, then 43% H₃PO₄ to extract the highly soluble DIC. Samples are analyzed for gas concentration and δ¹³C-DIC and δ¹³C-CH₄ in the headspace by direct injection. Isotope data are described in δ notation with units of per mil (‰), by:

$$\delta(\text{‰}) = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \times 10^3 \quad (2.9)$$

where R is the isotopic ratio of the heavy isotope relative to the lighter isotope (¹³C/¹²C) for both standard and sample. C isotope ratios are commonly reported relative to the PDB (Pee Dee Belemnite) standard.

2.7.2 Organic acid analysis

Much of the easily decomposable C in peat profiles is derived from roots, root residues and root exudates (Kuzyakov and Domanski, 2000). Under anaerobic conditions, microbes in the soil produce a range of organic acids from plant residues, including acetic, lactic, formic and propionic acid (Killham, 1994). The plant root system also releases a wide range of labile C compounds, including ectoenzymes, organic acids, sugars, phenolics and amino acids (Marschner, 1995). Once released, these labile C compounds are easily available substrate for methanogenic bacteria to consume (Joabsson et al., 1999). An organic acid of particular interest is acetate, as it is a direct substrate for methanogenesis via acetate fermentation and is found in higher concentrations *in-situ* than other organic acids (e.g. Ström et al., 2012; 2015).

To determine the pore water concentration of dissolved labile substrate, *i.e.* organic acids, amino acids and carbohydrates, pore water samples can be analyzed using a high-pressure liquid chromatography (LC) tandem-ion-spray mass spectrometry (MS) system. The LC system can be equipped to meet the separation requirements of the three compound groups by changing the analytical column and guard column (details in Ström et al., 2012). Combined, the LS and MS analysis result in a complete separation of all compounds by element composition and molecular weight (Ström et al., 2012).

CHAPTER 3

MULTI-YEAR NET ECOSYSTEM CARBON BALANCE OF A RESTORED PEATLAND REVEALS A RETURN TO CARBON SINK

Bridging statement to Chapter 3

The return of the C sink functioning of peatlands is a goal of restoration. Previous North American research has indicated that an active ecological restoration approach has the best recovery outcome. However, the time frame needed for C sequestration to re-establish after active restoration remains unknown as studies beyond a decade post-restoration do not yet exist. To address this, the present chapter assesses the NECB of an extracted temperate peatland in Canada that was restored 14 years prior. Here, I combine three years of eddy covariance flux measurements of CO₂ and CH₄ with DOC fluxes to quantify a multi-year NECB that I then compare to a long-term NECB record at an undisturbed peatland. I use a remotely sensed vegetation monitoring index to visualize the ecosystem vegetation response prior to and after restoration and compare it to the surrounding undisturbed peatland as a validation measure. In this study, I demonstrate that the restored peatland is an annual sink for C in all three study years. This chapter confirms that actively restoring an extracted peatland can return the C sink functioning that is fundamental to re-initialize peat accumulation.

3.1 Abstract

Peatlands after drainage and extraction are large sources of carbon (C) to the atmosphere. Restoration, through re-wetting and revegetation, aims to return the C sink function by re-establishing conditions similar to that of an undisturbed peatland. However, the time needed to re-establish C sequestration is not well constrained due to the lack of multi-year measurements. We measured over three years the net ecosystem exchange of CO₂ (NEE), methane (F_{CH_4}) and DOC at a restored post-extraction peatland (RES) in southeast Canada (restored 14 years prior to the start of the study) and compared our observations to the C balance of an undisturbed reference peatland (REF) that has a long-term continuous flux record and is in the same climate zone. Small but significant differences in winter respiration driven by temperature were mainly responsible for differences in cumulative NEE between years. Low growing season inter-annual variability was linked to constancy of the initial spring water table position, controlled by the blocked drainage

ditches and presence of water storage structures (bunds and pools). Half-hour F_{CH_4} at RES was small except when *Typha latifolia*-invaded drainage ditches were in the tower footprint; this effect at the ecosystem level was small as ditches represent a minor fraction of RES. The restored peatland was an annual sink for CO_2 ($-90 \pm 18 \text{ g C m}^{-2} \text{ yr}^{-1}$), a source of CH_4 ($4.4 \pm 0.2 \text{ g C m}^{-2} \text{ yr}^{-1}$) and a source of DOC ($6.9 \pm 2.2 \text{ g C m}^{-2} \text{ yr}^{-1}$), resulting in mean net ecosystem uptake of $78 \pm 17 \text{ g C m}^{-2} \text{ yr}^{-1}$. Annual NEE at RES was most similar to wetter, more productive years at REF. Integrating structures to increase water retention, alongside re-establishing key species, have been effective at re-establishing the net C sink rate to that of an undisturbed peatland.

3.2 Introduction

Peatlands drained for peat extraction are a source of greenhouse gas (GHG) emissions to the atmosphere (Joosten et al., 2012; IPCC, 2014; Smith et al., 2014). When a peatland is drained and its vegetation removed, the internal GHG dynamics that result in carbon (C) uptake are fundamentally altered. The position of the water table is a primary control of the biogeochemical processes that drive GHG fluxes in peatlands (IPCC, 2014). An internal C balance – water table feedback in undisturbed ombrogenic peatlands (Frolking et al., 2010; Hilbert et al., 2000), generally results in the ecosystem being a carbon dioxide (CO_2) sink and methane (CH_4) source (Koehler et al., 2011; Roulet et al., 2007; Strachan et al., 2016). Drainage lowers the water table, reducing the CH_4 emitted at the ecosystem level (Strack and Zuback, 2013; Tuittila et al., 2000; Waddington and Day, 2007), although drainage ditches can continue to be localized sources of CH_4 (Sundh et al., 2000; Waddington and Day, 2007). The lack of primary productivity after vegetation is removed results in net CO_2 loss from the system (McNeil and Waddington, 2003; Tuittila et al., 2000; 2004; Waddington et al., 2010; Wilson et al., 2015; 2016). Post-extraction drainage impacts can persist for decades, ultimately leading to ongoing CO_2 emissions to the atmosphere (Aslan-Sungur et al., 2016, Rankin et al., 2018).

Restoring extracted peatlands offers opportunities to increase biodiversity (Parish et al., 2008; Ramshunder et al., 2012), improve water quality (Chimner et al., 2017; Wilson et al., 2011) and re-establish C uptake (Beyer and Höper, 2015; Dixon et al., 2014; Waddington et al., 2010; Wilson et al., 2013). Across the globe, various management actions are applied that respond to the degree and scale of disturbance (e.g. Evans et al., 2005; Rochefort et al., 2003). Re-wetting is most commonly applied and is the method discussed by the IPCC guidelines for national GHG inventories (IPCC, 2014). However, flooding during re-wetting has been shown to cause large CH_4

emissions (Beyer and Höper, 2015; Cooper et al., 2014; Hahn et al., 2015; Wilson et al., 2009;), that may not be limited to the initial years as originally assumed (Vanselow-Algan et al., 2015). As well, when considering industry-scale peat extraction, raising the water table may be insufficient at re-establishing C uptake due to a lack of propagule bank (Salonen, 1987) and the issue of frost heaving (Groeneveld and Rochefort, 2005).

The Moss Layer Transfer Technique (MLTT; Graf and Rochefort, 2016) is a restoration approach that over 25 years has moved from experimental trials to being applied broadly in extracted peatlands and the remediation of oil well-pads (Chimner et al., 2017; Karofeld et al., 2016; Strack et al., 2014; Waddington et al., 2010). This approach applies active re-introduction and protection of peatland plant species, in addition to re-wetting to re-establish the hydrologic regime (Graf and Rochefort, 2016). The MLTT aims to improve biodiversity, water quality and C uptake through ultimately re-establishing the self-regulatory mechanisms of a naturally functioning peat-accumulating ecosystem (Rochefort et al., 2003).

Research in undisturbed peatlands has shown that multi-year measurements are necessary to obtain reliable C balance estimates because of large, weather-driven inter-annual variability in C exchange (*e.g.* Flanagan and Syed, 2011; Peichl et al., 2014; Roulet et al., 2007). Ecosystem respiration (ER) is a function of plant productivity (autotrophic respiration) and temperature (heterotrophic respiration) whereas light, temperature, and nutrients are controls of gross primary productivity (GPP) (*e.g.* Lafleur, 2009; Lafleur et al., 2005; Lindroth et al., 2007; Nijp et al., 2015; Wang et al., 2014); therefore, variability between years can impact the annual balance between photosynthetic uptake and respiration loss of C (the net ecosystem exchange of CO₂ (NEE)). Water storage indicated by water table depth (WTD), and the anaerobic conditions it induces if saturated, is a key reason for slow decomposition in peatlands, and it can also be a strong correlate explaining annual NEE differences (Helfter et al., 2015; McVeigh et al., 2014; Strachan et al., 2016). Notably, the timing, severity and duration of drought can determine the difference between annual CO₂ uptake and release at an undisturbed peatland (Lafleur, 2009; Limpens et al., 2008; Lund et al., 2012).

Despite being a relatively small mass flux of C, the CH₄ flux is important to the net ecosystem carbon balance (NECB) and is a GHG with a strong radiative forcing. However, the CH₄ release (F_{CH_4}) from restored sites shows high inter-site variability (IPCC, 2014). This is partly due to the highly heterogeneous vegetation and hydrology response of different restoration

methods (Wilson et al., 2016). For instance, a water table at or above the surface limits CH₄ oxidation allowing larger CH₄ emissions (Beyer and Höper, 2015; Cooper et al., 2014; Wilson et al., 2009), and a shallow water table may stimulate sedge growth at the expense of Sphagnum regeneration (Poulin et al., 2013). WTD, as an indicator of the thickness of the unsaturated zone, is an indicator of potential CH₄ oxidation, while WTD, temperature and plant substrate inputs can directly influence CH₄ production (Lafleur, 2009; Whalen, 2005). Vascular plants have deeper roots that can enhance CH₄ production through the addition of easily decomposable root exudates and litter (Chanton et al., 2008; Prater et al., 2007). As well, plants adapted to non-aerated conditions enable plant-mediated CH₄ transport through their aerenchymous tissue, which can increase emissions by allowing the CH₄ to by-pass the zone of potential oxidation (Olefeldt et al., 2013; Treat et al., 2007). These linkages suggest that continued plant community changes may play an important role in CH₄ production and emission at restored sites.

Alongside the spectrum of restoration initiatives, CH₄ fluxes are also highly variable in space and time, which dictates the choice of flux measurement method. Long-term CO₂ budgets in undisturbed peatlands are measured with the eddy covariance (EC) technique, which spatially integrates fluxes over a wide source area (Baldocchi et al., 2003). Within the last decade, EC has also become a standard method for the measurement of F_{CH_4} (e.g. Rinne et al., 2007). Yet, the static chamber method is still used more often at restored sites, as application of EC is limited by the cost of the analytical sensors and heavier power requirements if a closed path analyser is used.

Of the ecosystem C flux components, the net export of dissolved organic carbon (DOC; F_{DOC}) is the least reported in restored (e.g. Strack and Zuback, 2013) and undisturbed (e.g. Christensen et al., 2012; Koehler et al., 2011; Levy and Gray, 2015; Nilsson et al., 2008; Roulet et al., 2007) peatland C balances. Yet, like CH₄, the DOC loss can be the same order of magnitude as the long-term rate of C accumulation (Roulet et al., 2007). F_{DOC} is the net gain or loss of DOC through water inputs (e.g. precipitation, run-on, groundwater) and outputs (e.g. runoff). Dissolved CH₄, dissolved inorganic carbon and particulate organic carbon also compose water borne losses, although generally these fluxes represent a small component of the ecosystem budget (Dinsmore et al., 2010) and so are not always measured along with DOC.

The Bois-des-Bel peatland (RES) is a MLTT-restored peat extraction site in southeast Canada where several studies of carbon exchange took place during the three initial years after restoration and again at 10 years (Strack and Zuback, 2013; Waddington and Day, 2007;

Waddington et al., 2003; 2008; 2010). Despite successful Sphagnum mosses re-establishment, the site was a source of C when measured at 10 years post-restoration, which the authors linked to dry midsummer conditions (Strack and Zuback, 2013). To address whether RES is now a C sink 14 years after being restored, we measured NEE and F_{CH_4} with EC over three years, as well as F_{DOC} , to calculate the NECB. The undisturbed peatland, Mer Bleue, was used for comparison (REF) as Mer Bleue is located in the same climate zone, has a similar vegetation assemblage and has a long-term C flux record (1998-present). While not all peatlands are alike, we would expect peatlands located in the same climate zone with similar hydrogeomorphological settings to display similar responses to climate variability and stress. This has been demonstrated in a number of comparative studies. The Mer Bleue peatland has a similar NECB to other bogs where long-term records are available (Dinsmore et al. 2010; Kohler et al. 2011; Roulet et al. 2007); these studies show the annual NECB varies over a fairly narrow range of approximately -10 to $-80 \text{ g C m}^{-2} \text{ yr}^{-1}$. Lund et al. (2010) showed that Mer Bleue shared many common elements and attributes when NEE, GEP and ER were analyzed against various ecological, physical and climatic variables. Further, the Mer Bleue NECB record shows the dynamic inter-annual variability typical of bogs but is less common in fens (cf. Nilsson et al., 2009). The objective of our study is to evaluate if the C sink function at the restored peatland has returned by comparing against the long-term record of an undisturbed peatland.

3.3 Materials and methods

3.3.1 Site description

The Bois-des-Bel peatland complex is located approximately 11 km northeast of Rivière-du-Loup, Quebec, Canada ($47^{\circ}58'1.95''\text{N}$ $69^{\circ}25'43.10''\text{W}$; Figure 3.1) and lies within a 16 km wide agricultural plain bordered to the north by the St. Lawrence River and to the south by the Appalachian foothills. The region was deglaciated about 12,000 years BP but was subsequently submerged under the Goldthwait Sea until 9,500 years BP (Dionne, 1977). The present-day peatland covers an area of 210 ha, at a mean elevation of 15 m ASL (Lavoie et al., 2001). Mean peat thickness is 2.2 m, and a maximum of 3.75 m, with a basal date of 6985 years BP (Lavoie et al., 2001; Lortie, 1983). The climate of the region is cool temperate, with a 30-year average annual temperature of $3.5 \pm 2.9 \text{ }^{\circ}\text{C}$ and annual precipitation of 964 mm, of which 270 mm is snowfall (1981-2010 climate normal, St-Arsene, Environment Canada). Precipitation is spread fairly equally across the year, with a minimum of 64 mm in April and a maximum of 95 mm in July. The

coldest temperatures occur during the month of January (-12.4 ± 2.6 °C) while the warmest month is July (17.6 ± 1.2 °C). Bois-des-Bel is one of the few remaining peatlands in the region that has not been extensively extracted for horticultural peat moss (Poulin et al., 2004). Nonetheless, a small sector of 11 ha was extracted by vacuum harvesting between 1972 and 1980. In 1999 and 2000, an 8.1 ha section was restored using the MLTT. Graf and Rochefort (2016) provide a detailed description of the restoration process used at the site.



Figure 3.1 – Locations of the undisturbed reference peatland (REF) and the restored peatland (RES) in eastern Canada.

The Mer Bleue peatland (45.41 N, 75.52 W) is 28 km² located 10 km east of Ottawa, Canada. Average annual air temperature is 6.4 ± 0.8 °C and annual precipitation is 943 mm, of which 235 mm falls as snow (1981-2010 climate normal, Ottawa, Environment Canada). Mer Bleue has hosted EC measurements of CO₂ and chamber measurements of CH₄ since 1998. For a complete site description, see Moore *et al.* (2002); Bubier *et al.* (2003); Lafleur *et al.* (2003); Roulet *et al.* (2007), and Brown *et al.* (2014).

3.3.2 Eddy covariance measurements, data processing and ancillary measurements

A micrometeorological tower was installed at RES in July 2013; however, our NECB analysis begins on 1 November 2013, for calculating the C balance over a hydrological year (1 November to 31 October). The 2013 EC setup consisted of an open path CO₂/H₂O analyzer (LI-7500/A, LI-COR, NE, USA), a fast response three-dimensional sonic anemometer (CSAT-3, Campbell Scientific, AB, CAN) and a finewire thermocouple (FW05, Campbell Scientific) connected to a Campbell Scientific CR1000 datalogger. In March 2014 by snowmelt, an open-path CH₄ analyzer (LI-COR LI-7700) was added and all EC measurements were made through a LI-COR LI-7550 analyzer interface unit. Instruments were mounted 1.3 m above the *Sphagnum* surface and data signals were recorded at 10 Hz.

A suite of environmental variables was measured continuously at the tower location to allow for flux data interpretation; a Campbell Scientific CR5000 datalogger was used to store half hourly values. Air temperature (T_a) and humidity were measured using an HMP45A (Vaisala, Vantaa, Finland), and soil temperature was measured at 0.05, 0.1, 0.2, 0.4, 0.6, 0.8 m below the *Sphagnum* surface using type T thermocouples (Omega Engineering, Stamford CT, USA). A net radiometer (CNR1, Kipp and Zonen, Delft, The Netherlands) mounted 1.5 m above the surface measured incoming and outgoing short- and long-wave radiation fluxes while a PQS1 PAR Quantum Sensor (Kipp and Zonen) measured photosynthetic photon flux density (PPFD). A ground heat flux plate (HFT3, Hukseflux, Delft, The Netherlands) and averaging soil thermocouple probe (TCAV, Campbell Scientific) were used to measure soil heat flux at 0.08 m below the *Sphagnum* surface and to calculate soil heat storage above the plate, respectively. Rainfall was captured with a tipping bucket rain gauge (TR-5251, Texas Electronics, Dallas, TX, USA) and soil volumetric water content (SWC) in the top 0.2 m was measured using a CS616 probe (Campbell Scientific). Snowfall was estimated from the St-Arsene station located 7 km west of RES. Water table depth was recorded near the tower location using a Levellogger with an associated Barologger to correct for barometric pressure changes (3001 Series, Solinst, ON, CAN). The Kruskal-Wallis test by ranks was used to test differences in monthly median meteorological conditions between years, with the Wilcoxon rank-sum test used to determine which years were significantly different.

DOC concentration and discharge at a weir outflow were measured between mid-April and December of 2014 to 2016. Discharge was manually measured approximately bi-weekly and

regressed against continuous water level measurements (3001 Series, Solinst, ON, CAN) to estimate discharge continuously; discharge was assumed to be zero during the frozen period (1 December to 1 March). DOC samples collected at the outflow were passed through 0.45 μm paper filters (Macherey-Nagel MN 85/90) and acidified before being analyzed for DOC content on a total organic carbon analyzer (Shimadzu TOC-V). As no significant relationship between discharge and DOC concentration was found, F_{DOC} ($\text{g m}^{-2} \text{ period}^{-1}$) was estimated following Method-5 in Walling and Webb (1985):

$$F_{\text{DOC}} = \left\{ \left[\frac{K \sum_{i=1}^n (C_i Q_i)}{\sum_{i=1}^n Q_i} \right] Q_r \right\} / A \quad (3.1)$$

where K (d season^{-1}) is a correction factor to convert from a daily to seasonal time step, C_i (g L^{-1}) is the instantaneous [DOC], Q_i (L d^{-1}) is the instantaneous discharge, Q_r (L d^{-1}) is the mean discharge over the sampling period and A (m^2) is the total drainage area of the site. F_{DOC} during snowmelt was estimated using snow water equivalents (SWE) to be able to compare with previous studies at RES (Strack and Zuback, 2013; Waddington et al., 2008). Waddington *et al.* (2008) estimated a snowmelt F_{DOC} of 8.3 g C m^{-2} for 137 mm SWE. Data of snow on the ground at the onset of snowmelt (Rivière-du-Loup, Environment Canada) provided SWE (e.g. 100 cm \sim 100 mm SWE) that was then used to weight the results of Waddington *et al.* (2008). We did not measure DOC input in rainfall, however, DOC concentration in rainfall was previously measured as $3.5 \pm 2.2 \text{ mg L}^{-1}$ at RES (Waddington et al., 2008). To estimate DOC input to the system, we multiplied this DOC concentration by the total amount of rainfall received during the respective years of our study period (Roulet et al., 2007).

The turbulent fluxes of CO_2 and CH_4 were computed using the EddyPro software (version 6.1.0, LI-COR Biogeosciences). We applied a double rotation to correct for sonic anemometer tilt, removed spikes in the high frequency data (Vickers and Mahrt, 1997), and used block averaging to remove the mean value from the half-hourly time series and a covariance maximization procedure to detect time lags. Low- and high-pass filtering effects were accounted for using analytical spectral corrections following Moncrieff *et al.* (1997) and Moncrieff *et al.* (2004). The WPL term was used to compensate for temperature- and humidity-induced density fluctuations (Webb et al., 1980). For F_{CH_4} calculation, corrections for spectroscopic effects were incorporated into the WPL term following McDermitt *et al.* (2010) and F_{CH_4} was removed when the CH_4

analyzer signal quality was low (Relative Signal Strength Indicator (RSSI) < 20%). Half-hour fluxes were removed when turbulence was not fully developed or non-stationary (Mauder and Foken, 2011), or when data points were identified as outliers following Papale *et al.* (2006). A friction velocity threshold of 0.12 m s^{-1} (95% confidence interval: $0.08\text{-}0.16 \text{ m s}^{-1}$) was used to remove data when turbulence was weak (Papale *et al.*, 2006). Only the highest data quality (quality flag = 0) was used during analysis and gap-filling of NEE and F_{CH_4} (Mauder and Foken, 2011). This conservative approach resulted in quality control checks removing 33% and 42% of NEE measurements during the growing season (defined as 1 May to 31 October, inclusive) and non-growing season, respectively. Methane data removal was 42% and 43% for the same periods. Over the three years, on average 61% of the NEE growing season time series was gap-filled while the non-growing season was 85% gap-filled. The methane time series was 71% gap-filled during the growing season and 97% modeled during the non-growing season period. Gap-filling methods are detailed in the paragraphs below.

We ran a 2D flux footprint parameterization (Kljun *et al.*, 2015; www.footprint.kljun.net) to acquire the extent and location of the tower footprint with the aim to evaluate the relative ditch area within the source area of the tower. Zero-plane displacement height and roughness length were estimated from tower measurements while the boundary layer height was derived following Appendix B in Kljun *et al.* (2015). The footprint model provides a half-hourly probability map of flux contribution per unit area ($\% \text{ m}^{-2}$) that was combined with a land cover classification map (WorldView-2 taken on 3 August 2014; DigitalGlobe Foundation) to derive sums of half-hourly probabilities of flux contributions from the ditch and bog land covers. The restoration area was classified as 96% restored field while ditches comprised 4%. The restored section is surrounded by forested peatland which limits fetch to 200 m toward the west, 150 m toward the north and south and 100 m toward the east (abuts an unrestored section). NEE and F_{CH_4} half-hourly values were excluded from the analyses when the half-hour footprint exceeded the fetch of the site.

To obtain a cumulative flux (ΣNEE and ΣF_{CH_4} ; g C m^{-2}), we used the marginal distribution sampling method (Reichstein *et al.*, 2005) to gap-fill, an extended lookup table method that accounts for temporal autocorrelation. NEE time series gaps were filled using PPFD ($\mu\text{mol m}^{-2} \text{ s}^{-1}$), T_a ($^{\circ}\text{C}$) and water vapour pressure deficit (VPD, kPa) as lookup table variables. For F_{CH_4} , we used soil temperature at 0.4 m below the moss surface (T_s , $^{\circ}\text{C}$), T_a and VPD. We chose T_s at 0.4 m

depth because previous studies have shown CH₄ production in peatlands to reach a maximum near the average summer water table position (Kotaiho et al., 2010; Sundh et al., 1994), which for our site is around 0.35 m. As the LI-7700 sensor was removed from the site over the winter periods (November to March), an exponential relationship between T_s and F_{CH_4} was used to model winter emissions to estimate annual emissions. This relationship was also applied during the shoulder seasons where large gaps existed, as measurements during these periods were few and displayed large scatter. A total flux measurement error was calculated based on error in determining the friction velocity threshold as well as a random measurement error estimate. We calculated ΣNEE and ΣF_{CH_4} for 100 friction velocity thresholds derived according to Papale *et al.* (2006) (determined by bootstrapping nighttime NEE), and added the random error (Richardson *et al.*, 2006) to estimate a 95% CI on annual ΣNEE and ΣF_{CH_4} . The annual net ecosystem carbon balance (NECB) is the sum of ΣNEE , ΣF_{CH_4} and ΣF_{DOC} for the individual years.

3.3.3 Spatial and temporal controls of F_{CH_4} and spectral decomposition

Methane production in anoxic soils is linked to microbial activity and is limited by temperature and substrate availability, among other biotic and abiotic factors (Basiliko et al., 2007; Dunfield et al., 1993). A strong seasonality in T_s and vegetation productivity can result in a noticeable low-frequency (*e.g.* weeks to months) component of F_{CH_4} (Rinne et al., 2007). In contrast, the spectral signature of the flux footprint is expected to vary at a higher frequency (*e.g.* hours) in relation to rapid changes in footprint composition, with instantaneous effects on flux measurements. To decompose F_{CH_4} into low ($F_{CH_4_{lf}}$; nmol m⁻² s⁻¹) and high ($F_{CH_4_{hf}}$; nmol m⁻² s⁻¹) frequency components, we used a modification of the Singular Spectrum Analysis (SSA) that accounts for missing data in a time series (Schoellhamer, 2001). The time series analysis technique decomposes signals into linearly superimposed frequency-specific sub-signals that can then be reconstructed at the corresponding temporal scale (Mahecha et al., 2007). A frequency of longer than one week was selected for $F_{CH_4_{lf}}$ and between 2 hours and 7 days for $F_{CH_4_{hf}}$. Frequencies smaller than 2 hours were not analyzed so that noise was reduced during periods of low RSSI signal strength (Helbig et al., 2017). Further methodological details and discussion on the use of SSA in EC studies can be found in Mahecha *et al.* (2007). The control of flux footprint composition (*i.e.* contribution of ditches) and wind direction (*i.e.* *Typha latifolia* cover) on F_{CH_4} was analyzed using the $F_{CH_4_{hf}}$ signal while the effect of T_a , T_s and WTD as seasonal controls were analyzed

using the F_{CH_4-lf} signal. For F_{CH_4-lf} , we created simple and multiple linear regression models for the variables T_a , T_s , WTD, GPP, NEE and Year and their interaction terms in R using the `lm` function (R Core Team 2017).

3.3.4 NEE partitioning

The bulk partitioning method developed by Runkle *et al.* (2013) was used to partition NEE into gross primary productivity (GPP; $\mu\text{mol m}^{-2} \text{s}^{-1}$) and ecosystem respiration (ER; $\mu\text{mol m}^{-2} \text{s}^{-1}$). A rectangular hyperbola function (for GPP) and an empirical Q_{10} model (for ER) was fit to the entire non-gap-filled half-hourly NEE dataset, according to the equation:

$$NEE = -GPP + ER = \frac{GPP_{max} \alpha PPF D}{GPP_{max} + \alpha PPF D} + ER_{base} Q_{10}^{\frac{T_a - T_{ref}}{\gamma}} \quad (3.2)$$

Here, GPP_{max} ($\mu\text{mol m}^{-2} \text{s}^{-1}$) is the theoretical light-saturated rate of canopy photosynthesis, α ($\mu\text{mol m}^{-2} \text{s}^{-1}$) is the initial quantum efficiency, ER_{base} ($\mu\text{mol m}^{-2} \text{s}^{-1}$) is basal respiration at the reference temperature $T_{ref} = 15 \text{ }^\circ\text{C}$, Q_{10} is the temperature sensitivity of ER to T_a , and γ is a constant of $10 \text{ }^\circ\text{C}$ (Mahecha *et al.*, 2010). $Q_{10} = 1.32$ was fixed in the first iteration before deriving the final GPP_{max} , α and ER_{base} outputs following the method outlined in Reichstein *et al.* (2005). To derive ER, we combined nighttime gap-filled NEE with modelled daytime ER. GPP was then calculated as the residual of NEE and ER. Daytime NEE was used to obtain daytime ER to account for potential light-imposed leaf respiration inhibition (Wehr *et al.*, 2016) as well as issues with extrapolating nighttime T_a -ER relationships to daytime conditions (Lasslop *et al.*, 2010). To evaluate any potential effects of tower source area on NEE, Equation 3.1 was used to calculate parameters of the light response curves for July-August (*i.e.* peak LAI) half-hour NEE measurements binned by wind direction. Equation 3.1 was also used to calculate the average NEE for $PPFD = 1800 \mu\text{mol m}^{-2} \text{s}^{-1}$ (NEE_{cap} ; $\mu\text{mol m}^{-2} \text{s}^{-1}$).

3.3.5 Vegetation survey

A non-destructive vegetation survey was completed 14 years post-restoration to determine the percentage cover of vascular and non-vascular plants on the former peat fields and drainage ditches. Plots of 1x1 m were surveyed every 10 m over the total length of each of the eight restored peat fields (30 m width by circa 300 m length). The location of the plots alternated between the left, center and right in a zig-zag fashion over the field, resulting in 260 locations surveyed. Three of 11 ditches closest to the flux tower were surveyed using the same method without the zig-zag

alterance. In each plot, percentage vascular cover was evaluated for all functional groups while non-vascular plant cover was evaluated in 0.25 m x 0.25 m subplots located in the lower left (west) corner of the vascular vegetation plots.

3.3.6 Enhanced vegetation index

For remote sensing applications, the enhanced vegetation index (EVI) was developed to allow improved vegetation monitoring by better discriminating the canopy from the background signal while also reducing the influence of atmospheric constituents (Huete et al., 2002). It combines reflectance in near infrared (NIR), red (R) and blue (B) bands within the shortwave spectrum as

$$EVI = G * ((NIR - R)/(NIR + C1 * R - C2 * B + L)) \quad (3.3)$$

G is a gain factor with a value of 2.5, the coefficients C1 and C2 are used to control for atmospheric aerosol content and are set at 6 and 7.5, respectively, and L is the canopy background adjustment and has a value of 1 (Huete et al., 1994; 1997). We used Landsat EVI data obtained from the USGS (Masek et al., 2006; Vermote et al., 2016) and extracted values of EVI for pixels centered on the RES tower and a section of the nearby undisturbed peatland. We were not interested in the intra-seasonal variability in EVI; rather, EVI was used as a broad characterization of the state of the ecosystem recovery following restoration. As the satellite return period is approximately 2 weeks and the availability of data is dependent on a lack of cloud cover, we used a median summer EVI value (June 1 to August 31) to represent each growing season from 1984 to 2016.

3.4 Results

3.4.1 Vegetation characteristics

A decade and a half after restoring the degraded peatland with the Moss Layer Transfer Technique, mosses (*Sphagnum rubellum*, *S. fuscum*, *S. magellanicum*, *S. cuspidatum* and *Polytricum strictum*) cover more than 90% of RES at an average thickness of 0.3 m. Sedges (*Eriophorum vaginatum*, and *Carex* spp.) cover 33% of the site and ericaceous shrubs (*Chamaedaphne calyculata*, *Rhododendron groenlandicum*, *Kalmia angustifolium*, *Vaccinium oxycoccus*, and *V. angustifolium*) cover 39% (Table 3.1). Within this time since restoration, hummock and hollow microtopography has formed (Pouliot et al., 2011). Trees, *Picea mariana* and *Larix laricina*, are also beginning to expand across the site. The remnant ditches were originally filled with loose peat and vegetative material; however, subsidence relative to the highly

compressed cutover peat and a higher pH allowed *Typha latifolia* to successfully invade wetter areas. Dense colonization in the ditches during the early stage of restoration has been reducing over time (Poulin et al., 2013), possibly due to local acidification from the developing *Sphagnum* carpets reducing vascular plant access to nutrients (Poulin et al., 2009). At this stage, *T. latifolia* continue to be present in 2 of 7 ditches; these fell within the tower source area toward the NW and SW sections of the peatland (Table 3.1). Overall fractional cover of remnant ditch (FC_{ditch}) within the footprint was on average 3% over the study period, which is similar to the site proportion of 4% (Table 3.1).

Table 3.1 – Percent vegetation cover and ditch cover (FC_{ditch}) for three 30° direction bins for the area of the mean growing season 80% probability tower flux footprint.

Physiographic feature	Functional Type	30-60° (NE)	200-230° (SW)	290-320° (NW)	All directions
Field	Vascular	66	76	72	75
	Ericaceous shrubs	36	42	42	39
	Sedges	27	35	26	33
	<i>Typha latifolia</i>	0	1	10	0
	Non-vascular	55	74	51	69
	<i>Sphagnum</i>	50	67	33	61
	Ditch	Vascular	85	83	73
	Ericaceous shrubs	63	53	41	51
	Sedges	30	23	25	29
	<i>Typha latifolia</i>	0	6	19	6
	Non-vascular	41	39	57	44
	<i>Sphagnum</i>	14	7	2	8
FC _{ditch}		7	2	4	4

The microtopography of the reference peatland is made up of hummocks, hollows and lawns. *Sphagnum* mosses (*S. capillifolium*, *S. fuscum*, and *S. mangellanicum*) compose the base layer and are overlain mainly by ericaceous shrubs (*C. calyculata*, *K. angustifolium*, and *R. groenlandicum*). Secondary components of the community include the deciduous shrub *Vaccinium myrtilloides*, and a sparse cover of *E. vaginatum* (~ 2% cover) (Bubier et al., 2003; Kalacska et al., 2013; Malhotra et al., 2016; Moore et al., 2002).

3.4.2 Meteorological conditions

No single year experienced an abnormal mean annual T_a but, over the growing season (defined as 1 May to 31 October, inclusive), average T_a at RES was warmer than the St-Arsene 30-year (1981-2010) average (termed the climate normal) in the months of July 2014, June, August and September 2015 and August 2016, and cooler than normal in July 2015 (Figure 3.2a). During the non-growing season, March 2014 and February 2015 were cooler than normal while March 2015 and November through February 2016 were warmer than normal (Figure 3.2a). Monthly medians of daily T_a were significantly different between years for October through February and in July (Kruskal-Wallis test, $p < 0.05$) (Figure 3.2a). Monthly medians of daily PPFD were not significantly different between years except for April (Kruskal-Wallis test, $p < 0.05$) (Figure 3.2b). Both 2014 and 2015 had below normal precipitation, receiving about 700 mm over the course of each year while 2016 received 947 mm, which is within 1 SD of the 30-year mean (964 mm). Maximum rainfall occurred during the month of October in 2014 and 2016 and July in 2015 (Figure 3.2c). Winter T_a and snow accumulation on the ground impacted the maximum depth of frost. The 2015 spring followed a cold winter (Figure 3.3a) when the soil froze > 0.4 m relative to the moss surface (Figure 3.4). This contrasts with the other winters where the soil froze < 0.10 m, due to greater snow insulation in 2014 (data not shown) and abnormally warm conditions in 2016 (Figure 3.2a).

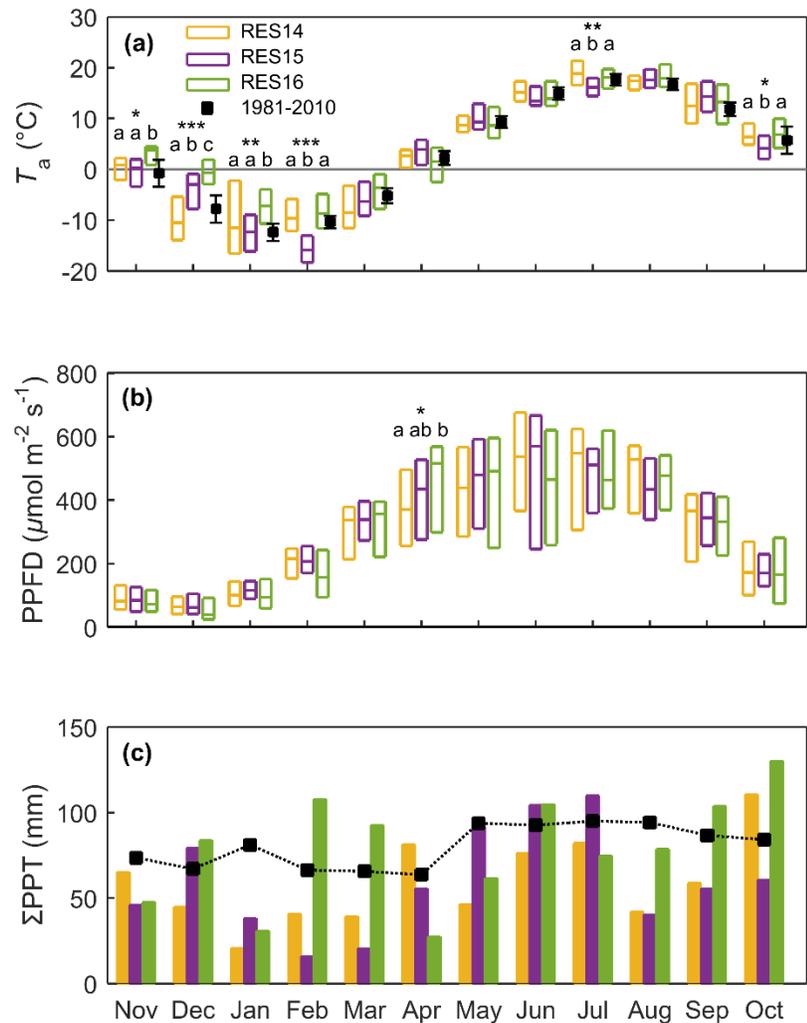


Figure 3.2 – Daily (a) air temperature (T_a ; $^{\circ}\text{C}$), (b) photosynthetic photon flux density (PPFD; $\mu\text{mol m}^{-2} \text{s}^{-1}$), and (c) cumulative precipitation (ΣPPT ; mm) for individual months 14, 15 and 16 years post-restoration at the restored peatland. (a) and (b) boxes show 25th and 75th percentiles; lines inside the boxes show medians. Monthly medians with asterisks are significantly different between years (Kruskal-Wallis test; $*\alpha = 0.05$ / $**\alpha = 0.01$ / $***\alpha = 0.001$), with letters denoting which of the years are significantly different (Wilcoxon rank-sum test). Letters should be compared only within one month. Black squares in (a) and (c) show 30-year climate normals (1981-2010) from the St-Arsene meteorological station.

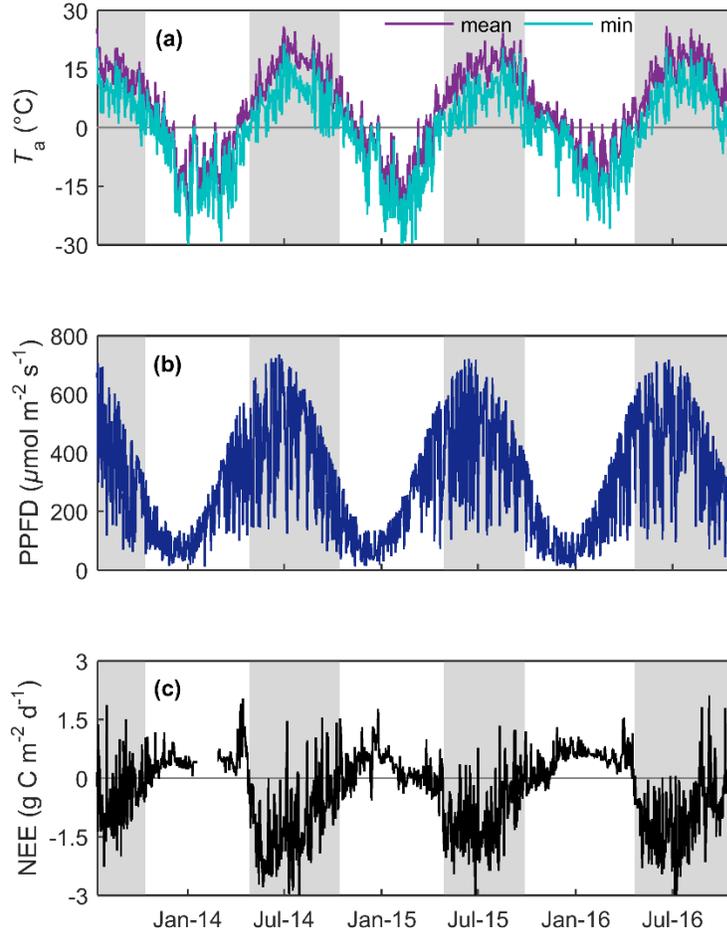


Figure 3.3 – Daily (a) air temperature (T_a ; mean, min; °C), (b) photosynthetic photon flux density (PPFD; $\mu\text{mol m}^{-2} \text{s}^{-1}$) and (c) gap-filled net ecosystem exchange (NEE; $\text{g C m}^{-2} \text{d}^{-1}$). Grey shaded areas outline carbon uptake periods of the restored peatland 14, 15 and 16 years post-restoration. Note that NEE data from 2014 is missing in the months of January and February due to sensor malfunction.

Average growing season values of T_a , T_s and WTD did not significantly differ among years, although 2015 was generally cooler and wetter, experiencing 0.5°C lower T_a , 2 to 3°C lower T_s and highest WTD (Table 3.2). Two large single-day rain events in September (57 mm) and October (48 mm) are mainly responsible for 2016 having the highest total precipitation of the 3 years (Table 3.2). Throughout the study period, daily WTD ranged from 0.6 – 0.1 m below the moss surface (Figure 3.4). WTD showed rapid responses to precipitation, resulting in variations of up to 0.33 m within a few days (Figure 3.4). The timing of water table drawdown differed each season with

WTD reaching a maximum during July in 2014, September in 2015 and August in 2016. Recurrent rainfall maintained the water table position in 2015 until August and the overall intensity of drawdown was less than in other years (Figure 3.4).

Table 3.2 – Average (\pm SD) growing season (1 May to 31 October, inclusive) methane flux (F_{CH_4}), air temperature (T_a), soil temperature (T_s), water table depth (WTD) and cumulative precipitation (ΣPPT) at the restored peatland 14, 15 and 16 years post-restoration.

	RES14	RES15	RES16
F_{CH_4} (mg C m ⁻² d ⁻¹)	17.1 \pm 9.8	16.6 \pm 9.1	14.9 \pm 7.0
T_a (°C)	13.5 \pm 5.5	12.9 \pm 5.4	13.4 \pm 5.6
T_s (°C)	11.2 \pm 2.3	8.0 \pm 4.9	10.4 \pm 3.3
WTD (cm)	-29 \pm 12	-26 \pm 10	-31 \pm 12
ΣPPT (mm)	414	446	554

3.4.3 Net ecosystem exchange of CO₂

Daily NEE ranged from an uptake of CO₂ of > 2 g C m⁻² d⁻¹ during the growing season to a loss of < 1.7 g C m⁻² d⁻¹ during cloudy days and the shoulder seasons (Figure 3.3c). The shift from winter loss to net uptake during the spring (defined as 1 March to 30 April, inclusive) was well defined (April 26 \pm 3 days) and coincided with minimum daily T_a exceeding 0°C (Figure 3.3a). The transition during autumn to net release was more variable (October 10 \pm 11 days) and occurred as T_a approached 0°C but was also due to seasonal light limitation (Figure 3.3b). Monthly medians of daily NEE were negative from May through October and positive otherwise, except for April 2015, which was also negative (Figure 3.5). Of the growing season period, September was the only month with significant difference in monthly medians of daily NEE among years (Kruskal-Wallis test; $p < 0.05$), despite significant inter-annual differences in GPP and particularly ER for the same period (Figure 3.5). Within-year variability in daily NEE was low in December through March; however, inter-annual differences in monthly medians of daily NEE were significant (Kruskal-Wallis test; $p < 0.001$) (Figure 3.5). April showed the greatest range in monthly medians of daily NEE (Kruskal-Wallis test; $p < 0.001$) which was driven by significantly more positive ER in 2014 and GPP (higher primary productivity) in 2015 (Figure 3.5). Significantly lower GPP and ER during July 2015 effectively offset each other resulting in no statistical difference in July NEE monthly medians among years (Figure 3.5).

Rates of net CO₂ uptake during the growing season were similar among years while respiration rates during the coldest months, particularly the near-zero respiration experienced in late-winter of 2015, had a comparatively large impact on inter-annual variability in Σ NEE (see Figure 3.6b). Annual Σ NEE was -94 ± 10 (\pm 95% CI), -105 ± 7 and -70 ± 7 g C m⁻² in 2014, 2015 and 2016, respectively, resulting in a study period average Σ NEE of -90 ± 18 (\pm SD) g C m⁻² yr⁻¹ (Table 3.3).

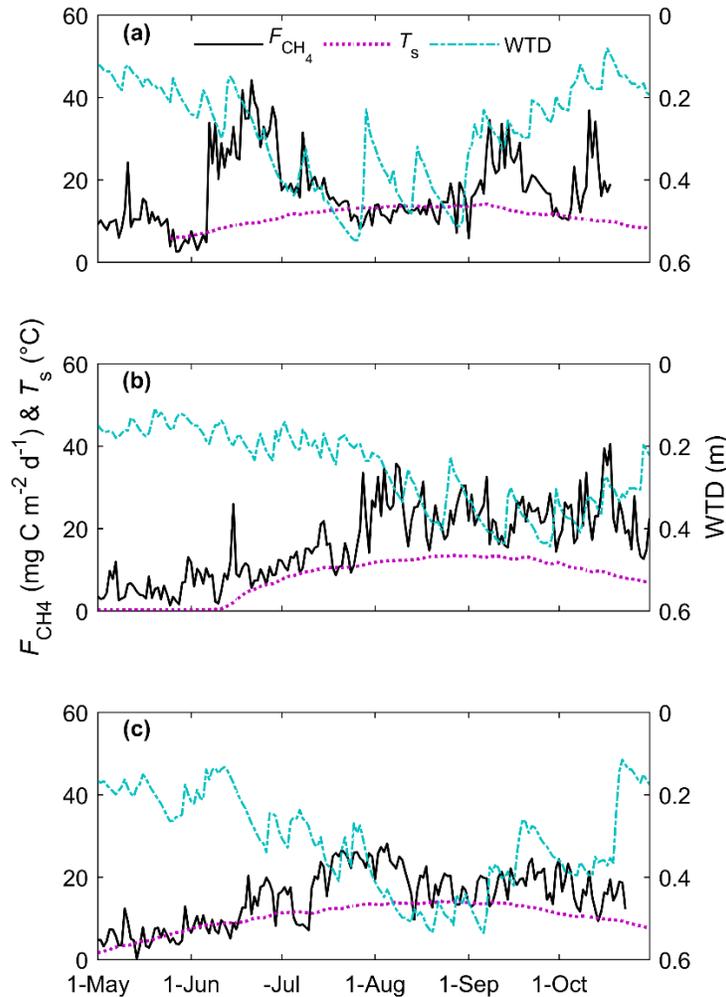


Figure 3.4 – Daily values of methane flux (F_{CH_4} ; mg C m⁻² d⁻¹), soil temperature (T_s ; °C) and water table depth (WTD; cm) between 1 May and 31 October at the restored peatland (a) 14, (b) 15 and (c) 16 years post-restoration. Note that T_s values are missing in May 2014 and that T_s in 2015 was frozen until mid-June.

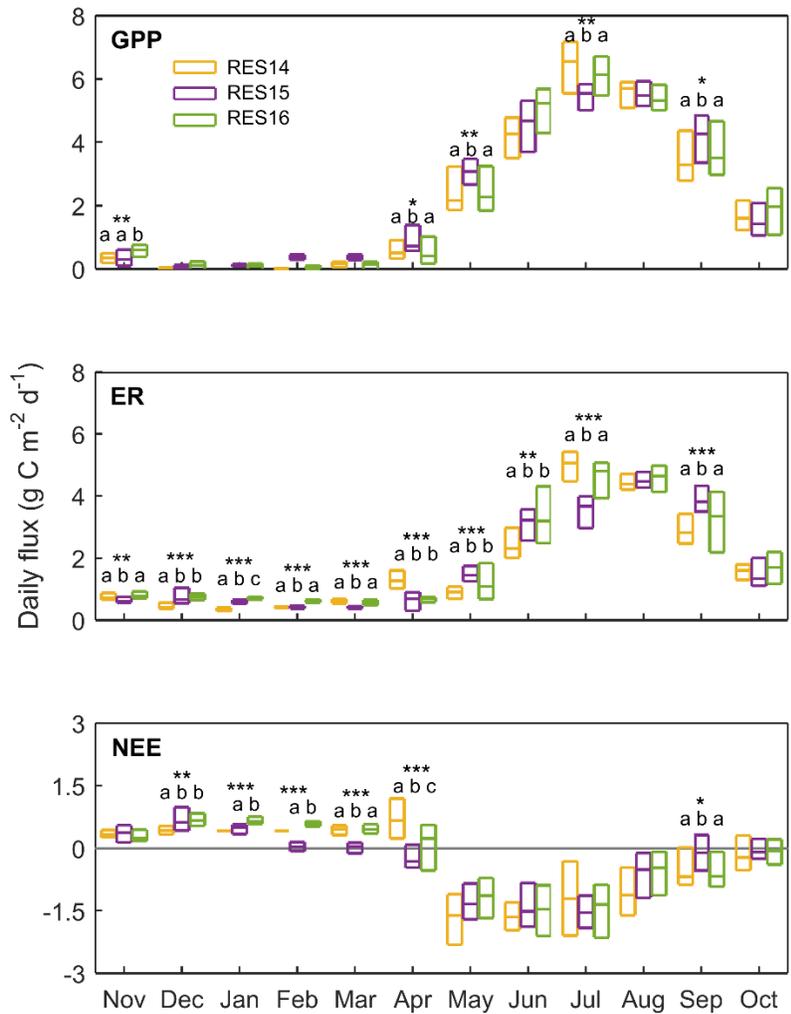


Figure 3.5 – Daily gross primary productivity (GPP; $\text{g C m}^{-2} \text{d}^{-1}$), ecosystem respiration (ER; $\text{g C m}^{-2} \text{d}^{-1}$) and net ecosystem exchange (NEE; $\text{g C m}^{-2} \text{d}^{-1}$) for individual months during the 14th, 15th and 16th year post-restoration at the restored peatland. Boxes show 25th and 75th percentiles; lines inside the boxes show medians. Monthly medians with asterisks are significantly different (Kruskal-Wallis test; * $\alpha = 0.05$ /** $\alpha = 0.01$ /***/ $\alpha = 0.001$), with letters denoting which of the years are significantly different (Wilcoxon rank-sum test). Letters should be compared only within one month. Note that NEE data from 2014 is missing in the months of January and February due to sensor malfunctioning. Also note that statistical tests were not performed on winter GPP as values should be zero; non-zero values result from the residual of NEE and ER.

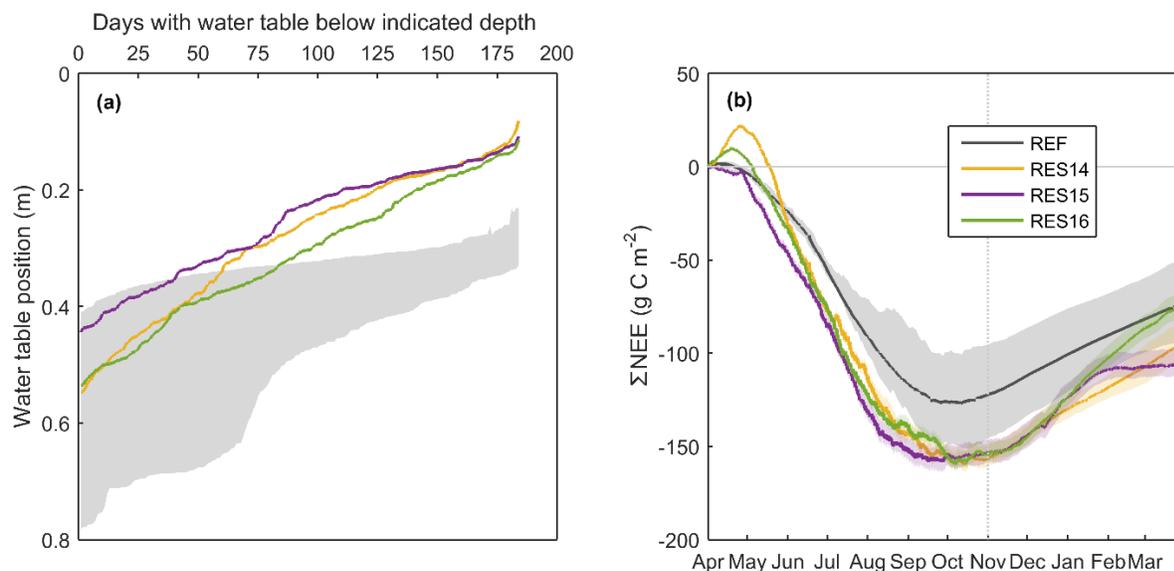


Figure 3.6 – (a) Water table exceedance curves over the growing season in the 3 study years at the restored Bois-des-Bel peatland (RES; lines) compared to the reference Mer Bleue peatland (REF; grey shaded range). (b) Comparison of annual Σ NEE (g C m^{-2}) at RES ($\pm 95\%$ CI; coloured shading) with the 17-year mean and standard deviation (grey shading) at REF. In this figure, the start of the hydrological year (Nov-Mar) is shown after October 31 to more easily display and compare the snow-free season.

Table 3.3 – Cumulative ($\pm 95\%$ CI) growing season fluxes and annual balance (\pm SD) of the restored peatland in $\text{g C m}^{-2} \text{ yr}^{-1}$.

		NEE	GPP	ER	F_{CH_4}	F_{DOC}	NECB
RES14	GS	-175 ± 5	709	530	3.3 ± 0.1	-	-
	Annual	-94 ± 10	743	647	4.4 ± 0.1	9.2	-80 ± 11
RES15	GS	-145 ± 5	693	523	3.1 ± 0.1	-	-
	Annual	-105 ± 7	759	624	4.5 ± 0.2	6.6	-94 ± 7
RES16	GS	-159 ± 4	723	571	2.8 ± 0.1	-	-
	Annual	-70 ± 7	762	681	4.2 ± 0.1	4.8	-61 ± 7
mean \pm SD	GS	-160 ± 15	708 ± 15	541 ± 26	3.2 ± 0.1	-	-
	Annual	-90 ± 18	754 ± 10	651 ± 29	4.4 ± 0.2	6.9 ± 2.2	-78 ± 17

3.4.4 Ecosystem methane flux

Daily F_{CH_4} ranged from $0 \text{ mg C m}^{-2} \text{ d}^{-1}$ to a maximum emission of $45 \text{ mg C m}^{-2} \text{ d}^{-1}$ during the growing season (Figure 3.4), and up to $57 \text{ mg C m}^{-2} \text{ d}^{-1}$ during the spring period (data not shown). The sub-weekly F_{CH_4} signal, $F_{\text{CH}_4, hf}$, could not be explained by FC_{ditch} ($p > 0.05$). Visual

inspection instead determined that $F_{CH_4_{hf}}$ was influenced by wind direction, with higher magnitude values originating almost exclusively from the NW section of RES (Figure I.1), which is where a disproportionate amount of *T. latifolia* is located (Table 3.1). The NW section was sampled more in the spring and less in the growing season because of shifting footprints (Figure I.1). *T. latifolia* was proportionately sampled during the growing season, nonetheless, as the SW was an important source area for F_{CH_4} measurements during this period (Table 3.1; Figure I.1).

Multi-year values of daily $F_{CH_4_{lf}}$ (above-weekly signal) most strongly correlated with T_s ($F_{1,490} = 210.0, p < 0.0001$), with an R^2 of 0.30. Other linear regression equations resulted in a significant but lower F statistic while slightly improving R^2 , with the category Year coming forward as a significant effect (Table 3.4).

Table 3.4 – Multiple linear models using daily values to examine potential drivers of methane flux at the restored peatland, RES. Statistics were applied to the entire study period dataset, growing season only (GS), and Spring combined with GS.

Period	Effect	F statistic	p value	R^2
Study period	T_s	$F_{1,490} = 209.9$	<0.0001	0.30
	$T_s + NEE$	$F_{2,489} = 140.7$	<0.0001	0.36
	$T_s + NEE + T_s * NEE$	$F_{3,487} = 104.1$	<0.0001	0.39
	$T_s + GPP + Year$	$F_{3,487} = 85.4$	<0.0001	0.41
	$T_s + GPP + Year + T_s * GPP$	$F_{4,486} = 72.9$	<0.0001	0.42
RES14 GS	NEE	$F_{1,134} = 12.2$	<0.0001	0.08
RES15 Spring + GS	WTD + T_s	$F_{2,172} = 77.1$	<0.0001	0.47
RES15 GS	WTD	$F_{1,154} = 139.5$	<0.0001	0.47
RES16 Spring + GS	WTD + T_s	$F_{2,173} = 62.6$	<0.0001	0.40
RES16 GS	WTD	$F_{1,158} = 117.1$	<0.0001	0.42

Variation in $F_{CH_4_{lf}}$ during 2014 showed a weak but significant interaction with NEE ($F_{1,134} = 12.2, p < 0.0001, R^2 = 0.08$), whereas the years 2015 and 2016 were significantly correlated with WTD and T_s ($F_{2,172} = 77.1, p < 0.0001, R^2 = 0.47$; $F_{2,173} = 62.6, p < 0.0001, R^2 = 0.40$). In both 2015 and 2016, $F_{CH_4_{lf}}$ most strongly correlated with WTD when only growing season values were included ($F_{1,154} = 139.5, p < 0.0001, R^2 = 0.47$; $F_{1,158} = 117.1, p < 0.0001, R^2 = 0.42$).

Annual ΣF_{CH_4} was 4.4 ± 0.1 ($\pm 95\%$ CI), 4.5 ± 0.2 and 4.2 ± 0.1 g C m⁻² in 2014, 2015 and 2016, respectively, with a study period average of 4.4 ± 0.2 g C m⁻² yr⁻¹ (Table 3.3). A range of 9-18% of gap-filled emissions occurred during the spring, 67-75% during the growing season and the remaining 13-19% during the cold season.

3.4.5 Dissolved organic carbon flux

Concentration of DOC at the outflow was lowest during the snowmelt period at 30 ± 8 mg L⁻¹ and generally peaked in the driest months, averaging 86 ± 13 mg L⁻¹ over the data collection period (data not shown). Discharge at the weir peaked during snowmelt and was frequently zero for portions of July through September (data not shown). Snowmelt F_{DOC} was estimated to be 7.1, 4.7 and 4.7 g C m⁻² in 2014, 2015 and 2016 respectively, based on a SWE of 118, 77 and 77 mm. F_{DOC} after snowmelt until December was determined to be 3.6, 3.5 and 2.2 g C m⁻², respectively using Equation 3.1. The mean annual input of DOC in precipitation was estimated to be 1.6, 1.6 and 2.1 g C m⁻² yr⁻¹, yielding an annual net DOC export estimate of 9.2, 6.6 and 4.8 g C m⁻² yr⁻¹ in 2014, 2015 and 2016, respectively (mean $\Sigma F_{\text{DOC}} = 6.9 \pm 2.2$ g C m⁻² yr⁻¹; Table 3.3).

3.4.6 Net ecosystem carbon balance

Combining the annual import and export of C from RES yields a 3-year mean NECB of -78 ± 18 g C m⁻² yr⁻¹, with 61 to 94 g C m⁻² accumulated annually (Table 3.3). Of the components, NEE is the largest and most variable while F_{CH_4} is the smallest and varies the least. F_{DOC} is comparatively small as well and combined with F_{CH_4} equates to only 11% of mean NEE.

3.4.7 Reference peatland carbon balance

Annual ΣNEE at the reference peatland over the 17-year period (1999 to 2015) indicated that the peatland was always a CO₂ sink, with -73 ± 40 (mean \pm SD) g C m⁻² yr⁻¹ taken up annually on average. The large range in annual ΣNEE of -10 to -135 g C m⁻² yr⁻¹ (Roulet et al. 2007 and unpublished data) (Figure 3.6b) was associated with a wide range of growing season wetness conditions and water table positions (Figure 3.6a). Annual ΣF_{CH_4} (Brown et al., 2014) and ΣF_{DOC} were 6 ± 4 g C m⁻² yr⁻¹ and 17 ± 3 g C m⁻² yr⁻¹, respectively, yielding a 17-year NECB for the reference peatland of -50 ± 40 g C m⁻² yr⁻¹ (Table 3.3).

3.4.8 Canopy structure changes: Abandonment to present

EVI was used to demonstrate variations in canopy structure (e.g. leaf area index and canopy architecture) at RES following the cessation of extraction in 1980. EVI was low (~ 0.2) during the

first decade in accordance with the absence of vegetation; between year variability increased during the second decade of abandonment because of some spontaneous regeneration (Figure 3.7). EVI increased rapidly in the years immediately following the application of the MLTT in 2000 (year 0) and doubled within 2 years. Both EVI magnitude and inter-annual pattern were similar between the restored (RES) and undisturbed (NAT) sections of the Bois-des-Bel peatland complex within 5 years of restoration.

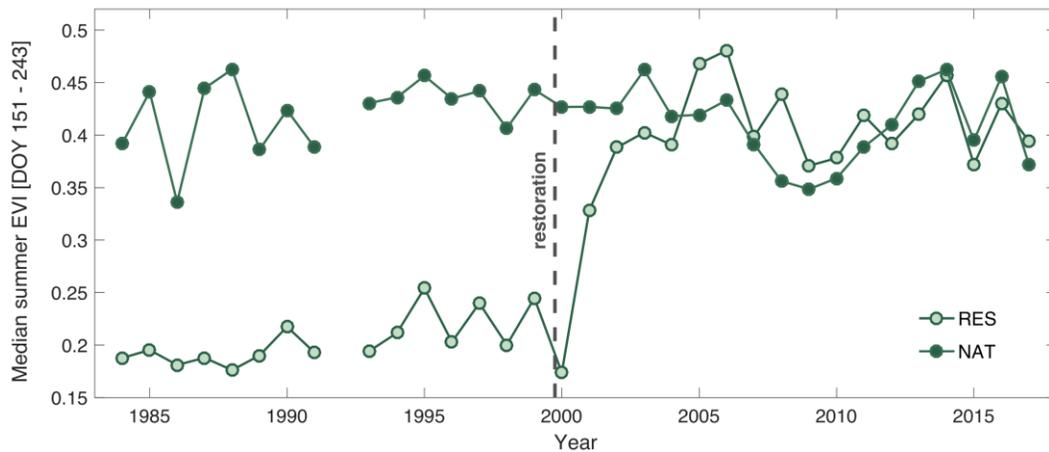


Figure 3.7 – Comparison of median summer (day of year 151 to 243) enhanced vegetation index (EVI) from 1984 to present at the restored (RES) and undisturbed (NAT) sections of the Bois-des-Bel peatland complex. RES was an active peat extraction site until 1980 and was restored using the moss layer transfer technique during the autumns of 1999 and 2000.

3.4.9 Site inter-comparisons

Annual NEE at RES was within the range of mean values reported for long-term undisturbed peatlands in temperate and boreal regions (Figure 3.8). Our NEE results were similar to a 5-year chamber flux record at a 7 years re-wetted temperate peatland (Wilson *et al.*, 2016) but had a smaller standard deviation. In contrast, NEE from abandoned sites and a young restored site (restored 2 years prior) showed high CO₂ emissions to the atmosphere with large inter-annual variability (Figure 3.8).

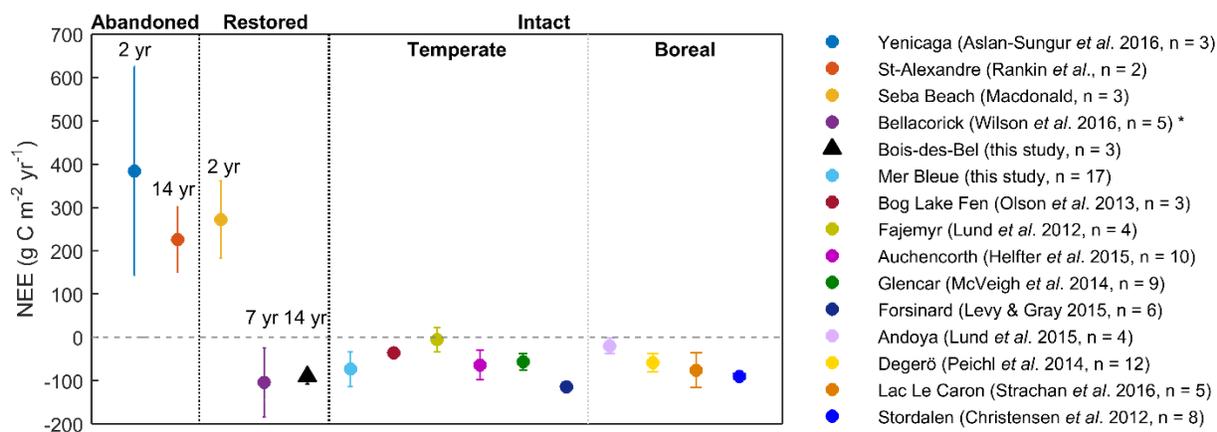


Figure 3.8 – Mean (\pm SD) annual net ecosystem exchange of CO₂ (NEE; g C m⁻² yr⁻¹) at peatland sites with multiple year eddy covariance CO₂ datasets. Negative values indicate net CO₂ uptake from the atmosphere to the ecosystem. In the legend, n is the number of study years, while the years indicated above abandoned and restored site points refer to the number of years since abandonment/restoration prior to the start of the measurements. Figure adapted from Wilson *et al.* (2016). *The annual NEE at Bellacorick was derived by up-scaling chamber measurements.

3.5 Discussion

With hydrological regulation and re-established vegetation cover, we have measured net C uptake in a peatland following industrial peat extraction. Our results show that 14 years following restoration, the restored peatland took up 78 g C m⁻², on average annually over a 3-year period, with relatively little difference among years.

The CH₄ flux was the smallest contributor to the C balance, with growing season (1 May-31 October) CH₄ emissions (2.8-3.3 g C m⁻²) at the lower end but within the range of EC studies on other northern hemisphere peatlands (Table I.1). Similar emissions have been measured at the reference peatland (Brown *et al.*, 2014), a treed fen in western Canada (Long *et al.*, 2010), a collapse-scar bog in Interior Alaska (Euskirchen *et al.*, 2014), and high-Arctic moist tundra sites

with short growing seasons (Friborg et al., 2000; Parmentier et al., 2011). Our CH₄ exchange is greater than EC and chamber measurements in drained and degraded peatlands (<1 g C m⁻²; Strack and Zuback, 2013; Rankin et al., 2018; Wilson et al., 2016) and less than re-wetted sites (9-40 g C m⁻²; Beyer and Höper, 2015; Franz et al., 2016; Hendriks et al., 2007; Herbst et al., 2011; Lee et al., 2017; Wilson et al., 2016). This is an expected finding given that our average growing season water table position was ~0.30 m below the moss surface and did not exhibit the water level extremes of drained or flooded sites. Oxidation of diffusing CH₄ through the newly formed moss layer was likely an important process in reducing emissions, partially counteracted by the water table remaining within the rooting zone of the vascular plants. Similar to the first few years post-restoration (Waddington and Day, 2007), plot-scale measurements performed during the study period indicate the *E. vaginatum* was the primary source of CH₄ emission from restored fields (data not shown). Yet, the magnitude of *E. vaginatum*-mediated flux was less than that of *E. vaginatum* plots at the reference peatland (Lai et al., 2014) and other undisturbed peatlands (Greenup et al., 2000; Joabsson and Christensen, 2001; Ström and Christensen, 2007; Ström et al., 2012; Waddington et al., 1996). Our lower CH₄ flux result is similar to that of other post-restoration studies (Strack et al., 2016; Tuitilla et al., 2000; Wilson et al., 2009). The lower fluxes have been explained by the slow re-establishment of microbial communities after prolonged drying (Juottonen et al., 2012).

Net water borne losses of dissolved organic carbon were a slightly larger contributor than CH₄ to the annual NECB at the restored peatland (Table 3.3). DOC concentration at the outflow was similar to measurements reported at 10 years post-restoration, while DOC export was consistent with growing season observations at 3 and 10 years (Strack and Zuback, 2013; Waddington et al., 2008). Net DOC export (7 ± 2 g C m⁻² yr⁻¹) was at the lower end of the range reported for undisturbed peatlands (7-17 g C m⁻² yr⁻¹; Koehler et al., 2011; Levy and Gray, 2015; Nilsson et al., 2008; Olefeldt and Roulet, 2012; Worrall et al., 2003) and the reference peatland (17 ± 3 g C m⁻² yr⁻¹).

NEE of CO₂ dominated the magnitude and inter-annual variability of the NECB. Inter-annual differences in NEE appeared to be mainly driven by extremes in winter weather rather than growing season variability, the latter being more important at the reference peatland (Roulet et al., 2007). Largest CO₂ uptake occurred at 15 years post-restoration (-105 g C m⁻²) when deeper frost penetration during an abnormally cold winter reduced respiration losses; lowest annual uptake at

16 years post-restoration (-70 g C m^{-2}) coincided with an abnormally warm winter with higher respiration rates (Figure 3.6b). Meanwhile, significant inter-annual differences in daily GPP and ER during the growing season months had little effect on NEE. A coupling between the gross fluxes was evident (Figure 3.5), and can be explained by a portion of ER being related to GPP through autotrophic respiration (Frolking et al., 2002; Moore et al., 2002). In contrast to our results, the 17-year study period of the reference peatland showed large differences in summer water table depth exceedance. REF had greater extreme WTD and longer periods of time where the water table was lower (Figure 3.6a). The differences in water storage between years are reflected in large differences in Σ NEE during August and September (Figure 3.6b). Despite this, REF was a net C sink in all years, suggesting that the carbon balance – water table feedback of a undisturbed peatland creates a long term dynamic equilibrium.

The shape of the water exceedance curves at the restored peatland in the three study years was more similar to the dry end of the range of years at REF, even as minimum WTD fell within the wet end of the range (Figure 3.6a). A wetter initial condition helps to explain how a higher minimum water table position was maintained. During spring, the water table at RES peaked 0.02 to 0.1 m below the moss surface in comparison to the reference peatland which peaked 0.16 to 0.31 m below the surface (data not shown). There are several structures (pools and bunds) that were incorporated into the restoration plan to increase water retention during the critical early restoration period. These structures, alongside the blocked drainage system, appear to be effectively retaining snowmelt runoff. Rapid recharge during rain events also appears to prevent continual drawdown of the water table during mid-summer water deficit periods (Figure 3.4). The current water table dynamics suggest that the relatively constrained water table at RES is due to external controls (site engineering) rather than internal hydrological controls at this stage. Ten years after restoration, the newly forming *Sphagnum* layer had a lower bulk density (McCarter and Price, 2013; Waddington et al., 2011) and soil water retention (Waddington et al., 2011) compared to surface *Sphagnum* layers in the surrounding undisturbed peatland. Large pores in the newly formed layer were found to restrict capillary transfer of water from the highly compact cutover peat, limiting hydrological connectivity between the two layers (McCarter and Price, 2015). It is expected that self-regulatory mechanisms will become more important as accumulation of new peat restores the critical feedbacks among production, decomposition and the hydrology of the site (Belyea and Baird, 2006; Eppinga et al., 2009; Frolking et al., 2001; 2010; Hilbert et al., 2000).

Nonetheless, the effect of a wetter initial condition on growing season NEE is positive, as net CO₂ uptake in all three years was similar to the higher productivity measured during wetter years at REF. A higher cover of *E. vaginatum* may be helping to maintain net CO₂ uptake during drier periods, when moss photosynthesis is reduced due to water stress and the onset of desiccation. Evidence of this was found when comparing NEE in *Sphagnum* and vascular plant plots at 10 years post-restoration (Strack and Zuback, 2013). Vegetation composition changes are still ongoing with *E. vaginatum* being gradually outcompeted by *Sphagnum* (Poulin *et al.*, 2013). It is possible that the C sink strength will reduce somewhat with the decline of *E. vaginatum* cover, as the co-occurrence of *E. vaginatum* and *Sphagnum* has been linked to higher CO₂ uptake efficiency than pure stands (Kivimäki *et al.*, 2008). Broad comparability in EVI at the restored site and surrounding undisturbed peatland over the last few years suggests that the developing vegetation in general has a normal response to environmental factors and does not appear to be experiencing any residual stress from the non-natural soil profile.

To the best of our knowledge, the only other peatland restoration sites reporting long-term datasets are the work of Renou-Wilson *et al.* (2016; 2018) and Bellacorick, a re-wetted industrial cutaway peatland in Ireland. At 7 through 12 years post-re-wetting, the re-wetted Irish peatland displayed considerably higher inter-annual variation relative to our restored Canadian peatland and other undisturbed peatlands (Figure 3.8). The higher variation measured was attributed to the Irish site being in transition in terms of vegetation composition, water retention capacity and GHG dynamics in general (Wilson *et al.*, 2016). The rehabilitation plan of the cutaway Irish peatland included ditch blocking and the creation of bunds and pools that, alongside high annual rainfall, allowed the rapid colonization of wetland species not typically found in Atlantic blanket bogs (Wilson *et al.*, 2013). Inundation has enabled a transition to a CO₂ sink, by suppressing aerobic respiration, but has also enabled higher CH₄ emissions (9 g C m⁻² yr⁻¹) and estimated DOC losses (Wilson *et al.*, 2013; 2016). Crucially, accumulation of new organic material is less than that of our restored Canadian site at the same age (Lucchese *et al.*, 2010; Wilson *et al.*, 2016), despite a considerably longer growing season (Wilson *et al.*, 2013). The authors suggest that the spread of *S. cuspidatum*, which has readily decomposable litter (Belyea, 1996; Hogg, 1993), may be responsible for the lower organic matter accumulation (Wilson *et al.*, 2016). A positive aspect of maintaining a water table below the surface is that *S. rubellum* and *S. fuscum*, two hummock-forming species, are currently dominant at our restored peatland. Hummock-forming species are

expected to maximize C uptake due to better capillary water transport ability and higher decay resistance (Rydin et al., 2006). It appears that an ideal set of hydrological conditions has been restored at our experimental Canadian peatland causing reintroduced vegetation to evolve toward undisturbed reference peatlands, allowing CO₂ uptake to be maximized and CH₄ and DOC losses to be minimized.

This study therefore indicates that C uptake can be re-established within 14 years of restoration with the Moss Layer Transfer Technique. Maintaining a water table below the surface is a necessary step if the aim of restoration is to mitigate C emissions to the atmosphere. In the short term, cutover peat may help to constrain CH₄ emissions by limiting CH₄ production. With site regrading, the effects of drainage ditches can be minimized; however, we have shown that the presence of remnant ditches does not necessarily equate to large ecosystem CH₄ release, despite *T. latifolia* invasion, due to natural ongoing infilling and their overall small proportional areal extent. While internal hydrological controls have not quite re-established, structures put in place during the restoration process appear to be sufficient to maintain steady CO₂ uptake throughout the growing season, causing a stable C sink interannually. It is likely that ecosystem resiliency will return once a thick enough *Sphagnum* layer establishes, that is capable of exerting control over the water table during summer drawdown.

CHAPTER 4

CUTOVER PEAT LIMITS METHANE PRODUCTION CAUSING LOW EMISSION AT A RESTORED PEATLAND

Bridging statement to Chapter 4

The results of Chapter 3 indicate that CH₄ emissions were lower at the restored peatland despite a water table near the surface and a relatively high vascular plant cover, known to increase CH₄ emission. To address why, the present chapter evaluates CH₄ production and oxidation in the restored peat fields and former drainage ditches at the restored peatland. I combine stable isotope measurements of CH₄ and co-occurring DIC that provide an indirect method to evaluate CH₄ production and oxidation with pore water concentrations of CH₄, CO₂ and acetate and finally surface flux measurements. I comprehensively map the pathways of CH₄ production and movement through the soil in the restored fields and former ditches to help pin-point the processes that may be contributing to emitted CH₄. This chapter brings together methods in a novel fashion to show that the legacy of cutover peat in reducing CH₄ production and emission could last for a period (decades) beyond the successful return of a carbon sink.

4.1 Abstract

Peatland degradation due to human activities is contributing to rising atmospheric CO₂ levels. Restoring the carbon (C) sink function in degraded peatlands and preventing further stored C losses is a key climate mitigation strategy, given the global scale of peatland disturbance. Active restoration at a post-extraction peatland in Canada has been shown to successfully re-establish net CO₂ uptake rates similar to undisturbed peatlands within a decade or two (Nugent et al., 2018). However, lower than expected CH₄ emissions suggest recovery of belowground C cycling processes may lag behind recovery of the surface net flux. Using closed chamber measurements over a warm season, we determined that restored *Sphagnum*, which covers two thirds of the site, was a net zero source of CH₄. Emissions from the restored site were primarily attributed to vascular plant substrate inputs, measured as acetate, and plant-mediated transport. The carbon isotopic fractionation factor for CH₄ and CO₂ in the restored former peat field pore water exhibited $\alpha < 1.060$ even deeper in the cutover peat profile (0.8 m depth), evidence of a dominance in acetoclastic methane production. In contrast, isotopic fractionation in the former drainage ditches showed a

balance of acetoclastic and hydrogenotrophic methanogenesis deeper in the profile, indicative of some bulk peat C turnover. This study shows that the legacy of cutover peat in reducing CH₄ production and thus emission, can aid in reducing the climate warming impact of newly restored peatlands.

4.2 Introduction

Peatlands maintain a large reservoir of once atmospheric CO₂ as stored soil organic matter, which has had a long-term cooling impact on the climate (Frolking and Roulet, 2007; Frolking et al., 2006). Long-term carbon storage in peatlands results from plant production of biomass exceeding decomposition of organic material (Moore et al., 1998). This is primarily related to organic matter decomposition rates which, in northern latitude peatlands (above 45°N), arise from low temperatures, partial to complete waterlogging and soil organic matter properties that limit microbial respiration (Moore and Basiliko, 2006). Anoxic conditions caused by shallower water tables also enable methane (CH₄) production that exceeds methanotrophic oxidation, causing peatlands to be a source of atmospheric CH₄ (Vasander and Kettunen, 2006). In contrast, peatlands that are vacuum-harvested for horticultural purposes are heavily disturbed systems no longer capable of sequestering carbon, and instead become persistent sources of CO₂ and very low CH₄ sources (e.g. Aslan-Sungur et al., 2016; Nugent et al., 2018; Nugent et al., accepted; Rankin et al., 2018). Restoring the hydrology and vegetation to that of an undisturbed peatland is necessary at vacuum-extracted sites to reduce net organic matter mineralization and to return the site to carbon accumulation (Rankin et al., 2018; Waddington and McNeil, 2002). The importance of peatlands as a global carbon store makes restoring all forms of degraded peatlands a key climate change mitigation strategy (Leifeld and Menichetti, 2018).

Over 25 years of ecological research in Canadian peatlands that have undergone drainage and extraction has led to the development of the moss layer transfer technique (MLTT) restoration approach (Graf and Rochefort, 2016). Large-scale application of the MLTT was recently shown to be successful in returning an impacted peatland to a carbon sink comparable to undisturbed peatlands within 14 years of restoration (Nugent et al., 2018). A persistent inter-annual carbon sink was achieved in part due to low annual emissions of CH₄ of $4.4 \pm 0.2 \text{ g C m}^{-2} \text{ yr}^{-1}$ (Nugent et al., 2018). The presence of former drainage ditches, which dissect the restored peat fields (Figure 4.1), did not emit a lot of CH₄ because they cover only a small area (Nugent et al., 2018). The CH₄ emitted from the entire restored peatland was lower than that of a reference undisturbed peatland, despite a shallower water table and much higher cover of *Eriophorum vaginatum* (Nugent et al., 2018). This result led to speculation that slow re-establishment of microbial communities after prolonged drying may be limiting CH₄ production rates (Juottonen et al., 2012). To address why net emissions were lower at the restored peatland, this study evaluates CH₄ production and

oxidation in the restored peat fields and former drainage ditches. We combine surface trace gas flux measurements with dissolved concentrations of CH₄, CO₂ and acetate, and stable isotope measurements of CH₄ and co-occurring dissolved total CO₂ (DIC, dissolved inorganic carbon). The stable isotope composition ($\delta^{13}\text{C}$) of CH₄ and DIC provides an indirect method to evaluate CH₄ production and oxidation.

In the water saturated zones of undisturbed peatlands, methanogenesis is expected to be the dominant terminal decomposition mechanism, due to anoxic conditions and a general absence of inorganic electron acceptors (Chaser et al., 2000a, b; Corbett et al., 2013a, b; Romanowicz et al., 1995). In peatlands, methanogenesis primarily occurs by either H₂/CO₂ reduction (hydrogenotrophic methanogenesis) or acetate fermentation (acetoclastic methanogenesis) and produces a net equimolar amount of CO₂ and CH₄ (Chanton, 2005). With both pathways, $\delta^{13}\text{C}$ of organic matter is fractionated to form a more enriched $\delta^{13}\text{C}$ -CO₂ and a more depleted $\delta^{13}\text{C}$ -CH₄ (Corbett et al., 2013). The degree of fractionation is dependent on the pathway, with more of a difference between CO₂ and CH₄ with H₂/CO₂ reduction than with acetate fermentation (Chaser et al., 2000a, b). This fractionation does not occur in CO₂ production by aerobic respiration or fermentation (Lapham et al., 1999). Transport of CH₄ from the soil to the atmosphere can result in isotopic fractionation, depending on the mode of transport. Aqueous diffusive transport does not result in significant isotopic fractionation, nor does ebullition as bubbles pass quickly through the peat to the atmosphere (Chanton, 2005). Gas transport via plants with aerenchyma likely causes ¹³C enrichment in the rhizosphere, but this process is difficult to differentiate from the effects of rhizospheric methane oxidation (Chanton, 2005).

Methanogenic archaea use a select few small molecules, e.g. acetate, H₂ and CO₂, supplied by the metabolic activities of other microbes as substrate. Acetate is considered the most important carbon intermediate in terrestrial anaerobic systems, rarely accumulating as it is rapidly produced and consumed (Hines et al., 2008). However, *Sphagnum*-containing peatlands such as bogs and poor fens tend to favor methanogenesis from H₂/CO₂ reduction (Chanton et al., 1995, 2005; Chaser et al., 2000a, b; Kelly et al., 1992; Lansdown et al., 1992; Popp et al., 1999); in these systems, acetate has the potential to accumulate in the absence of vascular plants (Hines et al., 2008). Labile carbon is generally found in the root environment of vascular plants, supplied by root residues and root exudates (Kuzyakov and Domanski, 2000). The plant root system is continuously releasing a wide range of labile carbon compounds, such as organic acids, amino acids and carbohydrates,

which serve as easily available substrate for microbial decomposition (Joabsson et al., 1999; Proctor and He, 2017). Root release of acetate and precursors to acetate can have a substantial effect on CH₄ production in the soil (Joabsson et al., 1999; Ström and Christensen, 2007; Ström et al., 2003, 2005, 2012). However, acetate concentrations found in the pore water and from *Eriophorum scheuchzeri* root exudation equate to only a few hours of CH₄ flux, suggesting a continuous input is needed to maintain the acetate fermentation pathway (Ström et al., 2012).

Previous studies in extracted peatlands that have been restored have found low or even insignificant CH₄ emissions (Komulainen et al., 1998; Nugent et al., accepted; Strack and Zuback, 2013; Strack et al., 2014; 2016; Tuittila et al., 2000; Waddington and Day, 2007; Wilson et al., 2009). Lower emissions relative to undisturbed peatlands could be due to greater overall CH₄ oxidation (during diffusion or rhizosphere oxidation) or reduced CH₄ production, or both. Rewetting causes the water table to rise relative to its drained position, but greater seasonal fluctuations can occur (McCarter and Price, 2015). Some rewetting efforts have resulted in flooded landscapes; however, our focus is on systems with a water table restored to below the surface. In deeper water table systems, CH₄ oxidation has the potential to significantly reduce the amount of CH₄ emitted (Roulet et al., 1993). Symbiosis among methanotrophic bacteria and *Sphagnum* has been reported to supply a significant portion of moss carbon by oxidizing peat CH₄, even below the water table (Raghoebarsing et al., 2005). As well, vascular plants such as *E. vaginatum* can promote a high degree (> 90%) of rhizospheric CH₄ oxidation (Ström et al., 2005). Drainage is an environmental stress that has the potential to adversely affect methanogen populations over decades (Juottonen et al., 2012). Acetoclastic methanogens tend to be physically fragile (Dannenberg et al., 1997), which suggests their population would react more to stress (Hines et al., 2008). The recalcitrant nature of cutover peat (Anderson et al., 2006; Basiliko et al., 2007; Glatzel et al., 2004; Juottonen et al., 2012), overlain by a restored *Sphagnum* layer, where *Sphagnum* is known to have antimicrobial compounds (Hines et al., 2008), could be an environment that inhibits methanogenesis. Acetate accumulation in the pore water profile would indicate acetate was a major end product of anaerobic metabolism rather than CH₄ production, suggesting methanogenesis inhibition (Hines et al., 2008).

In Canada, approximately 34,000 ha of vacuum-harvested peatlands are currently, or will soon be, in need of active restoration (ECCC, 2018). A surface net carbon uptake was successfully restored at a formerly vacuum-harvested peatland in Canada, but a mechanistic understanding of

subsurface carbon cycling is needed to better understand the results of Nugent *et al.* (2018). We hypothesized that the physiochemical nature of the underlying cutover peat was acting to inhibit CH₄ production, and that CH₄ release from the restored peat fields occurred primarily via plant-mediated transport. Using surface flux measurements, substrate supply and CH₄ production and oxidation in the former drainage ditches and restored peat fields, our objective was to identify the causes of the lower than expected ecosystem CH₄ release found in the Nugent *et al.* (2018) study.

4.3 Methods

4.3.1 Site description

Our study took place at the restored Bois-des-Bel peatland near Rivière-du-Loup, Québec, Canada (47°58'1.95"N 69°25'43.10"W). The peatland complex is 210 ha, of which 11.5 ha was vacuum-harvested in the 1970's. The MLTT restoration approach was used to restore 8.1 ha in the autumn of 1999 (Figure 4.1), in the first ever landscape scale attempt. Graf and Rochefort (2016) provide a detailed description of the restoration process while Nugent *et al.* (2018) have a more complete description of the geographical history of the Bois-des-Bel complex and its post-restoration biophysical characteristics. The climate of the region is cool-temperate and experiences an average annual temperature of 3.5 ± 2.9 °C with 962 mm of precipitation, of which 270 mm is snowfall over November–March (1981-2010 climate normal, St-Arsene, Environment Canada). Precipitation is spread fairly evenly over the months with the coldest month being January (-12.4 ± 2.6 °C) and the warmest month July (17.6 ± 1.2 °C).

4.3.2 Flux measurements

The experimental set up focussed on comparing vascular and non-vascular plant communities in the restored peat fields and former drainage ditches at the restored peatland. Six vascular plots and three non-vascular plots were set up in the features (field, ditch), respectively, for a total of 18 plots. Plot selection was done based on the dominant vegetation within the respective features, with *E. vaginatum* and *Sphagnum* spp. chosen in the restored peat field while plots with *Typha latifolia* and bare ditch areas were selected in the former ditches. While the bare ditch plots were initially devoid of vegetation, vascular plants did spread through the area over the course of the season. Sprouts within the collars were removed on a regular basis. Boardwalks were used to span the former ditches and to traverse the restored peatland. An additional six *Sphagnum* plots were created in the adjacent undisturbed peatland, located within the same peatland complex, which was used as a reference site.



Figure 4.1 – Site map of the post-extraction restored peatland Bois-des-Bel in Québec, Canada. The restored peat fields (green shading) are separated at 30 m intervals by former drainage ditches (blue lines), which have been infilled but are depressed.

Net CO₂ and CH₄ flux measurements were carried out using the closed chamber technique on permanently installed collars. A laser gas analyzer (LGR-UGGA, Los Gatos Research, CA, USA)

connected to a clear polycarbonate chamber enabled simultaneous measurements of CO₂ and CH₄ (and H₂O) concentration at 1 Hz. A rectangular chamber (60 x 60 x 30 cm; 0.108 m³) and collar combination was used at the restored field plots while a cylindrical chamber (100 cm height x 26 cm diameter; 0.053 m³) and collar combination was deployed in the former ditches, to accommodate vertical growth of *T. latifolia*. We equipped the chambers with fans to maintain a well-mixed headspace, as well as a cooling system to prevent excessive warming during closure. NEE and CH₄ flux were calculated from the linear change in CO₂ and CH₄ headspace concentration, respectively, over a measurement period of 2 min. A tarp was used to block incoming radiation within the chamber over a successive closure. Gross primary productivity (GPP) was calculated from the difference between the unshrouded measurement (NEE) and the fully dark measurement which provided ecosystem CO₂ respiration (ER).

Gas temperature (T_{SAMPLE}, °C) was measured at 1 Hz by the LGR-UGGA while photosynthetically active radiation (PAR; $\mu\text{mol m}^{-2} \text{s}^{-1}$) was recorded every 10 sec during chamber closure by a quantum sensor. Following chamber deployment, soil temperature (T_{SOIL}) at 2, 5, 10, 15, 20, 25 and 30 cm was measured next to each collar using a digital thermocouple temperature probe, while water table depth (WTD) was manually measured at adjacent wells. Dataloggers (CR5000 and CR23X, Campbell Scientific, AB, CAN) were used to record half hourly air temperature (T_{AIR}), and T_{SOIL} at multiple depths (5, 10, 20, 40, 60, 80 cm) in the restored field and former ditch locations over the measurement season using type T thermocouples (Omega Engineering). Paired Leveloggers and Barologgers (Model 3001, Solinst, Ontario, Canada) determined half hourly WTD in proximity to the T_{SOIL} profiles.

A total of 600 chamber closures were performed over the snow-free season of 2016. Standard chamber flux calculations (Bubier et al., 2002) were made for linear changes in headspace CO₂ and CH₄ over time. In the case where CH₄ bubbling was captured with the LGR-UGGA, a piece-wise linear fitting routine modified from Goodrich *et al.* (2011) was used to separate linear from non-linear CH₄ increase in headspace concentration. Methane ebullition occurred repeatedly in the ditch plots and was characterized by a sudden break in the slope of the CH₄ mixing ratio over short durations (generally < 20 sec). The first difference of the CH₄ mixing ratio time series and standard deviation of the first difference were used to distinguish non-linear events. In total, 78 non-linear events passed the criteria in 2016 and were separated out from the linear dataset. The linear slope before and after the concentration jump was determined in order to quantify jump

magnitude as well as baseline magnitude, which theoretically should continue during bubble events (Goodrich et al., 2011). Bubble magnitude was calculated as the difference between the jump magnitude and baseline magnitude and then converted to CH₄ mass released (mg CH₄) using chamber volume, temperature and pressure. The fraction of total emissions attributed to the ebullition pathway was estimated by calculating the cumulative ebullitive and diffusive flux over the periods where sampling took place.

4.3.3 Pore water sample collection and analyses

In-situ concentration of dissolved organic carbon (DOC), DIC and dissolved CH₄ (dCH₄) was determined using six replicate sets of pore water samplers installed 0.2 m and 0.8 m below the former ditch and restored field surface, respectively, as well as at the reference site. Pore water samplers were made of a 0.2 m length of ABS pipe (25 mm I.D.) closed at both ends, slotted at the middle 0.1 m, and covered in mesh to prevent clogging. Tygon tubing connected to one end was extended above the soil surface to allow for water collection by syringe from a stopcock. Installations occurred 30 days in advance of sampling and temporally representative samples were obtained by removing 60 mL of pore water from each sampler 48 hours before sampling (Strack and Waddington, 2008). The headspace degassing technique (Ioffe and Vitenberg 1984) was used to acquire gas from the water samples. Ambient air was drawn into the syringe in equal volume to the collected pore water (30 mL) and the sample was degassed by shaking the sample vigorously (Waddington and Day 2007). Gas samples were then transferred to evacuated 12 mL sealed vials (Exetainers, Labco, UK) and stored in a cooler for transport to McGill University, Montreal, Canada for analysis. Gas concentrations of CH₄ and CO₂ were determined using a gas chromatograph (Mini-2, SRI Instruments, California, USA). The remaining water sample was passed through 0.45 µm paper filters (Macherey-Nagel MN 85/90) and acidified before being analyzed for DOC concentration on a total organic carbon analyzer (TOC-V, Shimadzu, Maryland, USA).

Pore water sampling to determine δ¹³C and acetate concentration was undertaken on DOY 163 (June 11, 2016), 200-201 (July 18-19, 2016), 216-217 (August 3-4, 2016) and 242 (August 29, 2016). The experimental set-up targeted the root zone (0.2 m) and below the root zone in the cutover peat (0.8 m) using “sipper” sets (rhizosphere and deep) permanently installed in the flux collars. Sippers are 6 mm diameter stainless steel tubes with mesh-covered holes drilled at the base and a length of Tygon tubing with a stopcock. Sippers were flushed with a small amount of soil

water prior to slowly drawing 20 mL using a syringe. Stable carbon isotope samples were filtered in the field through 0.1 μm in-line syringe filters (Whatman Grade GF/D glass microfiber) and injected into 11 mL evacuated glass vials sealed with 20 mm-thick butyl rubber septa. Samples were duplicated and acidified in the field with 1 mL of 30% H_3PO_4 , and stored upside down on ice before being express shipped to Florida State University, Tallahassee, FL, USA. A 2-hour wait period was followed in the case of same-day sampling for $\delta^{13}\text{C}$ and acetate. Duplicate acetate samples were filtered in the field through 0.1 μm in-line syringe filters into 5 mL plastic vials and frozen prior to being shipped to Lund University, Lund, Sweden. Acetate concentration was additionally sampled directly from the roots of *T. latifolia* and *E. vaginatum* plants. This was undertaken by threading individual roots through a tiny hole in a syringe with attached Tygon tubing and stopcock. Three roots were sampled from for six plants of each species (36 roots total), with a blank syringe (root hole included) placed in the vicinity of each sampled plant (12 blanks total). Deionized water was replaced in the root syringes 24 hours prior to sampling in order to have a temporally representative sample. Note that $\delta^{13}\text{C}$ and acetate sampling in the field plots was prevented beyond June by a water table deeper than 0.2 m and by strong resistance when drawing up pore water from 0.8 m. Extraction was made difficult by the nature of the cutover peat, which had low porosity caused by subsidence after drainage (Waddington and McNeil, 2002).

Isotope samples were brought to ambient pressure with helium, pressurized to one atmosphere and shaken to extract gas into the headspace. The gas concentration and isotopic ratio in the headspace were determined by direct injection on a gas chromatograph combustion-interfaced isotope ratio mass spectrometer (MAT Delta V, Finnigan, USA). The stable isotope analysis is described in further detail in Corbett *et al.* (2015). We determined the dominant CH_4 production pathway at the sampling points in the soil profile using two stable isotope abundance metrics. First, acetate fermentation (acetoclastic methanogenesis) yields CH_4 whose $\delta^{13}\text{C}$ values fall within a typical range of -65 and -50‰ whereas CH_4 from H_2/CO_2 reduction (hydrogenotrophic methanogenesis) has $\delta^{13}\text{C}$ values typically between -110 and -60‰ (Hornibrook and Aravena, 2010; Whiticar *et al.*, 1986). Second, the apparent fractionation factor for carbon (α) (see in Equation 2.8) is a measure of the separation between CH_4 and co-occurring CO_2 (Chaser *et al.*, 2000a; Hornibrook *et al.*, 1997; Whiticar *et al.*, 1986). The factor is referred to as apparent, because while CO_2 is a precursor for CO_2 reduction, it is not an immediate precursor for CH_4 formed from acetate fermentation (Chanton *et al.*, 2006). Nonetheless, variation in α is

interpreted to represent variations in CH₄ production mechanism. Microbial culture-derived α values for H₂/CO₂ reduction are found to range between 1.031 and 1.077, while α values between 1.007 and 1.027 are characteristic of acetate fermentation (Chaser et al., 2000a; Conrad et al., 2002; Hornibrook et al., 1997, 2000a, 2000b). In general, values of $\alpha > 1.065$ and $\alpha < 1.055$ are characteristic of environments dominated by H₂/CO₂ reduction and acetate fermentation, respectively (Whiticar et al., 1986; Whiticar, 1999).

Organic acid concentrations, e.g., acetic acid/acetate, were analyzed using a high-pressure liquid chromatography tandem-ion-spray mass spectrometry system. The system consisted of a chromatography system (ICS-2500, Dionex, Sunnyvale, California, USA) and a triple quadrupole mass spectrometer (2000 Q-trap, Applied Biosystems, Foster City, California, USA). Further analysis details and quality controls can be found in Ström *et al.* (2012). Results are presented in μM of acetate, given that acetate dominates at $\text{pH} > 4.76$. Other organic acids, namely, citric, formic, glycolic and lactic, were also detected, but were present at insufficient amounts to pursue further analysis.

4.3.4 Statistical analysis

Statistical analyses were performed on the DOY 163 to DOY 243 means of the flux and pore water concentration sample groups (i.e. five vegetation groups, two depths). All data were tested for normal distribution using the Shapiro-Wilk test before further analyses. To test for significant differences between groups, the Mann-Whitney U test was used to test significance between two non-parametric sample groups, while the Student's t -test was used for parametric data. For three or more groups, the Kruskal-Wallis one-way analysis of variance was used to test non-parametric data while an ANOVA was used to test parametric data. All statistical analyses were done using R (R Core Team 2017). Results of the statistics were regarded as significant if p values were ≤ 0.05 .

4.3.5 Greenness index

Canopy greenness at the restored peatland was monitored using a digital camera, which took daily JPEG images with red (R), green (G) and blue (B) channels at solar noon. The images were analyzed using the Phenocam GUI application, available as a MATLAB[©] program (phenocam.sr.unh.edu/webcam/tools), to calculate the green chromatic coordinate (g_{cc}), where:

$$g_{cc} = \frac{G}{R+G+B}, \quad (4.1)$$

for a predefined region of interest (ROI) (Sonnentag et al., 2012). We selected two ROIs within each image: an area of restored peat field and a restored drainage ditch with *T. latifolia*.

4.4 Results

4.4.1 Surface fluxes

Net CO₂ exchange at the surface of the restored peatland showed differing seasonal patterns in the restored peat fields and former drainage ditches (Figure 4.2a, b). *T. latifolia* in former ditches were a source of CO₂ prior to leaf-out and after senescence (delimited by the greenness index) but had the highest net CO₂ uptake rate mid-season (July & August), with a mean (\pm SE) light-saturated NEE of $-13.3 \pm 1.0 \mu\text{mol m}^{-2} \text{s}^{-1}$, where negative measurements are net uptake by the ecosystem (Figure 4.2a; Table 4.1). Bare ditches were a low source of CO₂ with a mid-season mean CO₂ release of $2.5 \pm 0.4 \mu\text{mol m}^{-2} \text{s}^{-1}$ (Figure 4.2a, c; Table 4.1). *E. vaginatum* and *Sphagnum* in the restored peat fields actively took up CO₂ throughout the study period (May 15 to November 1, 2016), but at a significantly slower rate than *T. latifolia* (Kruskal-Wallis, $p < 0.0001$), of about $-3.5 \mu\text{mol m}^{-2} \text{s}^{-1}$ on mid-season sunny days (Figure 4.2b; Table 4.1). The warmest and driest period of the season was in August (Nugent et al., 2018), during which restored peat field NEE exhibited lower uptake and bare ditch CO₂ emission peaked. Meanwhile, *T. latifolia* net CO₂ uptake was the maximum recorded (Figure 4.2a, b). Early in the season (May & June), restored peat field *Sphagnum* plots exhibited significantly higher light-saturated NEE than the reference natural peatland *Sphagnum*, due to higher GPP (Table 4.1). Mid-season full-light NEE, ER and GPP was not statistically different between restored and reference *Sphagnum* (Kruskal-Wallis test, $p = 0.071$), but, late season (September-November) NEE and ER at the reference peatland was significantly less negative and more positive, respectively, than in the restored *Sphagnum* (Kruskal-Wallis test, $p < 0.001$) (Table 4.1).

Diffusive CH₄ flux measured simultaneously with NEE exhibited seasonal changes in all restored peatland plots except those dominated by *Sphagnum* (Figure 4.2c, d). Net CH₄ emission from bare ditch area increased from $98 \pm 25 \text{ nmol m}^{-2} \text{s}^{-1}$ during the early season to $1174 \pm 296 \text{ nmol m}^{-2} \text{s}^{-1}$ mid-season (Figure 4.2c; Table 4.1). Bare ditch emission reduced sharply once the water table dropped below the surface in August and did not recover with a late season rise in water table (Figure 4.2c; Table 4.1). *T. latifolia* had the second highest mid-season net CH₄

emission, of $266 \pm 213 \text{ nmol m}^{-2} \text{ s}^{-1}$ (Table 4.1), with net CH_4 flux peaking in advance of light-saturated NEE, seasonally (Figure 4.2a, c).

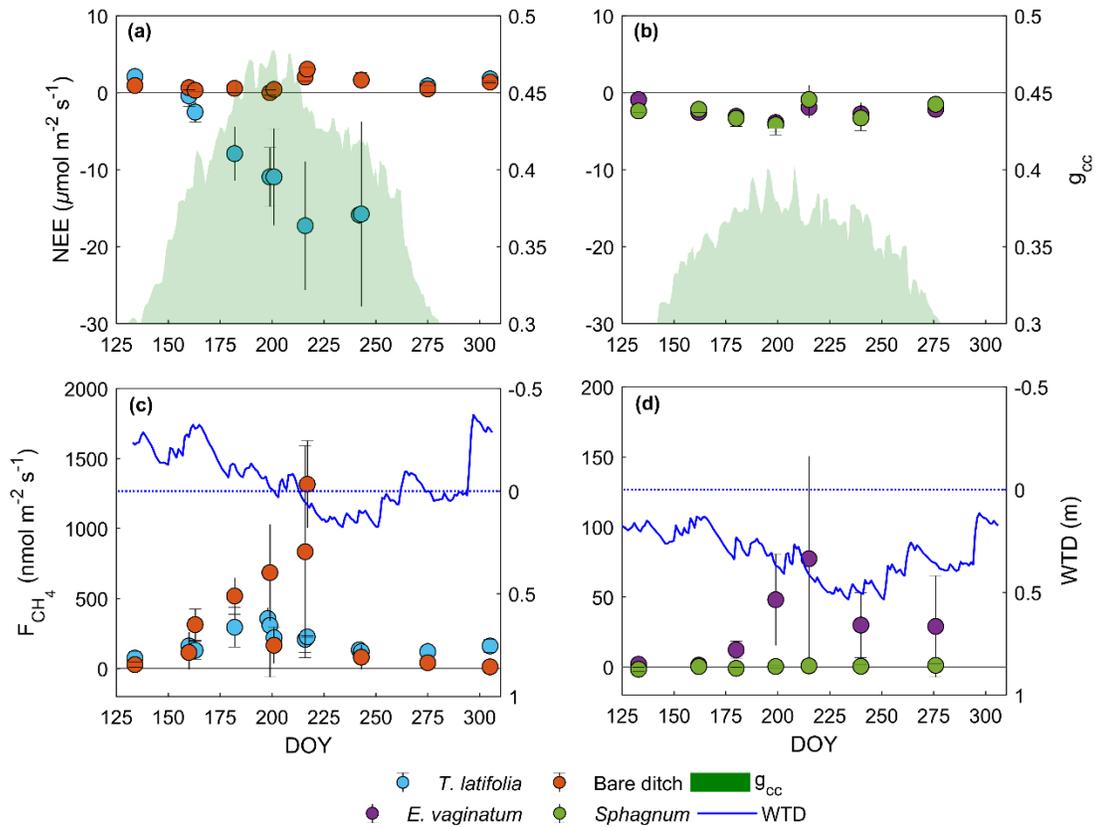


Figure 4.2 – Mean (\pm SD) instantaneous net ecosystem exchange of CO_2 (NEE, in $\mu\text{mol m}^{-2} \text{ s}^{-1}$) when photosynthetically active radiation (PAR) is greater than $1000 \mu\text{mol m}^{-2} \text{ s}^{-1}$ in: (a) former drainage ditch plots (*T. latifolia* and Bare ditch), and, (b) restored peat field plots (*E. vaginatum* and *Sphagnum*). Negative values represent net CO_2 uptake by the ecosystem while positive values are release to the atmosphere. The green shading in (a) and (b) is an index of greenness (g_{cc}) derived from digital imagery for the former ditches and restored fields. Mean (\pm SD) instantaneous CH_4 flux (F_{CH_4} , in $\text{nmol m}^{-2} \text{ s}^{-1}$) in: (c) former ditch and (d) restored field plots is graphed with continuous water table depth (WTD in m). Instantaneous NEE and F_{CH_4} were measured simultaneously using a laser gas analyzer. Note that the left y-axis in (c) and (d) have different ranges.

Table 4.1 – Mean (SE) fluxes of carbon at the surface-air interface during the early (May & June), mid (July & August) and late (September–November) season. Fluxes are net ecosystem exchange of CO₂ (NEE), ecosystem respiration (ER), gross primary productivity (GPP), and CH₄. NEE is the mean of measurements when PAR was greater than 1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$. CO₂ units are $\mu\text{mol m}^{-2} \text{s}^{-1}$; CH₄ units are $\text{mmol m}^{-2} \text{s}^{-1}$.

Feature	Plant community	Early season			Mid season			Late season					
		NEE	ER	GPP	CH ₄ flux	NEE	ER	GPP	CH ₄ flux	NEE	ER	GPP	CH ₄ flux
Restored field	<i>E. vaginatum</i>	-2.2 (0.5)	1.5 (1.1)	-3.7 (1.2)	1 (1)	-3.5 (0.3)	3.6 (1.7)	-7.1 (1.9)	73 (16)	-3.1 (0.6)	0.7 (0.1)	-3.8 (0.6)	34 (11)
	<i>Sphagnum</i>	-3.0 (0.3)	1.9 (0.7)	-4.9 (0.9)	-5 (1)	-3.4 (0.5)	3.1 (1.3)	-6.3 (1.4)	3 (2)	-2.2 (0.6)	1.0 (0.1)	-3.4 (0.7)	0.4 (0.2)
Former drainage ditch	<i>T. latifolia</i>	1.3 (1.1)	0.7 (0.05)	0.6 (1.2)	139 (15)	-13.3 (1.0)	4.5 (0.5)	-17.9 (1.3)	266 (18)	1.1 (0.2)	1.1 (0.2)	0.0	129 (22)
Restored Ecosystem	Bare ditch	1.3 (0.3)	1.3 (0.3)	0.0	98 (25)	2.5 (0.4)	2.5 (0.4)	0.0	1174 (296)	0.8 (0.3)	0.8 (0.3)	0.0	29 (19)
Reference peatland	<i>Sphagnum</i>	-5.6 (2.0)	2.3 (1.5)	-7.9 (3.0)	8 (8)	-7.3 (2.1)	4.4 (1.2)	-11.7 (2.0)	20 (9)	-6.0 (1.7)	2.4 (1.2)	-8.4 (2.3)	31 (77)
		-1.3 (0.2)	1.0 (0.2)	-2.3 (0.3)	17 (6)	-3.5 (0.5)	3.7 (0.6)	-7.2 (0.7)	50 (7)	-1.7 (0.4)	2.3 (0.3)	-4.0 (0.5)	31 (21)

Net CH₄ emission from *T. latifolia* also decreased alongside water table lowering in August, but fluxes remained at $129 \pm 22 \text{ nmol m}^{-2} \text{ s}^{-1}$ after senescence, similar to mean emissions ($139 \pm 15 \text{ nmol m}^{-2} \text{ s}^{-1}$) prior to leaf out (Table 4.1). *E. vaginatum* net CH₄ flux increased from 0 to $73 \pm 159 \text{ nmol m}^{-2} \text{ s}^{-1}$ mid-season as the water table position reached $\sim 0.3 \text{ m}$ below the surface (Figure 4.2d; Table 4.1). Lower fluxes occurred during the water deficit period in August and did not recover alongside late season water table rise, although *E. vaginatum* remained a source of $34 \pm 11 \text{ nmol m}^{-2} \text{ s}^{-1}$ (Figure 4.2d; Table 4.1). Restored *Sphagnum* was on average a null CH₄ source throughout the season, measuring low uptake ($\sim -8 \text{ nmol m}^{-2} \text{ s}^{-1}$) to low release ($< 10 \text{ nmol m}^{-2} \text{ s}^{-1}$) (data not shown). Fluxes from *Sphagnum* overlain by shrub species were similar to *Sphagnum*-only collars and were a net zero emission (data not shown). Comparatively, the reference site *Sphagnum* was a mean source over the season, with emissions peaking at $50 \pm 7 \text{ nmol m}^{-2} \text{ s}^{-1}$ and had a significantly higher flux during the early season compared to restored *Sphagnum* and *E. vaginatum* (Table 4.1).

Methane ebullition occurred most often in bare ditch areas, less frequently in *T. latifolia* plots, during a single campaign in one *E. vaginatum* plot and never in *Sphagnum* plots. Ebullition was recorded five times during *E. vaginatum* sampling on June 5, 2016 and had a mean bubble mass of 0.005 mg CH_4 ($0.004\text{--}0.006 \text{ mg CH}_4$) (data not shown). Bubbling occurred 29 times during 42 sampling occasions in the bare ditches and had a mean bubble mass of 0.09 mg CH_4 (range: $0.01\text{--}0.47 \text{ mg CH}_4$) (data not shown). Bubbles from *T. latifolia* plots had a lower mean bubble mass, of 0.03 mg CH_4 (range: $0.003\text{--}0.17 \text{ mg CH}_4$) and occurred 44 times during 179 sampling occasions (data not shown). In both ditch plot types, ebullition ceased by early August when the water table dropped below the ditch surface. The frequency of bubble events occurring from the former ditches over the sampling period was estimated to be 1,820/day and the mean flux was estimated at $42 \text{ nmol m}^{-2} \text{ s}^{-1}$, corresponding to 9% of total emissions (ebullitive & diffusive) over the sampling period.

4.4.2 Pore water carbon concentration

Concentration of dCH₄ was significantly higher 0.8 m below the surface (i.e. cutover peat) in the former ditches compared to the restored peat fields (Mann-Whitney *U* test, $p < 0.0001$) (Figure 4.3a; Table 4.2). Pore water sampling 0.2 m below the surface (i.e. root zone) of the restored peat fields was not possible after the month of June due to seasonal water table drawdown;

values shown in Figure 4.3a and 4.3b after DOY 175 were determined from pore air samples. In contrast, the former ditch water table did not drop more than 0.17 m below the surface during the 2016 season (Figure 4.2c). dCH₄ concentration in the root zone and in the cutover peat were statistically different in the bare ditch areas (Mann-Whitney *U* test, $p=0.011$) and in *T. latifolia* plots (Mann-Whitney *U* test, $p<0.0001$). *T. latifolia* dCH₄ was significantly lower than bare ditch dCH₄ at both sampling depths (Mann-Whitney *U* test, $p<0.0001$). Bare ditch dCH₄ had an early-season peak, coinciding with a rainy period that preceded the beginning of the seasonal water table drawdown (Figure 4.2c). Meanwhile, dCH₄ at the two depths below *T. latifolia* showed a synchronized seasonal pattern, with stable or increasing concentration during early season, a mid-season decrease and stable concentration during late-season. A comparison of June–August measurements in the restored peatland and reference peatland determined that bare ditch, *T. latifolia* and reference *Sphagnum* plots were not significantly different at 0.8 m depth (Kruskal-Wallis test, $p=0.078$; Table 4.2). In contrast, concentration at 0.2 m depth was significantly lower in restored peat fields and *T. latifolia* plots and significantly higher in bare ditch plots compared to the reference plots (Mann-Whitney *U* test, $p<0.0001$; Table 4.2).

Concentration of dissolved CO₂ was significantly higher in the former ditches than in the restored peat fields (Mann-Whitney *U* test, $p<0.0001$), and in the cutover peat compared to the root zone in all plot types (Mann-Whitney *U* test, $p<0.0001$) (Figure 4.3b; Table 4.2). DIC appeared to peak mid-season in the former ditches while the inverse appeared the case in the restored peat fields (Figure 4.3b). DIC in June–August was significantly higher in the former ditches compared to the reference peatland at 0.2 m (Mann-Whitney *U* test, $p=0.0017$) and at 0.8 m (Mann-Whitney *U* test, $p<0.001$; Table 4.2). DIC in the restored peat fields differed significantly from reference values at 0.8 m depth (Kruskal-Wallis test, $p<0.0001$; Table 4.2).

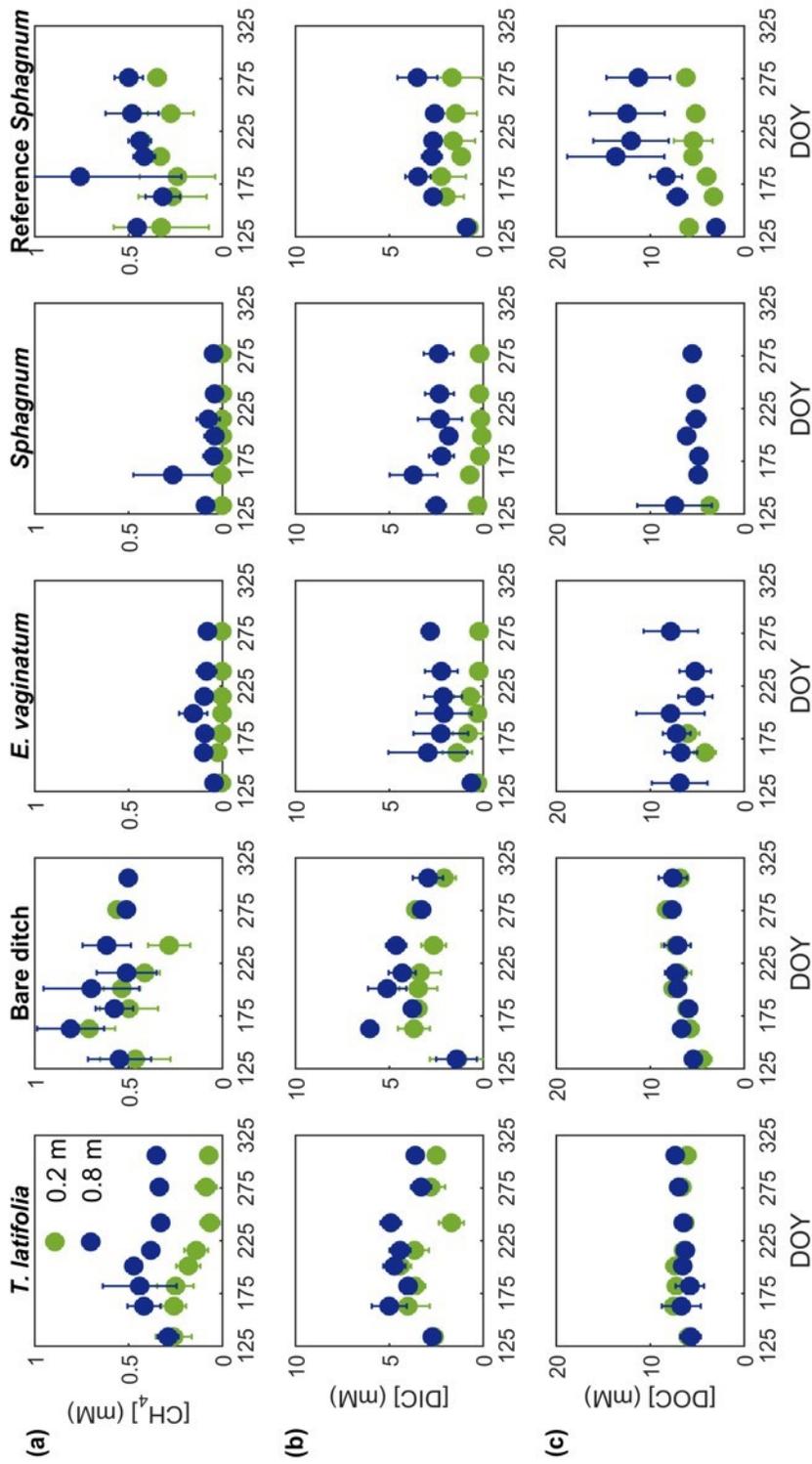


Figure 4.3 – Mean (\pm SD) concentration of (a) dissolved inorganic carbon (DIC), (b) dissolved inorganic carbon (DIC), and, (c) dissolved organic carbon (DOC) at 0.2 m (root zone) and 0.8 m (cutover peat) below the surface of the restored peatland and reference peatland over the study period. *E. vaginatum* and *Sphagnum* root zone sampling resulted in gaseous samples after DOY 175. Measurements from reference *Sphagnum* plots occurred in the undisturbed peatland that surrounds the restored peatland.

DOC concentration in the cutover peat was not significantly different in the former ditch and restored peat field *E. vaginatum* plots whereas restored *Sphagnum* values were significantly lower, when grouped seasonally (Kruskal-Wallis test, $p=0.002$). DOC at 0.2 m depth was significantly higher in the former ditch than the restored peat field (Kruskal-Wallis test, $p<0.001$), but not amongst the former ditch plots and restored peat field plots, respectively (Mann-Whitney *U* test, $p=0.32$, $p=0.88$). *T. latifolia* root zone DOC appeared to decrease over the season whereas concentrations appeared to increase slightly in the three other former ditch cohorts (Figure 4.3c). DOC at 0.8 m depth was significantly higher in the reference peatland compared to the restored peatland (Mann-Whitney *U* test, $p<0.0001$). Meanwhile, DOC at 0.2 m depth was significantly higher in the restored peatland former ditches compared to the reference site (Mann-Whitney *U* test, $p<0.001$; Table 4.2).

4.4.3 Acetate concentration

Acetate concentration in the restored peat fields could not be measured beyond the June campaign (DOY 163) due to the position of the water table and strong resistance to water extraction at 0.8 m depth (Figure 4.4). Mean (SE) acetate concentration in the root zone of *E. vaginatum* plots in June was $28.6 \pm 6.7 \mu\text{M}$ compared to $34.8 \pm 8.3 \mu\text{M}$ in the cutover peat (Table 4.2). Concentration in the root zone and cutover peat of restored *Sphagnum* was $8.6 \pm 1.8 \mu\text{M}$ and $39.1 \pm 14.7 \mu\text{M}$, respectively (Table 4.2). Within the former ditches, the *T. latifolia* root zone had the highest mean concentration ($14.9 \pm 2.3 \mu\text{M}$) on DOY 163, compared to 6.2-8.5 μM otherwise. *T. latifolia* root zone was the only sampling cohort to exhibit a significant seasonal pattern (Kruskal-Wallis test, $p=0.007$ Figure 4.4b). A root isolation experiment found *T. latifolia* root exudation of acetate to peak mid-season (Figure 4.4a), whereas *E. vaginatum* root exudation did not change over the season (Figure 4.4f).

Table 4.2 – Mean (SE) concentration at 0.2 m and 0.8 m depth in June–August of dissolved organic carbon (DOC), dissolved CH₄ (dCH₄), dissolved inorganic carbon (DIC), acetate in pore water and root exudates, as well as mean stable isotope composition ($\delta^{13}\text{C}$) of CH₄ and apparent fractionation factor for carbon (α).

Feature	Vegetation	Depth (m)	[DOC] (mM)	[dCH ₄] (mM)	[DIC] (mM)	[Acetate] (μM) [†]	Root [Acetate] (μM)	$\delta^{13}\text{C}\text{-CH}_4$ (‰) [†]	α [†]
Restored field	<i>E. vaginatum</i>	0.2	6.0 (0.4)	0.04 (0.01)	0.49 (0.11)	28.6 (6.7)	9.0 (1.2)	-62.4 (1.9)	1.043 (0.002)
		0.8	7.0 (0.5)	0.30 (0.14)	2.39 (0.21)	34.8 (8.3)	-	-57.9 (0.4)	1.049 (0.001)
	<i>Sphagnum</i>	0.2	4.9 (0.2)	-	0.18 (0.02)	8.6 (1.8)	-	-	-
		0.8	5.0 (0.2)	0.12 (0.02)	1.42 (0.32)	39.1 (14.7)	-	-63.0 (3.3)	1.053 (0.004)
Former drainage ditch	<i>T. latifolia</i>	0.2	7.0 (0.1)	0.17 (0.02)	3.54 (0.21)	8.8 (1.2)	9.0 (2.0)	-54.1 (0.4)	1.044 (0.001)
		0.8	6.4 (0.2)	0.40 (0.02)	4.75 (0.12)	8.3 (0.7)	-	-63.7 (0.4)	1.059 (0.001)
Reference peatland	<i>Bare ditch</i>	0.2	6.8 (0.3)	0.49 (0.05)	3.29 (0.21)	4.1 (0.5)	-	-56.6 (0.5)	1.051 (0.001)
		0.8	7.2 (0.2)	0.66 (0.05)	5.03 (0.21)	7.0 (1.3)	-	-63.5 (0.5)	1.062 (0.001)
Reference peatland	<i>Sphagnum</i>	0.2	4.5 (0.3)	0.35 (0.02)	2.21 (0.15)	-	-	-	-
		0.8	11.0 (0.8)	0.50 (0.05)	2.84 (0.11)	-	-	-	-

[†]Restored field averages only include samples collected in June as subsequent sampling was prevented by a water table deeper than 0.2 m and strong resistance when drawing up pore water from 0.8 m.

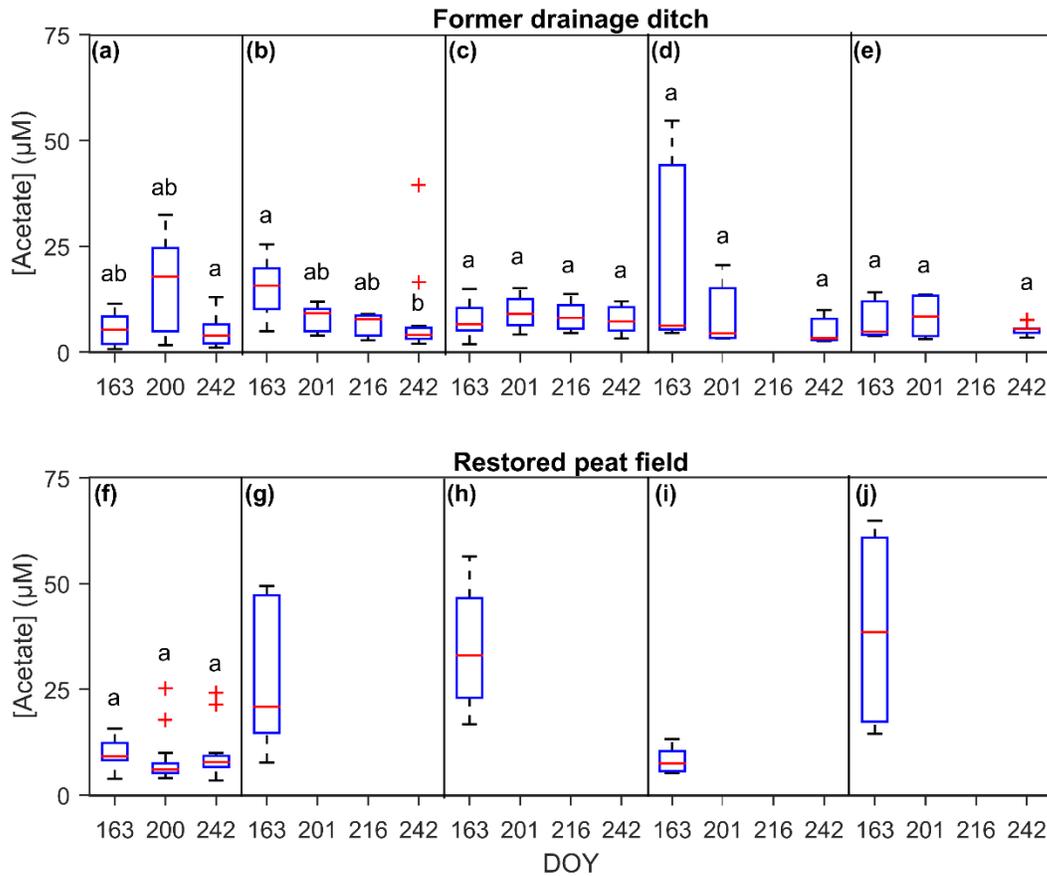


Figure 4.4 – Pore water acetate concentration (μM) in the former drainage ditches (top panel) and restored peat fields (bottom panel). Concentration was measured from *T. latifolia* in (a) isolated roots, (b) root zone (0.2 m depth), and (c) cutover peat (0.8 m depth); from bare ditch in (d) root zone, and (e) cutover peat; from *E. vaginatum* in (f) isolated roots, (g) root zone, and (h) cutover peat; and from *Sphagnum* in (i) root zone, and (j) cutover peat. Isolated root samples were accumulated in syringes in a deionized water medium over a 24-hour period. Sampling in the restored fields only occurred on DOY 163, with the exception of root sampling. Significant differences between sampling dates were evaluated using the Kruskal-Wallis test ($\alpha = 0.05$).

4.4.4 Carbon isotopic composition of dCH_4 and DIC

Pore water $\delta^{13}C$ -DIC in samples extracted from the restored peatland ranged from -24‰ to -2‰, with the least enriched signature found in the root zone of restored *Sphagnum* (~-22‰) and *E. vaginatum* (-24‰ to -18‰) plots and the most enriched signature in bare ditch cutover peat (-10‰ to -2‰) (Figure 4.5; some data not shown due to missing $\delta^{13}C$ -CH₄).

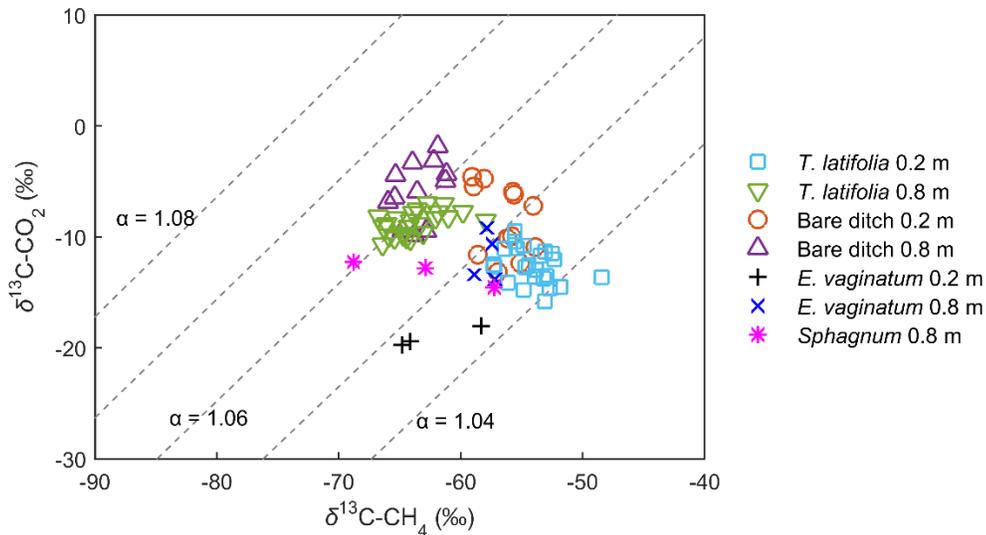


Figure 4.5 – Cross-plot showing stable isotope carbon composition (^{13}C) of DIC ($\delta^{13}C-CO_2$) and dissolved CH_4 ($\delta^{13}C-CH_4$) in pore water. Results are classified by depth below the surface (0.2 m and 0.8 m) and plant community (*T. latifolia* in former ditches, bare ditch, *E. vaginatum* in restored peat fields and *Sphagnum* in restored peat fields). Dashed diagonal lines show equal fractionation between dissolved CH_4 and co-occurring DIC, with the apparent fractionation factor (α) decreasing from top-left to bottom-right. Values of α above 1.065 suggest H_2/CO_2 reduction is the dominant methanogenesis pathway while values below 1.055 suggest acetate fermentation is dominating (Conrad, 2005).

June–August mean (SE) $\delta^{13}C$ -DIC in the cutover peat below *E. vaginatum*, *Sphagnum*, *T. latifolia* and bare ditch plots was $-11.8 \pm 1.1\text{‰}$, $-13.2 \pm 0.7\text{‰}$, $-8.8 \pm 0.2\text{‰}$ and $-5.8 \pm 0.8\text{‰}$, respectively (data not shown). Mean $\delta^{13}C$ -DIC in the root zone of the above respective communities was $-21.2 \pm 1.0\text{‰}$, $-22.1 \pm 0.5\text{‰}$, $-12.8 \pm 0.3\text{‰}$ and $-8.5 \pm 0.9\text{‰}$ (data not shown). The $\delta^{13}C$ -DIC signature beneath bare ditch area (0.2 & 0.8 m depth) did not exhibit seasonal change ($p=0.063$). Instead, one bare ditch plot had significantly less depleted values than the other two plots (Kruskal-Wallis test, $p<0.001$). Individual *T. latifolia* plots became less enriched in $\delta^{13}C$ -DIC over the course of four sample dates, but, when the plots were analyzed together, no seasonal pattern emerged (Kruskal-Wallis test, $p=0.11$) (Figure 4.5). The $\delta^{13}C$ -DIC signature in *T. latifolia* cutover peat, on

the other hand, did show a seasonal shift toward less enriched values during mid-season (Kruskal-Wallis test, $p=0.020$).

Pore water $\delta^{13}\text{C-CH}_4$ ranged from least enrichment in the samples taken at 0.8 m depth (-69‰ to -57‰) to most enrichment (max -48‰) in the *T. latifolia* root zone (*T. latifolia* 0.2 m in Figure 4.5). Mean $\delta^{13}\text{C-CH}_4$ in the cutover peat below *E. vaginatum*, *Sphagnum*, *T. latifolia* and bare ditch plots was $-57.9 \pm 0.4\text{‰}$, $-63.0 \pm 3.3\text{‰}$, $-63.7 \pm 0.4\text{‰}$ and $-63.5 \pm 0.5\text{‰}$, respectively (Table 4.2). Mean $\delta^{13}\text{C-CH}_4$ in the root zone was $-62.4 \pm 1.9\text{‰}$ for *E. vaginatum*, $-54.1 \pm 0.4\text{‰}$ for *T. latifolia* and $-56.6 \pm 0.5\text{‰}$ in bare ditch plots (Table 4.2); three pore water samples were extracted from beneath *Sphagnum* on DOY 163, but all were below the $^{13}\text{C-CH}_4$ detection limit, as was the case in three of six *E. vaginatum* samples. The $\delta^{13}\text{C-CH}_4$ signature of bare ditch cutover peat did not significantly change over the season (Kruskal-Wallis test, $p=0.96$), whereas root zone $\delta^{13}\text{C-CH}_4$ became significantly more enriched over the course of the season (Kruskal-Wallis test, $p=0.033$; Figure 4.5). The signature of the *T. latifolia* root zone also exhibited significant seasonal enrichment (Kruskal-Wallis test, $p=0.044$), while the cutover peat beneath *T. latifolia* was least enriched on the two mid-season sampling dates (DOY 201 & 216) (Figure 4.5).

The apparent fractionation factor for $\text{DIC} \rightarrow \text{CH}_4$, α , ranged from a mean of ~ 1.045 in the root zone (0.2 m) of *T. latifolia* and *E. vaginatum* to a mean of 1.062 in bare ditch cutover peat (0.8 m) (Table 4.2). Cutover peat samples generally grouped above 1.06, with the exception of *E. vaginatum* (Figure 4.5). *Sphagnum* cutover peat showed a relatively large range in α , but, amongst only three samples. Root zone samples (0.2 m) generally grouped below 1.05, although this was the case only later in the season in bare ditch areas (Figure 4.5).

4.5 Discussion

4.5.1 Surface carbon exchange

Methane emissions measured at a post-extraction peatland restored 16 years prior reveal that *Sphagnum*-dominated areas were a net zero source of CH_4 over the warm season. This is a significant finding as approximately two thirds of the restored peatland was pure *Sphagnum* or *Sphagnum* with Ericaceous shrubs (*Chamaedaphne calyculata*, *Rhododendron groenlandicum*, etc.) (Nugent et al., 2018). Comparatively, *Sphagnum* plots in the reference peatland surrounding the restored site emitted CH_4 at rates similar to other dry *Sphagnum* peatlands (Lai et al., 2014; Moore et al., 2011; Strack et al., 2004; 2006). *E. vaginatum* tussocks, which occupied roughly a third of the restored site, emitted CH_4 at a rate ($73 \text{ nmol m}^{-2} \text{ s}^{-1}$ during mid-season) that was within

the range of *Eriophorum* emissions in undisturbed peatlands (20-433 nmol m⁻² s⁻¹) (Green and Baird, 2011; Greenup et al., 2000; Lai et al., 2014; Moore et al., 2011; Öquist and Svensson, 2002; Ström and Christensen, 2007; Ström et al., 2005; Waddington et al., 1996), as well as the range reported in restored peatlands (6-142 nmol m⁻² s⁻¹) (Cooper et al., 2014; Komulainen et al., 1998; Marinier et al., 2004; Tutuila et al., 2000; Wilson et al., 2009; 2016). Diffusive CH₄ flux from the former ditches, which occupy 4% of the restored site, was high in non-vegetated areas when the water table was at or above the surface. Ebullition was a regular pathway until the water table fell below the surface of the former ditches. The mean magnitude of CH₄ released during bubble events was similar to events at a temperate poor fen (Goodrich et al., 2011). Although no attempt was made to calculate the daily ebullition rate, as our temporal resolution was too coarse, nonetheless ebullition was estimated to account for 9% of total emissions from the former ditches. Plant-mediated CH₄ emission from *T. latifolia*, which densely occupied two of seven inner ditches in the restored section (Figure 4.1), was similar to rates measured at a temperate freshwater *Typha angustifolia*-dominated marsh (Strachan et al., 2015). At our site, *T. latifolia* attenuated former ditch emissions when the water table was above the surface but was a continual source even once the water table dropped below the surface and diffusive fluxes in the bare sections were significantly reduced by oxidation. The former ditches were a CH₄ emission hotspot within the site as was expected owing to the preferential water holding, a pattern also seen at other restored or rewetted peatlands (e.g. Cooper et al., 2014; Vanselow-Algan et al., 2015; Wilson et al., 2013, 2016).

Our flux measurements from the restored peat fields can be compared in more detail to those of the Mer Bleue peatland, which is located within the same climate zone as our study site and has similar water storage (Nugent et al., 2018). At Mer Bleue, *Sphagnum* with *Chamaedaphne calyculata* emitted CH₄ at a rate of 36–72 nmol m⁻² s⁻¹ during mid-summer even as the water table approached 0.5–0.6 m below the surface (Moore et al., 2011). Mid-summer peak *E. vaginatum* emission at Mer Bleue was 145–433 nmol m⁻² s⁻¹, whereas only two of six *E. vaginatum* collars at our restored site had fluxes above 100 nmol m⁻² s⁻¹ (data not shown). Thus, there appear to be factors reducing surface emission of CH₄ across the restored peat fields, although clearly more so in *Sphagnum*-dominated areas. A further point to consider is that *E. vaginatum* is a pioneer species in post-extraction peatlands that is expected to disappear as *Sphagnum* growth progresses (Lavoie

et al., 2005; Poulin et al., 2013). Consequently, CH₄ emission from the restored fields could decrease further with *E. vaginatum* decline.

Measurements of NEE reveal that the restored peat field vegetation was sequestering CO₂ at a higher rate than the reference peatland in the early and late season. NEE at the restored site had an additional boost mid-season from the highly productive *T. latifolia*. Despite their low extent, the impact of *T. latifolia* at the site scale cannot be discounted as mid-season GPP modelled from eddy covariance NEE was about 5 μmol m⁻² s⁻¹ higher than our chamber-derived GPP in the restored peat fields alone (Table 4.1). Ecosystem NEE and GPP were higher during the early and late season as well, but this is likely an artifact of the low measurement resolution of our study. For instance, late season sampling did not include a date in September, so mean NEE would be biased toward the cooler temperatures and lower light levels of October and November. The fraction of ditch that was within the eddy covariance tower footprint was on average 3% over three years of measurements, as such the ditches were minimally under sampled at the ecosystem level (4% areal cover; Nugent et al., 2018). NEE measurements in the restored peat fields do not differ from fluxes at undisturbed peatlands (e.g. Joabsson and Christensen, 2001; Ström and Christensen, 2007), indicating that restoration has effectively returned the C sink function.

4.5.2 Belowground carbon cycling

Pore water measurements indicate that areas of restored peatland *Sphagnum* had the lowest concentration of dCH₄, DIC and DOC at the peatland complex. *E. vaginatum* in the restored peat fields also exhibited lower dCH₄ and DIC relative to concentrations in the former ditches. dCH₄ concentration beneath the restored peatland *E. vaginatum* was substantially lower than that of natural *E. vaginatum*-dominated areas at a palsa peatland in Sweden (Ström and Christensen, 2007) and at Mer Bleue (Beer and Blodau, 2007). On the other hand, dCH₄ beneath *E. vaginatum* in this study exceeded concentrations at a nearby spontaneously recolonized post-extraction peatland (Mahmood and Strack, 2011) and early-restoration values at our own site (1–3 years post-restoration; Waddington and Day, 2007). This suggests a progressive shift in CH₄ pool accumulation over time post-restoration moving towards, although still distinct from, undisturbed peatland conditions. Our restored peat field flux measurements demonstrate that CH₄ precursors (acetate, H₂ and CO₂) were present in great enough concentration to maintain CH₄ production below *E. vaginatum*. However, a zero release of CH₄ early in the season suggests that time was needed to accumulate the CH₄ pool. Comparatively, the reference peatland had relatively high

early season pore water CH₄ concentration and net emission. The winter preceding the study period had abnormally warm conditions, causing only the top 0.10 m of the restored peatland to freeze (Nugent et al., 2018). Comparative measurements at the reference peatland are lacking, but, are unlikely to drastically differ given the proximity of their locations. This suggests that winter and/or early spring CH₄ production was higher at the reference portion of the study site.

The reference peatland *Sphagnum* plots exhibited a seasonal increase in DOC in the deeper peat layer commonly seen at undisturbed peatlands (e.g. Blodau et al., 2007; Waddington and Roulet, 1997). In contrast, neither the restored peat fields nor former ditches showed significant seasonal DOC accumulation (Figure 4.3c). Radiocarbon evidence has shown dissolved organic matter (DOM) up to 3 m depth to be younger than the surrounding bulk peat (Chanton et al., 2008), indicating the importance of vertical carbon movement in peatlands. Our restored peat field mean DOC concentration was similar to measurements done four years prior (~ 5.8 mM), during which DOC chemistry was determined to be less labile than at the reference peatland (Strack et al., 2015). The not fully recovered DOC chemistry was attributed to a hydrological disconnect between the cutover peat and new *Sphagnum* growth, caused by the high bulk density of the cutover peat (McCarter and Price, 2013; Strack et al., 2015). In *Sphagnum* peatlands, CO₂ and CH₄ is generally derived from a combination of DOM and bulk peat decomposition whereas labile DOM appears to be the main methanogenesis substrate in sedge-dominated peatlands (Chanton et al., 2008). The greater reliance on bulk peat may be one of several reasons why *Sphagnum* peatlands typically produce low amounts of CH₄ compared to sedge-dominated peatlands (Bridgman et al., 2013). At the restored peatland, the limited contact in the restored peat fields between cutover peat pore water and new litter appeared to be a factor reducing labile DOM input to deeper peat. This would in turn reduce priming effects of the DOM on the recalcitrant peat (Basiliko et al., 2012).

In general, dCH₄, DIC and DOC concentrations were higher in the former ditches compared to the reference peatland, with the exception of deeper peat DOC. This shows an active turnover of C in the former ditches. Bare ditch area accumulated the highest dCH₄ concentrations, equal at both sampling depths, and did not exhibit the seasonal drawdown seen beneath *T. latifolia* (Figure 4.3a). The seasonal pattern in the *T. latifolia* plots illustrates that net CH₄ removal (rhizospheric oxidation and plant-mediated transport) exceeded production during the mid-season months.

Acetate was present in the restored peat fields at a significantly higher concentration ($\sim 30 \mu\text{M}$) than in the former ditches ($\sim 8 \mu\text{M}$), but was at the low end of the range found at undisturbed *Sphagnum* and sedge-dominated peatlands ($5 \mu\text{M}$ to $>1000 \mu\text{M}$) (Avery et al., 1999; Blodau et al., 2007; Ström et al., 2003; 2012; 2015). Concentrations derived from the restored area *E. vaginatum* root exudates remained about $9 \mu\text{M}$ over the summer which, while a low concentration, was occurring over approximately one third of the site. Comparatively, acetate concentration in the pore water of Mer Bleue ranged from 10 to $50 \mu\text{M}$ (Blodau et al., 2007), with lowest acetate levels coinciding with the timing of peak CH_4 emissions from plant communities (Lai et al., 2014; Moore et al., 2011). Notes that methods used in this study and in Blodau *et al.* (2007) do differ, making the result not directly comparable. *T. latifolia* root exudation at the restored site peaked mid-season even as acetate and CH_4 concentration was declining in the pore water toward a minimum at the end of August. In contrast, acetate levels in bare ditch areas did not vary significantly over the season. It seems likely that *T. latifolia* were the primary source of labile C substrate for acetoclastic methanogenesis occurring throughout the former ditches.

4.5.3 CH_4 production pathways and oxidation

A $\delta^{13}\text{C}$ -DIC value that is closer to the isotopic signature of organic matter ($\sim -26\text{‰}$) in conjunction with ^{13}C - CH_4 enrichment is evidence that CH_4 oxidation was occurring in the restored peat fields at 0.2 m depth (Singleton et al., 2018). Stable isotope values in the cutover peat (0.8 m) additionally reveal that acetate fermentation was the dominant methanogenesis pathway, although data are confined to mid-June only. *E. vaginatum* roots at the restored site reached a mean depth of 0.24 m, with no roots extending beyond 0.3 m (data not shown). As the maximum depth reached by the water table was ~ 0.5 m, 0.8 m depth sampling presumably should have been unaffected by vascular plant rhizospheric inputs and oxidation. It is suspect then that none of the $\delta^{13}\text{C}$ samples from the restored peatland showed H_2/CO_2 reduction dominating ($\alpha > 1.065$). Comparatively, $\delta^{13}\text{C}$ data of DIC and CH_4 at Mer Bleue ($\alpha > 1.069$) suggested that acetate fermentation was of less importance and that H_2/CO_2 reduction dominated from 0.35 m depth up to a sampling maximum of 3.7 m (Beer and Blodau, 2007). The stable isotopic signature does not define the relative importance of methanogenesis in terms of total respiration, merely the relative importance of the two CH_4 production pathways (Hines et al., 2008). The reduced importance of H_2/CO_2 reduction at depth in the restored peat fields may be a sign of the insignificance of methanogenesis rather than the dominance of acetate fermentation. A lack of CH_4 concentration build-up in the restored

field cutover peat points toward production limitations in the recalcitrant peat. Lower DOM compared to the reference peatland suggests that bulk peat C turnover was slower, thus not supporting CH₄ production. Substrate supply for CH₄ production instead was likely from *E. vaginatum* growth, with methanogenesis occurring close to the roots and CH₄ being rapidly consumed or transported to the atmosphere via plant tissues.

It is possible that the importance of oxidation in this system is more than we hypothesize. In a thawing permafrost peatland, the most oxidized CH₄ and highest methanotroph abundances were found to occur in peat that was inundated >90% of the time (Singleton et al., 2018). The same study found that CH₄ concentration, which increased with depth, was the key driver of methanotroph community patterns within the bog section (Singleton et al., 2018). We would argue that the very low concentrations found within the saturated peat profile of the restored fields would not be a hospitable location for methanotrophs, lending toward the interpretation that production is the limiting factor within the cutover peat.

The relatively enriched $\delta^{13}\text{C}$ -DIC signature in the former ditches throughout the season, on the other hand, conclusively demonstrates methanogen activity (Corbett et al., 2013). *T. latifolia* root zone samples were the most enriched in $\delta^{13}\text{C}$ -CH₄ ($-54.1 \pm 0.4\text{‰}$), while $\delta^{13}\text{C}$ α values were ~ 1.045 , illustrating more acetoclastic production or consumption by oxidation. Here, the higher surface flux measurements suggest production better explains the isotopic results. Although H₂/CO₂ reduction did not dominate at 0.8 m depth, an α of 1.055 to 1.065 shows that recalcitrant peat in the former ditches was supporting CH₄ production, contrary to the restored peat fields.

4.6 Conclusion

Our study has shown that bulk peat carbon turnover is low at a post-extraction restored *Sphagnum* peatland. Because the saturated zone contributes relatively little to ecosystem respiration (Blodau et al., 2007), a successful ecological restoration has resulted in net CO₂ uptake at rates similar to undisturbed *Sphagnum* peatlands (Nugent et al., 2018). Net CH₄ production and emission in the restored peat fields, however, was reduced and appeared to occur only with *E. vaginatum* substrate input and plant-mediated transport. The lack of a hydrogenotrophic methanogenesis signature in the restored peat fields indicates decomposition of the recalcitrant cutover peat was limited. The much higher C turnover and CH₄ emission seen in the former drainage ditches appeared to be related to *T. latifolia* labile C inputs, evidenced by a strong acetoclastic methanogenesis signature in the *T. latifolia* rhizosphere. A mixed methanogenesis

signature deeper in the former ditch profile is evidence that older organic matter decomposition was occurring within the ditch confines. This study shows that, 16 years after restoration, approximately two thirds of the restored peatland (restored peat field areas with little *E. vaginatum* cover) remained a minimal source of CH₄. Greater hydrological connectivity between the *Sphagnum* layer and underlying cutover peat is expected as new peat continues to develop. On this basis, carbon turnover of the new peat, with potential DOM priming of the bulk peat, over time would limit the impacts of the cutover peat on the surface flux. The legacy of cutover peat in reducing CH₄ production and emission could last for a period (decades) beyond the successful return of a carbon sink, aiding in reducing the climate warming impact of newly restored extracted peatlands.

CHAPTER 5

PROMPT ACTIVE RESTORATION OF PEATLANDS SUBSTANTIALLY REDUCES CLIMATE IMPACT

Bridging statement to Chapter 5

Peatland restoration may be an effective climate change mitigation strategy. However, the success of peatland restoration for long-term C management through its impact on the radiative forcing of climate has not been yet been accurately investigated. To address this research gap, in the present chapter I use the case study of the Canadian horticultural peat moss industry to quantify the net climate impact of restoring peatlands, accounting for the time spent in an unrestored state. I use a space-for-time substitution from an eddy covariance tower series of undisturbed, unrestored, and restored post-extraction peatlands to drive an impulse-response model of radiative forcing. In this study, I demonstrate that prompt restoration is equally important to the restoration approach used in reducing the climate impact of extracted peatlands. The results of this study show that using best practices in peatland restoration can enable it to be a climate change mitigation tool.

5.1 Abstract

Restoration of peatlands after peat extraction could be a benefit to the climate system. However, a multi-year ecosystem-scale assessment of net carbon (C) sequestration is needed. We investigate the climate impact of active peatland restoration (rewetting and revegetation) using a chronosequence of C gas exchange measurements across post-extraction Canadian peatlands. An atmospheric perturbation model computed the instantaneous change in radiative forcing of CO₂ and CH₄ emissions/uptake over 500 years. We found that using emission factors specific to an active restoration technique resulted in a radiative forcing reduction of 89% within 20 years compared to IPCC Tier 1 emission factors based on a wide range of rewetting activities. Immediate active restoration achieved a neutral climate impact (excluding C losses in the removed peat) about 155 years earlier than did a 20-year delay in restoration. A management plan that includes prompt active restoration is key to utilizing peatland restoration as a climate change mitigation strategy.

5.2 Introduction

Peatlands play an important role in the global carbon (C) cycle. While their annual uptake of C is relatively small compared to many other ecosystems, the persistent uptake and maintenance

of the large store of sequestered atmospheric carbon dioxide (CO₂) in peatlands has led to net climate cooling due to their long-term negative radiative greenhouse gas (GHG) forcing (Frolking and Roulet, 2007; Frolking et al., 2006). Radiative forcing of a peatland is the difference between the atmospheric CO₂ sequestered since peatland formation (millennia) and recent perturbations (decades) to methane (CH₄) fluxes (Frolking et al., 2006). Northern peatlands are estimated to contain ~500 Gt C (Scharlemann et al., 2014; Yu et al., 2010) which is approximately 58% of the amount contained in the atmosphere (402.8 ± 0.1 ppm CO₂ in 2016 ~862 Gt C) (Dlugokencky and Tans, 2017). However, more than 50% of the global wetland area, including peatlands, has been lost since 1700 CE because of land use change (Davidson, 2014). Roughly 10% of remaining global peatlands are degraded by land use changes (such as peat extraction, agriculture, grazing and forestry) representing a carbon stock of 80.8 Gt C that is being diminished at a rate of ~1.91 Gt C annually (Leifeld and Menichetti, 2018). Degradation results in mineralization of stored peat, releasing large amounts of CO₂, but generally reducing CH₄ to minimal levels except from drainage ditches, which can act as hotspots for CH₄ emissions (Wilson et al., 2016).

Soil C sequestration and avoided GHG emissions through restoration of degraded peatlands are climate change mitigation strategies shown to be more cost effective in terms of nitrogen addition required and land area demand than rehabilitating agricultural land (Leifeld and Menichetti, 2018). However, the success of peatland restoration for long-term C management through its impact on radiative forcing is not well known. A few studies have examined the GHG fluxes from restored peatlands using periodic (non-continuous) chamber measurements (e.g. Renou-Wilson et al., 2019; Strack and Zuback, 2013; Swenson et al., 2019; Wilson et al., 2016) but the spatial and temporal extrapolation required to achieve an annual balance introduces errors (Bubier et al., 1999), limiting its utility to investigate climate impacts.

A full accounting of GHG emissions from the drainage and rewetting of organic soils (i.e. peatlands) is required in national GHG inventory reports to the UNFCCC (IPCC, 2014). The IPCC methodology uses a tiered approach for emission accounting based on the scale and quality of available data. The simplest reporting method, Tier 1, applies default values for emission/removal factors multiplied by the areas of land-use change affected by specified activities to estimate emissions for the project or sector of interest. For managed wetlands, the default emission factors provided are often averages from chamber GHG flux measurements gathered for an eco-region (e.g. boreal, temperate and tropical). The Tier 2 approach is similar conceptually to Tier 1, but

substitutes emission factors from country-specific emissions, usually obtained through scale-appropriate empirical measurements. Tier 3 is the most detailed approach and involves the simulation of land-use change impacts based on models of the underlying processes controlling emissions.

With Tier 1, the IPCC uses a global warming potential (GWP) metric approach to compare the relative climate impact of GHGs with different atmospheric lifetimes and radiative efficiencies. Emissions/removals of different GHGs are converted to an equivalency in metric tonnes of CO₂ (CO₂-eq). The sign of the CO₂-eq determines whether the perturbation to the system in question (e.g. ecosystem, sector) has a net warming or cooling effect on global climate. A major shortcoming of the GWP is that it treats emissions as single pulses rather than continuous and evolving emissions or removals through biosphere-atmosphere interactions (Neubauer and Megonigal, 2015). As well, the time integration for GWPs is arbitrary and does not recognize the time integration of a continuous gas exchange; a 100-year integration horizon was adopted by the Kyoto Protocol and continues to be in effect (Lashof, 2000). Less common, but more informative, is the approach of directly modeling the atmospheric dynamics of GHGs (Dommain et al., 2018; Frohling and Roulet, 2007; Frohling et al., 2006; Helbig et al., 2017; Lohila et al., 2010; Neubauer, 2014; Neubauer and Megonigal, 2015), which uses time integrations more appropriate for continuous ecosystem exchanges. An atmospheric perturbation model driven by continuous measurements of net GHG fluxes can account for the temporally variable rates of GHG exchange found in ecosystems (Neubauer and Megonigal, 2015).

We use the case study of the Canadian horticultural peat moss industry to quantify the net climate impact of restoring peatlands. Approximately 34,000 ha of Canadian peatlands are, or have been, drained for peat extraction, of which 18,000 ha are under active management (ECCC, 2018). Land-use regulations vary in detail and extent by province but there is now a need to demonstrate commitment to restoration before new sites can be opened (Rochefort et al., 2003). Restoration planning that meets the conditions for responsible horticultural peat moss production certification is increasingly an industry and consumer expectation. The IPCC definition of restoration is a process of assisting the recovery of an ecosystem that has been degraded which, in the case of drained peatlands, always has to include rewetting (IPCC, 2014). The Canadian horticultural peat moss industry employs an active restoration strategy that incorporates the moss layer transfer technique (Graf and Rochefort, 2016) in addition to rewetting. A multi-year continuous

measurement study of ecosystem-scale active restoration of a post-extraction peatland showed annual net CO₂ sequestration within 14 years (Nugent et al., 2018). To quantify the efficiency of peatland restoration actions, however, the time spent in an unrestored state needs to be accounted for. Here, we used a space-for-time substitution from an eddy covariance tower series at an undisturbed, 2 unrestored, and 2 restored post-extraction peatlands in Canada with an atmospheric perturbation model to evaluate the net (CO₂ + CH₄) radiative forcing of restoration actions. Our Tier 2 level results are compared with the net radiative forcing of average rewetting actions provided by IPCC Tier 1 emission factors, and also with not restoring post-extraction peatlands. We hypothesize that active restoration (Tier 2) will achieve a neutral climate impact more quickly than average rewetting actions (Tier 1), and that not restoring will cause an increasing positive radiative forcing over a 500-year timeframe.

5.3 Methods

5.3.1 Data sources

This study is based on net ecosystem flux measurements of CO₂ (NEE), CH₄ and dissolved organic carbon (DOC) from horticulture-extracted peatlands. The study sites were part of a paired unrestored/restored eddy covariance tower project in eastern (Québec) and western (Alberta) Canada that took place between July 2013 and November 2016 (Nugent et al., 2018; Rankin et al., 2018). The active restoration approach, known as the moss layer transfer technique, applied at the study sites incorporates site re-grading, rewetting (ditch blocking and/or infilling), revegetating with material from donor peatlands, protection with straw mulch, and phosphate fertilization where required (see Graf and Rochefort, 2016 for more details). The eastern restored site, Bois-des-Bel, has undergone periodic flux monitoring since being restored in the autumn of 1999 (e.g. Nugent et al., 2018; Petrone et al., 2003; Strack and Zuback, 2013; Waddington and Day, 2007; Waddington et al., 2003; 2008; 2010). The well-studied Mer Bleue bog (1998 to present eddy covariance record; Roulet et al., 2007) located near Ottawa, ON, Canada was used as a representative undisturbed peatland. Mer Bleue is currently the best record to use as the endpoint of the restoration trajectory, as its long-term record captures the wide range in variability when estimating a mean flux. Greenhouse gas flux monitoring occurred continuously over the growing season/year at the eastern and western Canadian paired unrestored/restored sites and undisturbed peatland, and a standard data post-processing methodology was used (Nugent et al., 2018). Main site characteristics of the study sites are presented in Appendix II Table II.1, site-specific

measurement techniques and instrumentation in Table II.2, site-specific gap-filling methods for CO₂ and CH₄ in Table II.3 and annual CO₂, CH₄ and DOC fluxes (mean ± 95%CI) in g C m⁻² yr⁻¹ in Table II.4. The 95% confidence interval of gap-filling was calculated based on error in determining the friction velocity threshold (Papale et al., 2006), as well as a random measurement error estimate (Richardson et al., 2006). A recent study comparing restored site fluxes of CO₂ and CH₄ at the plot-scale determined no significant difference between eastern and western Canada (Strack et al., 2016). As such, we compiled the data listed in Table II.4 into an unrestored and restored chronosequence that reflects the management history of Bois-des-Bel; that is, extraction over a ten-year period followed by 20 years without management (unrestored period) prior to restoration. We chose to not incorporate nitrous oxide (N₂O) fluxes into our GHG chronosequence because we had insufficient data from our study sites to make a defensible estimate of annual exchange (but see Appendix II.3). Chamber fluxes at the restored Bois-des-Bel site determined an N₂O flux that was most often not distinguishable from zero (data not shown), similar to the western Canada unrestored and restored sites (Brummell et al., 2017). A study of Estonian peatlands undergoing extraction found negative N₂O fluxes at their undisturbed reference sites (Salm et al., 2012). It seems likely that N₂O fluxes are a minor component of the total GHG balance when compared to the much larger CO₂ and CH₄ fluxes. For comparison, IPCC Tier 1 assumes a minimal N₂O flux when drained (0.03 g N m⁻² yr⁻¹) and a minimal flux after rewetting (IPCC, 2014).

5.3.2 Modelling radiative forcing

Radiative forcing was computed with an atmospheric perturbation model originally presented in Frohking et al. (2006). The model has been updated with revised radiative efficiencies, atmospheric lifetime numbers, and indirect radiative forcing effects in accordance with the latest IPCC synthesis report (Myhre et al., 2013). As well, the CO₂ portion of the model uses impulse response parameters from Joos et al. (2013) instead of an earlier parameterization. Sustained CO₂ and CH₄ fluxes estimated from the chronosequence of measured exchanges are treated as perturbations to a series of linear non-interacting, first-order atmospheric reservoirs (see Figure 1 in Dommain et al. 2018 for general structure of the model). The net (CO₂ + CH₄) radiative forcing (RF_{net}) was calculated as the sum of the individual gas contributions:

$$RF_{net}(t) = \sum_{i=0}^5 (\xi_i A_i f_i \cdot \int_0^t \Phi_i(t') e^{(t'-t)/\tau_i} dt'), \quad (5.1)$$

where ξ_i is a multiplier for indirect effects, A_i is the radiative efficiency of greenhouse gas i , f_i is the fractional multiplier for the net flux into reservoir i , $\Phi_i(t')$ is the net flux of a greenhouse gas i into the atmosphere at time t' , and τ_i is the adjustment or residence time of the reservoir i ; for model parameter values, see Table 3 in Dommain *et al.* (2018).

The atmospheric perturbation estimates were based on the chronosequence of CO₂, CH₄ and DOC fluxes detailed in Table 5.1; i.e. replacing the IPCC Tier 1 default values with the observed exchanges. The proportion of DOC exported that is ultimately emitted as CO₂ was chosen to be 0.9 ± 0.1 , the value proposed by the IPCC for calculating Tier 1 default annual emissions of CO₂ due to DOC export (IPCC, 2014). In a review of the fate of waterborne carbon from drained and rewetted peatlands, Evans *et al.* (2016) concluded that current observations support a value of 0.9 ± 0.1 . Applying this number ignores, however, that DOC breakdown can occur over a long temporal continuum along the river-lake-estuary-ocean system (Evans *et al.*, 2016). The CO₂ input into the model (CO_{2_tot}) is thus calculated as:

$$CO_{2_tot} = CO_2 + 0.9 \cdot DOC. \quad (5.2)$$

The CH₄ input into the model is calculated as:

$$CH_{4_tot} = 0.95 \cdot CH_4 + 0.05 \cdot CH_4\text{-Ditch}. \quad (5.3)$$

However, because the CH₄ emissions from drainage ditches at our study sites are already included in the annual CH₄ flux measured with eddy covariance, the ditch term in equation (5.3) is set to zero and the CH₄ input into the model is the measured value.

Table 5.1 – Canadian post-extraction peatland C fluxes compared to IPCC Tier 1 emission factors. Our study results are a space-for-time (chronosequence) collation of empirical measurements. IPCC Tier 1 emission factors are for drained peatlands managed for extraction and rewetted organic soils. Negative values are removal by the ecosystem while positive values are emission to the atmosphere.

		IPCC Tier 1 emission factor		Our study	
		Climate/ vegetation zone	Mean (95% CI) (g C m ⁻² yr ⁻¹)	Chrono- sequence	Mean (95% CI) (g C m ⁻² yr ⁻¹)
Drained/ Unrestored	CO ₂	Boreal and Temperate	280 (110-420)	UNR-1yr	445 (426-460)
				UNR- 15yr	216 (132-300)
	DOC	Temperate	31 (19-46)	UNR	35 (26-45)
	CH ₄	Boreal and Temperate	0.5 (0.1-0.8)	UNR	0.5 (0.3-0.7) ^b
	CH ₄ - Ditch	Boreal and Temperate	40.6 (7.6-73.5) ^a		n/a
Rewetted/R estored	CO ₂	Temperate Poor	-23 (-64-+18)	RES-1yr	504 (291-717)
				RES-4yr	145 (-12-302)
				RES-15yr	-90 (-110-69)
				RES-30yr	-73 (-136--9)
	DOC	Temperate	24 (14-36)	RES-15yr	8 (6-10)
				RES-30yr	17 (14-20)
	CH ₄	Temperate Poor	9.2 (0.3-44.5) ^c	RES-1yr	1.1 (0.5-1.7)
				RES-4yr	4.3 (0.7-7.9)
RES-15yr				4.4 (4.2-4.5)	
RES-30yr				6.0 (2.0-10.0)	

^a Site-level fractional cover of ditch is estimated to be 0.05 based on the mean of six studies in the land-use category reporting CH₄ emissions

^b CH₄ emissions from drainage ditches are included

^c CH₄ emissions from former ditches are not treated separately after rewetting

Table 5.2 outlines the Tier 2 scenarios run following model spin up (S2). For the unrestored and post-restoration periods, the 95% confidence range of the fluxes in Table 5.1, the confidence interval on the fraction of DOC converted to CO₂ (0.9 ± 0.1), and the standard error on the indirect

effects multiplier for CH₄ (1.65 ± 0.3) were used to establish an uncertainty bound. This includes sustained maximum (minimum) CO₂ removal and minimum (maximum) CH₄ emission to the atmosphere.

Table 5.2 – Atmospheric perturbation model scenario inputs. Scenario descriptions reference Table 5.1.

Tier	Scenario	Description
Tier 1	Average rewetting	Drained emission factors over 20 years Rewetted emission factors over 480 years
	Immediate average rewetting	Rewetted emission factors over 500 years
	No rewetting	Drained emission factors over 500 years
Tier 2	Active restoration	Unrestored chronosequence over 20 years Restored chronosequence over 480 years
	Immediate active restoration	Restored chronosequence over 500 years
	No restoration	Unrestored chronosequence over 500 years

The modified version of the model that does not include pre-extraction was used to run the IPCC emission factors detailed in Table 5.1 as time-invariant fluxes. Emission factors, taken from the IPCC 2013 Supplement to the 2006 Guidelines for National Greenhouse Gas Inventories: Wetlands (IPCC, 2014), were available for the categories: (1) Drained Organic Soils: Peat Extraction, and (2) Rewetted Organic Soils as an average with a 95% confidence interval. Emission factor units were standardized to $\text{g C m}^{-2} \text{ yr}^{-1}$ to facilitate inter-comparison in Table 5.1. The Tier 1 scenarios that were simulated with the modified model and uncertainty bounds computed using the same method as Tier 2 are presented in Table 5.2.

The model output, RF_{net} , is an annual time series of the radiative forcing due to cumulative GHG emissions or removals from an initial year. Following Frohling *et al.* (2006), the time that RF_{net} changes from positive (net warming) to negative (net cooling) is referred to as the radiative forcing switchover time. For this study, we discuss the instantaneous switchover time relative to radiative forcing in 1980 rather than the cumulative radiative forcing switchover time, which reflects GHG dynamics integrated over the history of the peatland (Neubauer, 2014).

5.4 Results

5.4.1 Chronosequence establishment

Our measurements in unrestored post-extraction peatlands show that not restoring after extraction leads to large CO₂ release to the atmosphere, both initially (UNR-1yr) and more than a

decade later (UNR-15yr; Figure 5.1). CO₂ emissions were lower at the older unrestored site due to some spontaneous plant regeneration in the drainage ditches and wetter areas of the site (Rankin et al., 2018). However, the lowest annual CO₂ emission from the older unrestored site is more than twice as much as the average uptake at our reference undisturbed peatland, Mer Bleue (REF) (Figure 5.1).

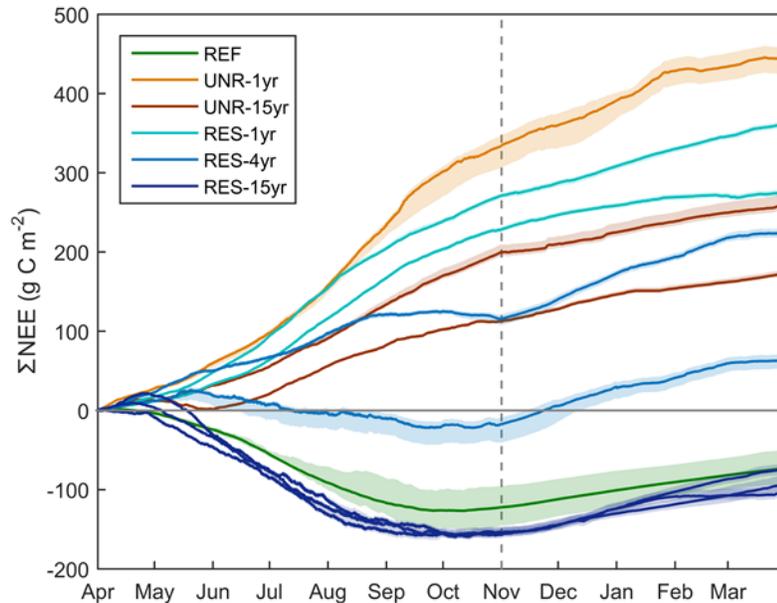


Figure 5.1 – Ten site years of annual cumulative net CO₂ flux (NEE) at Canadian post-extraction peatlands. NEE at unrestored (UNR) and actively restored (RES) peatlands are compared to a reference (REF) peatland, Mer Bleue. Displayed are the first year of UNR-1yr, two consecutive years of UNR-15yr, two consecutive years of RES-1yr, two years of RES-4yr measured at adjacent sites in the same year, three consecutive years of RES-15yr and the mean and standard deviation of 16 years of data at REF. Negative values represent cumulative net CO₂ removal from the atmosphere while positive fluxes are cumulative net CO₂ addition to the atmosphere. The shading on each line is the 95% confidence bound around the mean value. Note that the graph begins on April 1st to more easily display and compare the snow-free season (April–November).

At the newly actively restored site (RES-1yr), CO₂ emission rates were initially similar to that of the unrestored sites (Figure 5.1). Higher emissions during the first few years after active restoration have been linked to decomposition of the straw mulch layer, applied to maintain high humidity for the donor moss propagules (Waddington et al., 2003). By the fourth year (RES-4yr), declining

straw decomposition losses and productivity by the re-emerging vegetation layer had reduced the amount of CO₂ emitted annually (Figure 5.1). The importance of restoring a shallow water table to the amount of CO₂ emitted annually is seen by the difference between the two RES-4yr lines (Figure 5.1). A spatial gradient of restoration success was seen across the ~30 ha restored site, which was linked to a shallower water table (mean of 0.3 m vs. 0.6 m) advancing revegetation and thus productivity in some sections relative to others (data not shown). At the older restored site (RES-15yr), CO₂ uptake similar to that of REF was observed after 14 years (Nugent et al., 2018; Figure 5.1). The CO₂ sink was linked to a sufficiently shallow water table, attributed to effective water retention by berms put in place during the restoration process (Nugent et al., 2018).

The impact of after-use management of extracted peatlands on CH₄ emissions is primarily a function of the depth of the water table following rewetting. With a water table always below the surface, the unrestored sites released < 1 g CH₄-C m⁻² yr⁻¹ (Table II.4); as such, a single value is given for the unrestored state in Table 5.1. Very low CH₄ emissions were also observed during the initial years after restoration, before increasing in the third and fourth years to emissions similar to a decade and a half after restoration (Table II.4).

Net carbon loss from the peatland via DOC was greater at the unrestored sites and decreased substantially following restoration, to levels below that of REF (Table II.4) (Nugent et al., 2018). We found no statistical differences (Student's *t*-test, *p*>0.05) in net DOC export among the unrestored site ages as well as among the restored site ages (Table II.4) and, as such, a single value is given for the unrestored and restored states in Table 5.1.

5.4.2 Comparison with IPCC Tier 1 emission factors

The unrestored chronosequence fluxes are broadly similar to the IPCC Tier 1 emission factors (EFs) for a drained temperate peatland (Table 5.1). CO₂ emitted both on- and off-site are similar, although fixed IPCC Tier 1 values do not account for temporal trends in the GHG fluxes. Combining the IPCC Tier 1 CH₄ EFs using a ditch fractional cover of 0.05, representative of ditch density in Canadian extracted peatlands, results in a site-level mean of 2.5 g CH₄-C m⁻² yr⁻¹, five times greater than the chronosequence value (0.5 g CH₄-C m⁻² yr⁻¹) (Table 5.1). This outcome becomes important when accumulated in the atmosphere over several years (see Appendix II.4).

The CO₂ chronosequence captures the time needed after restoration to achieve a CO₂ sink, a period not explicitly included in the IPCC Tier 1 CO₂ EF (Table 5.1). A transition period, as well as a temporarily larger CO₂ sink, after restoration is discussed by the IPCC, but, insufficient

evidence was available to support the use of different default EFs; however, a transition period after restoration was highlighted as a primary reason to move toward Tier 2 methodology (IPCC, 2014). Because of limited scientific literature, long-term studies in undisturbed peatlands were combined with observations at rewetted sites to calculate the default CO₂ EF (IPCC, 2014). Notably, the CO₂ sink, once achieved in the chronosequence, is substantially larger than the IPCC Tier 1 value, while our restored DOC loss is less (Table 5.1). Discharge was greatly reduced at the main study site (RES-15yr in Figure 5.1) by ditch blocking and the creation of berms, which allowed the water table to rise significantly (McCarter and Price, 2013). We hypothesize that the DOC flux will become more similar to undisturbed peatlands as water storage stabilizes with improved hydrological connectivity between the *Sphagnum* moss layer and the cutover peat.

The CH₄ chronosequence shows a gradual increase in emissions with time since restoration, while remaining at the lower end of the IPCC Tier 1 5-95% confidence range (Table 5.1). Observation sites included in the IPCC Tier 1 EF cover a range of water table positions, soil temperatures and prior land use, which can all influence the amount of CH₄ produced and emitted. Inclusion of sites that were slightly flooded during rewetting helps to explain the large confidence range (IPCC, 2014). Maintaining a water table below the surface is a necessary step to mitigate CH₄ emissions (Strack et al., 2014). Active restoration achieves this, with approximately 5 g CH₄-C m⁻² less emitted annually at the Canadian sites compared to the average rewetting results contained in the IPCC (Table 5.1).

5.4.3 Climate impact of peatland restoration

The Tier 2 active restoration scenario accumulates the atmospheric effects of fluxes during a 20-year unrestored phase and after restoration (Figure 5.2), which follows the management history of the main study site. For a short period after restoration (in 2000 CE), the net radiative forcing (RF_{net}) continues to increase, reflecting the time needed for a restored site to transition to a carbon sink (Figure 5.2b). A small increase in RF_{net} around 2030 reflects a decrease in the amount of carbon sequestered annually, back to the rate of an undisturbed peatland (REF in Table 5.1). The radiative forcing switchover time (i.e. neutral climate impact) for this active restoration scenario is approximately 180 years (~2160 CE) (Figure 5.2b). The Tier 2 immediate active restoration scenario shows a similar pattern, except that it circumvents the cumulative effects in the atmosphere of 20 years spent unrestored. Immediate active restoration achieves a radiative forcing switchover within roughly 25 years (~2005 CE) of extraction ceasing. Not restoring, on

the other hand, results in a positive radiative forcing seven times more powerful than the negative forcing achieved by active restoration after 500 years. While both Tier 2 active restoration scenarios achieve a neutral climate impact, a Tier 1 average rewetting remains a positive radiative forcing, whether restored immediately or not (Figure 5.2b). The climate cooling effect of on-site CO₂ removal from the atmosphere is virtually cancelled out by climate warming from off-site CO₂ emissions from DOC breakdown. Thus, the CH₄ perturbation, which has a relatively short effective lifetime in the atmosphere, is reflected in RF_{net} approximately leveling off after two decades (Figure 5.2b). The uncertainty range of a Tier 1 average rewetting demonstrates that a net warming effect is much more likely than a net cooling effect (Figure 5.2a). The climate warming from the Tier 1 no rewetting scenario is 12 times greater than a Tier 1 average rewetting and 1.3 times greater than the Tier 2 no restoration scenario after 500 years. Radiative forcing associated with emissions from actual peat removal during extraction is likely adding to the net climate impact. However, a complete lifecycle assessment of peat extraction actions is required to quantify these effects.

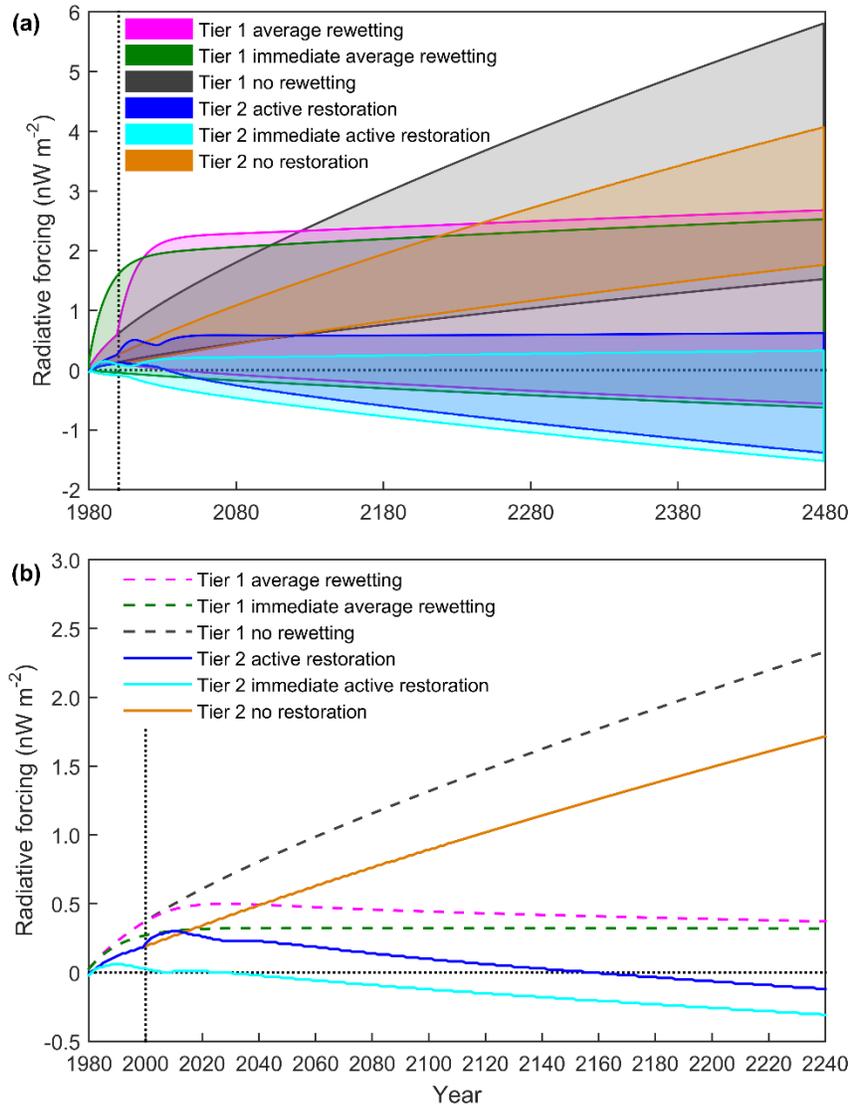


Figure 5.2 – Instantaneous net ($\text{CO}_2 + \text{CH}_4$) radiative forcing of post-extraction peatlands. Radiative forcing is nW m^{-2} per hectare of peatland, relative to extraction termination in 1980 CE. In the Tier 1 scenarios, emission factors were treated as time-invariant atmospheric perturbations, while the Tier 2 scenarios used sustained, varying atmospheric perturbations interpolated from the chronosequence (Table 5.1). Restoration occurs in 2000 CE in the Tier 1 average rewetting and Tier 2 active restoration scenarios, in 1980 CE in the immediate rewetting/restoration scenarios and does not occur in the no rewetting/restoration scenarios. The 500-year simulation confidence bounds are shown in (a) and the simulation average over the period 1980 to 2240 CE is shown in (b).

The climate benefit or cost of peatland restoration actions can be calculated by defining a reference and calculating the difference in net radiative forcing between the baseline (i.e., no

restoration action) and alternative management action. Immediate active restoration reduces the climate cost by 83% at 20 years (Table II.6). In comparison, an immediate average rewetting results in a climate cost reduction of 26% at 20 years (Table II.6). Restoring immediately using an active restoration approach rather than the average rewetting approach reduces the climate cost of the peatland by 89% at 20 years (Table II.6). The choice of 20 years is used here for illustrative purposes only; prompt restoration has the highest net benefit during the first few decades.

5.5 Discussion

Our findings reveal that not restoring post-extraction peatlands leads to decades more CO₂ emissions to the atmosphere, directly and downstream, with low CH₄ emission. Restoring a CO₂ sink can take over a decade with active restoration, but once achieved, low on-site CH₄ emissions and low off-site CO₂ losses help maximize carbon sequestration, even exceeding undisturbed peatland carbon uptake rates.

It is socially and environmentally responsible to set a post-extraction site on a trajectory to become a healthy peatland (Joosten et al., 2012). With successful restoration, the remaining carbon in the peat store is maintained and carbon sequestration sets the ecosystem on a course for eventual restoration of the lost peat – a process that may take thousands of years. Calculating the net ecosystem carbon balance by adding the carbon fluxes (CO₂ + CH₄ + DOC) reveals that an IPCC Tier 1 average rewetted peatland is a net source of 10 g C m⁻² yr⁻¹. In comparison, an actively restored peatland is a net sink of 78 g C m⁻² yr⁻¹ after 15 years, with the likelihood of this sink being reduced to a net sink of 50 g C m⁻² yr⁻¹ by 30 years as fresher litter accumulates, the decomposition of which will contribute to greater CO₂ loss. Consequently, active restoration appears to allow the horticulture peat moss industry to realize a goal of sustainable management, although it is not renewable within the timeframe of this study.

We have shown that beyond making a choice to restore, using an active restoration technique within a short time frame is important to properly utilize peatland management as a climate change mitigation strategy. Restoration offers a climate benefit when applied immediately and with intent to restore the integrity of the ecosystem (Figure 5.2). Active restoration accrues climate benefits once a site becomes an annual carbon sink, whereas IPCC Tier 1 average rewetting remains a positive radiative forcing over centuries. This case study illustrates that both timing of restoration and actions that result in favourable site conditions are important to actually achieve a sink. While this study demonstrates the radiative effects of a 20-year unrestored period, the

Canadian industry average between the end of peat extraction and restoration is now closer to three years and thus the climate impact would be more similar to the immediate active restoration scenario. Horticultural peat moss companies could improve their climate impact by limiting the period of deep drainage during extraction to reduce CO₂ emissions and by managing sites being extracted so that CH₄ emissions are as low as or lower than undisturbed peatlands. The reduction in climate impact associated with active restoration of Canadian post-extraction peatlands is small in the global context, as the radiative forcing of anthropogenic-derived CO₂ is increasing at rate of almost 0.3 W m⁻² per decade (Myhre et al., 2013). However, the extracted peatland area in Europe is large (Joosten, 2009), and other peatland disturbances (e.g. petrol industry infrastructure impacts, forestry, agriculture, grazing, erosion, roads) would also benefit from prompt active restoration in improving the chances of C sequestration recovery and reducing the climate impact. Wide-scale peatland restoration, done appropriately, can be an effective long-term climate change mitigation strategy.

CHAPTER 6

SYNTHESIS, CONCLUSIONS AND FUTURE DIRECTIONS

The global scale of peatland loss, drainage and use is worrisome as peatlands, when undisturbed, perform an essential function of removing CO₂ from the atmosphere, which has a cooling impact on the climate. A large amount of funding has recently been put toward restoring peatlands, in the hopes of returning lost ecological services, including climate regulation (Andersen et al., 2017). Of the restoration sites studied, most were less than a decade old and none were consistent annual C sinks. The timeframe needed for carbon functioning to re-establish is practical knowledge that is needed to justify and improve restoration practices. In this thesis, I have determined the timeframe and net climate impact of re-establishing a C sink at an actively restored post-extraction peatland.

6.1 Chapter syntheses

In Chapter 3, I show that a decade and a half was needed to return a stable C sink at an industrial peat extraction site in eastern Canada that was actively restored. NEE of CO₂ dominated the magnitude and inter-annual variability of the NECB, with inter-annual differences in NEE mainly driven by extremes in winter weather rather than growing season variability. This contrasted with the 17-year study period of the reference peatland, Mer Bleue, which showed large differences in NEE during August and September related to summer water table drawdown (Figure 3.6). Despite low summer water storage, Mer Bleue was a net C sink in all years, suggesting that the carbon balance – water table feedback of an undisturbed peatland creates a long-term dynamic equilibrium. This feedback does not appear to have re-established yet at the restored peatland. Instead, the current water table dynamics suggest that the relatively constrained water table at the restored peatland is due to site engineering rather than internal hydrological controls at this stage. However, it is likely that ecosystem resiliency associated with the carbon balance – water table feedback will return with the continued development of the live *Sphagnum*, detritus and peat layers.

In Chapter 3, I also address the effects of former drainage ditches, which have been found to be ‘hot spots’ for CH₄ emissions, particularly in rewetted peatlands. Using the eddy covariance technique, I show that the presence of remnant ditches does not necessarily equate to large

ecosystem CH₄ release due to their overall small proportional areal extent. A key outcome of this particular restoration has been a water table that remains below the peatland surface while being sufficiently shallow to maintain ecological functions. This study adds to other literature in showing that maintaining a water table below the surface is a necessary step if the aim of restoration is to mitigate CH₄ emissions to the atmosphere.

The ecosystem CH₄ flux was the smallest contributor to the C balance, similar in magnitude to other post-restoration studies. This was a surprising finding given that *E. vaginatum* occupied roughly a third of the restored site, with known capabilities for plant-mediated CH₄ transport. Broad comparability in the enhanced vegetation index (EVI) at the restored site and surrounding undisturbed peatland suggests that the developing vegetation was not experiencing any residual stress from the non-natural soil profile. However, the effect of cutover peat on the CH₄ flux warranted further investigation given the lower than expected annual CH₄ flux.

In Chapter 4, I reveal that the *Sphagnum*-dominated area, which covers approximately two thirds of the restored peatland, was a net zero source of CH₄. Pore water measurements indicate that the soil below *Sphagnum* had the lowest concentration of dissolved CH₄, DIC and DOC at the peatland complex, including the surrounding undisturbed peatland. Emissions from *E. vaginatum* were lower than at the undisturbed peatland, Mer Bleue, suggesting that factors might be reducing surface emission of CH₄ across the restored peat fields. In contrast, active C turnover was found in the former ditches at the restored site, along with relatively high ebullitive, diffusive and plant-mediated CH₄ release to the atmosphere. Acetate, a precursor to acetoclastic methanogenesis, was present in the restored peat fields at a significantly higher concentration than in the former ditches and was comparable to concentrations at the undisturbed peatland Mer Bleue. Restored field data limitations prevent being able to definitively say whether methanogenesis inhibition, suggested by a high acetate:CH₄ production ratio, led to the low rates of C loss as CH₄. However, a lack of CH₄ concentration build-up in the restored field cutover peat points toward production limitations in the recalcitrant peat. The lack of a hydrogenotrophic methanogenesis signature in the restored peat fields also indicates decomposition of the recalcitrant cutover peat was limited. In comparison, the much higher C turnover and CH₄ emission seen in the former ditches appeared to be related to *T. latifolia* labile C inputs, evidenced by a strong acetoclastic methanogenesis signature in the *T. latifolia* rhizosphere. A mixed methanogenesis signature deeper in the former ditch profile is evidence that older organic matter decomposition was occurring within the ditch confines. The

legacy of cutover peat in reducing CH₄ production and emission is found to have a beneficial impact by reducing the climate warming impact of the restored peatland.

In Chapter 5, I broaden my work by quantifying the radiative GHG forcing of climate impact of restoring peatlands. In the first dataset of its kind globally, I build a post-extraction space-for-time series by combining ten site-years of eddy covariance tower flux data at paired unrestored and restored post-extraction peatlands in eastern and western Canada, with the long-term record of the undisturbed peatland, Mer Bleue. My tower flux findings reveal that not restoring post-extraction peatlands leads to decades of CO₂ emissions to the atmosphere. Restoring a CO₂ sink can take over a decade with active restoration, but once achieved, low on-site CH₄ emissions and low fluvial CO₂ losses help maximize C uptake. Using an atmospheric perturbation model, I determine that not restoring a post-extraction site results in a positive radiative forcing seven times more powerful than the negative forcing achieved by active restoration after 500 years. Actively restoring a post-extraction site achieves a neutral climate impact between roughly 20 and 200 years depending on the promptness of the restoration. Model simulations using IPCC Tier 1 emission factors based on a wide range of rewetting activities, in contrast, yield a positive radiative forcing, whether restored promptly or not (Figure 5.2). Beyond making the crucial choice to restore, using an active restoration technique promptly is shown to be important to properly utilize peatland management as a climate change mitigation strategy.

6.2 Conclusions and broad context

Carbon sequestration and climate regulation are important ecosystem services provided by peatlands. Understanding GHG exchanges in managed peatlands is of critical importance in terms of climate change policy and mitigation (Joosten et al., 2012; UNEP, 2010), and is a necessity given that GHG accounting in managed peatlands is now required in national GHG inventory reports to the UNFCCC (IPCC, 2014). Due to a lack of restored peatland data, the IPCC default Tier 1 emission factors for the category ‘rewetted organic soils’ (i.e. peatlands) are based in part on data from undisturbed peatlands and are mainly comprised of scaled-up chamber data. However, a synthesis of the available literature has determined a need for long-term ecosystem-scale NECB monitoring in post-extraction peatlands, to account for the potentially large inter-annual variability experienced because of vegetation succession as well as weather variability. This thesis includes the first published study in a post-extraction peatland that, through measuring a multi-year NECB, definitively addresses the timeframe needed for the C sink function to re-

establish after restoration. When compiling the National Inventory Report, Environment and Climate Change Canada (ECCC) will be able to reference this work to calculate a Canadian-specific Tier 2 accounting of emissions and removals from drained and rewetted organic soils.

From an industry perspective, understanding the impact of active restoration on peatland GHG balances is critical for decision-making related to the after-use of extracted peatlands. The horticultural peat moss industry in Canada aims to be socially responsible by ensuring restoration of post-extraction sites is in accordance with government compliance as well as consumer expectations (CSPMA, 2014). One of the goals of the industry is to increase the percentage of its producers achieving the Veriflora® certification, of being a responsibly managed peatland (CSPMA, 2014). With the certification, the industry aims to appeal to the consumer choice of wanting a more sustainable product. The Veriflora® standard requires producers to measure and manage emissions and to implement best environmental sustainability practices. The scientific information provided in this thesis provides a basis for the industry to assess and manage its GHG emissions in the after-use stage. It further allows for an evaluation of the economic benefits of restoration, whether from a context of possible carbon credits or carbon taxation. Ultimately, this thesis assuages that the industry and Canadian government can have a scientifically-sound dialogue on after-use best practices when updating existing policies or introducing new protocols.

From a scientific perspective, a key objective of peatland biogeochemistry and flux research is to improve the predictive capability of coupled carbon-climate models. A more accurate characterization of the role of peatland ecosystems in climate regulation through the cycling and sequestration of C is needed to predict how peatlands develop under different climate conditions. While peatland models have been developed to simulate the feedbacks between peatland and atmosphere in the case of undisturbed peatlands, models that incorporate managed peatlands are lacking. This thesis provides essential knowledge to make modifications to some of the core biogeochemical functions of an undisturbed peatland model and provides flux data for model assessment. With a modified model, users would be able to answer long-term questions that cannot be addressed by empirical measurements, such as how long it will take to replace the quantity of peat extracted. Replacement of the peat is expected to take thousands of years, during which the climate will be changing, but such changes can be incorporated into the modelling approach, making it the ideal method for answering this pressing question.

6.3 Directions for future research

In this thesis, I quantify the net climate impact of restoring a post-extraction peatland compared to leaving it unrestored. To fully assess the climate impact of peatland extraction, however, the radiative forcing associated with emissions from actual peat removed during extraction needs to be quantified. Addressing this would require measuring emissions during the stages that make up the lifecycle of the horticultural peat moss product. Any stockpiling of peat, for instance, would be prime for C mineralization and CO₂ emission. The horticulture end-use stage would also need to be characterized to determine the amount of C that is lost compared to the amount that is incorporated belowground. Furthermore, measuring fluxes at a site undergoing extraction would improve our understanding of how much peat is being mineralized over the course of a year for the amount that is extracted during the few optimal weeks of good weather. This ratio might be surprising and could fuel changes in drainage and extraction techniques to minimize losses.

BIBLIOGRAPHY

- Abdalla, M., Hastings, A., Truu, J., Espenberg, M., Mander, Ü., & Smith, P. (2016). Emissions of methane from northern peatlands: A review of management impacts and implications for future management options. *Ecology and Evolution*, *6*(19), 7080–7102.
<https://doi.org/10.1002/ece3.2469>
- Alm, J., Schulman, L., Walden, J., Nykänen, H., Martikainen, P. J., & Silvola, J. (1999). Carbon Balance of a Boreal Bog During a Year with an Exceptionally Dry Summer. *Ecology*, *80*(1), 161–174. [https://doi.org/10.1890/0012-9658\(1999\)080\[0161:CBOABB\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1999)080[0161:CBOABB]2.0.CO;2)
- Alm, J., Shurpali, N. J., Minkinen, K., Aro, L., Hytönen, J., Laurila, T., ... Laine, J. (2007). Emission factors and their uncertainty for the exchange of CO₂, CH₄ and N₂O in Finnish managed peatlands. *Boreal Environmental Research*, *12*, 19.
- Amiro, B. (2010). Estimating annual carbon dioxide eddy fluxes using open-path analysers for cold forest sites. *Agricultural and Forest Meteorology*, *150*(10), 1366–1372.
<https://doi.org/10.1016/j.agrformet.2010.06.007>
- Andersen, R., Farrell, C., Graf, M., Muller, F., Calvar, E., Frankard, P., ... Anderson, P. (2017). An overview of the progress and challenges of peatland restoration in Western Europe. *Restoration Ecology*, *25*(2), 271–282. <https://doi.org/10.1111/rec.12415>
- Archer, D., Kheshgi, H., & Maier-Reimer, E. (1997). Multiple timescales for neutralization of fossil fuel CO₂. *Geophysical Research Letters*, *24*(4), 405–408.
<https://doi.org/10.1029/97GL00168>
- Archer, D., Kheshgi, H., & Maier-Reimer, E. (1998). Dynamics of fossil fuel CO₂ neutralization by marine CaCO₃. *Global Biogeochemical Cycles*, *12*(2), 259–276.
<https://doi.org/10.1029/98GB00744>
- Artz, R. R. E. (2009). Microbial Community Structure and Carbon Substrate use in Northern Peatlands. In A. J. Baird, L. R. Belyea, X. Comas, A. S. Reeve, & L. D. Slater (Eds.), *Carbon Cycling in Northern Peatlands* (pp. 111–129). Retrieved from <http://onlinelibrary.wiley.com/doi/10.1029/2008GM000806/summary>
- Aslan-Sungur, G., Lee, X., Evrendilek, F., & Karakaya, N. (2016). Large interannual variability in net ecosystem carbon dioxide exchange of a disturbed temperate peatland. *Science of The Total Environment*, *554–555*, 192–202.

- <https://doi.org/10.1016/j.scitotenv.2016.02.153>
- Aubinet, M., Feigenwinter, C., Heinesch, B., Laffineur, Q., Papale, D., Reichstein, M., ... Gorsel, E. V. (2012). Nighttime Flux Correction. In M. Aubinet, T. Vesala, & D. Papale (Eds.), *Eddy Covariance* (pp. 133–157). https://doi.org/10.1007/978-94-007-2351-1_5
- Aurela, M., Laurila, T., & Tuovinen, J.-P. (2004). The timing of snow melt controls the annual CO₂ balance in a subarctic fen. *Geophysical Research Letters*, *31*(16), L16119. <https://doi.org/10.1029/2004GL020315>
- Aurela, M., Riutta, T., Laurila, T., Tuovinen, J.-P., Vesala, T., Tuittila, E.-S., ... Laine, J. (2007). CO₂ exchange of a sedge fen in southern Finland—the impact of a drought period. *Tellus B*, *59*(5), 826–837. <https://doi.org/10.1111/j.1600-0889.2007.00309.x>
- Baldocchi, D. (2014). Measuring fluxes of trace gases and energy between ecosystems and the atmosphere – the state and future of the eddy covariance method. *Global Change Biology*, *20*(12), 3600–3609. <https://doi.org/10.1111/gcb.12649>
- Baldocchi, D. D. (2003). Assessing the eddy covariance technique for evaluating carbon dioxide exchange rates of ecosystems: Past, present and future. *Global Change Biology*, *9*(4), 479–492. <https://doi.org/10.1046/j.1365-2486.2003.00629.x>
- 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*(7), 1148–1165. <https://doi.org/10.1007/s10021-007-9083-2>
- Basiliko, N., Stewart, H., Roulet, N. T., & Moore, T. R. (2012). Do Root Exudates Enhance Peat Decomposition? *Geomicrobiology Journal*, *29*(4), 374–378. <https://doi.org/10.1080/01490451.2011.568272>
- Beer, J., & Blodau, C. (2007). Transport and thermodynamics constrain belowground carbon turnover in a northern peatland. *Geochimica et Cosmochimica Acta*, *71*(12), 2989–3002. <https://doi.org/10.1016/j.gca.2007.03.010>
- Bellisario, L. M., Bubier, J. L., Moore, T. R., & Chanton, J. P. (1999). Controls on CH₄ emissions from a northern peatland. *Global Biogeochemical Cycles*, *13*(1), 81–91. <https://doi.org/10.1029/1998GB900021>
- Belyea, L. R. (1996). Separating the effects of litter quality and microenvironment on decomposition rates in a patterned peatland. *Oikos*, *77*, 529–539.

- Belyea, L. R., & Baird, A. J. (2006). Beyond “the limits to peat bog growth”: Cross-scale feedback in peatland development. *Ecological Monographs*, *76*(3), 299–322. [https://doi.org/10.1890/0012-9615\(2006\)076\[0299:BTLTPB\]2.0.CO;2](https://doi.org/10.1890/0012-9615(2006)076[0299:BTLTPB]2.0.CO;2)
- Beyer, C., & Höper, H. (2015). Greenhouse gas exchange of rewetted bog peat extraction sites and a Sphagnum cultivation site in northwest Germany. *Biogeosciences*, *12*(7), 2101–2117. <https://doi.org/10.5194/bg-12-2101-2015>
- Billett, M. F., Palmer, S. M., Hope, D., Deacon, C., Storeton-West, R., Hargreaves, K. J., ... Fowler, D. (2004). Linking land-atmosphere-stream carbon fluxes in a lowland peatland system. *Global Biogeochemical Cycles*, *18*(1), GB1024. <https://doi.org/10.1029/2003GB002058>
- Blodau, C. (2002). Carbon cycling in peatlands — A review of processes and controls. *Environmental Reviews*, *10*(2), 111–134. <https://doi.org/10.1139/a02-004>
- Blodau, Christian, Basiliko, N., & Moore, T. R. (2004). Carbon turnover in peatland mesocosms exposed to different water table levels. *Biogeochemistry*, *67*(3), 331–351. <https://doi.org/10.1023/B:BIOG.0000015788.30164.e2>
- Blodau, C., Roulet, N. T., Heitmann, T., Stewart, H., Beer, J., Lafleur, P., & Moore, T. R. (2007). Belowground carbon turnover in a temperate ombrotrophic bog. *Global Biogeochemical Cycles*, *21*(1), GB1021. <https://doi.org/10.1029/2005GB002659>
- Brown, M. G., Humphreys, E. R., Moore, T. R., Roulet, N. T., & Lafleur, P. M. (2014). Evidence for a nonmonotonic relationship between ecosystem-scale peatland methane emissions and water table depth. *Journal of Geophysical Research: Biogeosciences*, *119*(5), 2013JG002576. <https://doi.org/10.1002/2013JG002576>
- Brummell, M. E., Lazcano, C., & Strack, M. (2017). The effects of *Eriophorum vaginatum* on N₂O fluxes at a restored, extracted peatland. *Ecological Engineering*, *106*, 287–295. <https://doi.org/10.1016/j.ecoleng.2017.06.006>
- 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*(4), 353–367. <https://doi.org/10.1007/s10021-003-0125-0>
- Bubier, J. L., Frohling, S., Crill, P. M., & Linder, E. (1999). Net ecosystem productivity and its uncertainty in a diverse boreal peatland. *Journal of Geophysical Research: Atmospheres*,

- 104(D22), 27683–27692. <https://doi.org/10.1029/1999JD900219>
- Bubier, J., Moore, T., Savage, K., & Crill, P. (2005). A comparison of methane flux in a boreal landscape between a dry and a wet year. *Global Biogeochemical Cycles*, 19(1), GB1023. <https://doi.org/10.1029/2004GB002351>
- Bubier, Jill 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(4), 353–367. <https://doi.org/10.1007/s10021-003-0125-0>
- Bubier, Jill L., Moore, T. R., Bellisario, L., Comer, N. T., & Crill, P. M. (1995). Ecological controls on methane emissions from a Northern Peatland Complex in the zone of discontinuous permafrost, Manitoba, Canada. *Global Biogeochemical Cycles*, 9(4), 455–470. <https://doi.org/10.1029/95GB02379>
- Buckmaster, C. R., Bain, S., & Reed, M. eds. (2014). *Global Peatland Restoration demonstrating SUCCESS*. IUCN UK National Committee Peatland Programme, Edinburgh, UK. ISBN 978-0-9570572-3-4.
- Chanton, J. P. (2005). The effect of gas transport on the isotope signature of methane in wetlands. *Organic Geochemistry*, 36(5), 753–768. <https://doi.org/10.1016/j.orggeochem.2004.10.007>
- Chanton, J. P., Bauer, J. E., Glaser, P. A., Siegel, D. I., Kelley, C. A., Tyler, S. C., ... Lazrus, A. (1995). Radiocarbon evidence for the substrates supporting methane formation within northern Minnesota peatlands. *Geochimica et Cosmochimica Acta*, 59(17), 3663–3668. [https://doi.org/10.1016/0016-7037\(95\)00240-Z](https://doi.org/10.1016/0016-7037(95)00240-Z)
- Chanton, J. P., Fields, D., & Hines, M. E. (2006). Controls on the hydrogen isotopic composition of biogenic methane from high-latitude terrestrial wetlands. *Journal of Geophysical Research: Biogeosciences*, 111(G4), G04004. <https://doi.org/10.1029/2005JG000134>
- Chanton, J. P., Glaser, P. H., Chasar, L. S., Burdige, D. J., Hines, M. E., Siegel, D. I., ... Cooper, W. T. (2008). Radiocarbon evidence for the importance of surface vegetation on fermentation and methanogenesis in contrasting types of boreal peatlands. *Global Biogeochemical Cycles*, 22(4), GB4022. <https://doi.org/10.1029/2008GB003274>
- Chapman, S. J., & Thurlow, M. (1996). The influence of climate on CO₂ and CH₄ emissions from organic soils. *Agricultural and Forest Meteorology*, 79(4), 205–217.

- [https://doi.org/10.1016/0168-1923\(95\)02283-X](https://doi.org/10.1016/0168-1923(95)02283-X)
- Chasar, L. S., Chanton, J. P., Glaser, P. H., & Siegel, D. I. (2000). Methane Concentration and Stable Isotope Distribution as Evidence of Rhizospheric Processes: Comparison of a Fen and Bog in the Glacial Lake Agassiz Peatland Complex. *Annals of Botany*, 86(3), 655–663. <https://doi.org/10.1006/anbo.2000.1172>
- Chasar, L. S., Chanton, J. P., Glaser, P. H., Siegel, D. I., & Rivers, J. S. (2000). Radiocarbon and stable carbon isotopic evidence for transport and transformation of dissolved organic carbon, dissolved inorganic carbon, and CH₄ in a northern Minnesota peatland. *Global Biogeochemical Cycles*, 14(4), 1095–1108. <https://doi.org/10.1029/1999GB001221>
- Chimner, R. A., Cooper, D. J., Wurster, F. C., & Rochefort, L. (2017). An overview of peatland restoration in North America: Where are we after 25 years? *Restoration Ecology*, 25(2), 283–292. <https://doi.org/10.1111/rec.12434>
- Christensen, T. R., Jackowicz-Korczyński, M., Aurela, M., Crill, P., Heliasz, M., Mastepanov, M., & Friborg, T. (2012). Monitoring the multi-year carbon balance of a subarctic peat mire with micrometeorological techniques. *AMBIO*, 41(3), 207–217. <https://doi.org/10.1007/s13280-012-0302-5>
- Christensen, T. R., Panikov, N., Mastepanov, M., Joabsson, A., Stewart, A., Öquist, M., ... Svensson, B. (2003). Biotic controls on CO₂ and CH₄ exchange in wetlands – a closed environment study. *Biogeochemistry*, 64(3), 337–354. <https://doi.org/10.1023/A:1024913730848>
- Clark, J. M., Lane, S. N., Chapman, P. J., & Adamson, J. K. (2007). Export of dissolved organic carbon from an upland peatland during storm events: Implications for flux estimates. *Journal of Hydrology*, 347(3), 438–447. <https://doi.org/10.1016/j.jhydrol.2007.09.030>
- Clymo, R. S. (1984). The Limits to Peat Bog Growth. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 303(1117), 605–654. <https://doi.org/10.1098/rstb.1984.0002>
- Conrad, R. (2005). Quantification of methanogenic pathways using stable carbon isotopic signatures: A review and a proposal. *Organic Geochemistry*, 36(5), 739–752. <https://doi.org/10.1016/j.orggeochem.2004.09.006>
- Conrad, R., Klose, M., & Claus, P. (2002). Pathway of CH₄ formation in anoxic rice field soil and rice roots determined by ¹³C-stable isotope fractionation. *Chemosphere*, 47(8), 797–

806. [https://doi.org/10.1016/S0045-6535\(02\)00120-0](https://doi.org/10.1016/S0045-6535(02)00120-0)
- Cooper, M. D. A., Evans, C. D., Zielinski, P., Levy, P. E., Gray, A., Peacock, M., ... Freeman, C. (2014). Infilled ditches are hotspots of landscape methane flux following peatland rewetting. *Ecosystems*, *17*(7), 1227–1241. <https://doi.org/10.1007/s10021-014-9791-3>
- Corbett, J. E., Burdige, D. J., Tfaily, M. M., Dial, A. R., Cooper, W. T., Glaser, P. H., & Chanton, J. P. (2013). Surface production fuels deep heterotrophic respiration in northern peatlands. *Global Biogeochemical Cycles*, *27*(4), 1163–1174. <https://doi.org/10.1002/2013GB004677>
- Corbett, J. E., Tfaily, M. M., Burdige, D. J., Cooper, W. T., Glaser, P. H., & Chanton, J. P. (2012). Partitioning pathways of CO₂ production in peatlands with stable carbon isotopes. *Biogeochemistry*, *114*(1–3), 327–340. <https://doi.org/10.1007/s10533-012-9813-1>
- Corbett, J. E., Tfaily, M. M., Burdige, D. J., Glaser, P. H., & Chanton, J. P. (2015). The relative importance of methanogenesis in the decomposition of organic matter in northern peatlands. *Journal of Geophysical Research: Biogeosciences*, *120*(2), 2014JG002797. <https://doi.org/10.1002/2014JG002797>
- Crill, P., Hargreaves, K., & Korhola, A. (2000). *The role of peat in Finnish greenhouse gas balances* (No. KTM-RAP--10/2000). Retrieved from Ministry of Trade and Industry website: http://inis.iaea.org/Search/search.aspx?orig_q=RN:32001740
- D'Acunha, B., Lee, S.-C., & Johnson, M. S. (2018). Ecohydrological responses to rewetting of a highly impacted raised bog ecosystem. *Ecohydrology*, *11*(1), e1922. <https://doi.org/10.1002/eco.1922>
- Dargie, G. C., Lewis, S. L., Lawson, I. T., Mitchard, E. T. A., Page, S. E., Bocko, Y. E., & Ifo, S. A. (2017). Age, extent and carbon storage of the central Congo Basin peatland complex. *Nature*, *542*(7639), 86–90. <https://doi.org/10.1038/nature21048>
- Davidson, N. C. (2014). How much wetland has the world lost? Long-term and recent trends in global wetland area. *Marine and Freshwater Research*, *65*(10), 934–941. <https://doi.org/10.1071/MF14173>
- Dawson, J. J. C., Billett, M. F., Hope, D., Palmer, S. M., & Deacon, C. M. (2004). Sources and Sinks of Aquatic Carbon in a Peatland Stream Continuum. *Biogeochemistry*, *70*(1), 71–92.

- Dimitrov, D. D., Grant, R. F., Lafleur, P. M., & Humphreys, E. R. (2010). Modeling the effects of hydrology on ecosystem respiration at Mer Bleue bog. *Journal of Geophysical Research: Biogeosciences*, *115*(G4), G04043. <https://doi.org/10.1029/2010JG001312>
- Dinsmore, K. J., Billett, M. F., Skiba, U. M., Rees, R. M., Drewer, J., & Helfter, C. (2010). Role of the aquatic pathway in the carbon and greenhouse gas budgets of a peatland catchment. *Global Change Biology*, *16*(10), 2750–2762. <https://doi.org/10.1111/j.1365-2486.2009.02119.x>
- Dionne, J.-C. (1977). La mer de Goldthwait au Québec. *Géographie physique et Quaternaire*, *31*(1–2), 61–80. <https://doi.org/10.7202/1000055ar>
- Dixon, S. D., Qassim, S. M., Rowson, J. G., Worrall, F., Evans, M. G., Boothroyd, I. M., & Bonn, A. (2014). Restoration effects on water table depths and CO₂ fluxes from climatically marginal blanket bog. *Biogeochemistry*, *118*(1–3), 159–176. <https://doi.org/10.1007/s10533-013-9915-4>
- Dlugokencky, E. and Tans, P. (2017). *Trends in atmospheric carbon dioxide*. National Oceanic & Atmospheric Administration, Earth System Research Laboratory, Boulder, Colorado, USA. <https://www.esrl.noaa.gov/gmd/ccgg/trends/global.html>
- Dommain, R., Frohling, S., Jeltsch-Thömmes, A., Joos, F., Couwenberg, J., & Glaser, P. H. (2018). A radiative forcing analysis of tropical peatlands before and after their conversion to agricultural plantations. *Global Change Biology*, *24*(11), 5518–5533. <https://doi.org/10.1111/gcb.14400>
- Dorrepaal, E., Cornelissen, J. H. C., Aerts, R., Wallén, B., & Logtestijn, R. S. P. V. (2005). Are growth forms consistent predictors of leaf litter quality and decomposability across peatlands along a latitudinal gradient? *Journal of Ecology*, *93*(4), 817–828. <https://doi.org/10.1111/j.1365-2745.2005.01024.x>
- Drollinger, S., Maier, A., & Glatzel, S. (2019). Interannual and seasonal variability in carbon dioxide and methane fluxes of a pine peat bog in the Eastern Alps, Austria. *Agricultural and Forest Meteorology*, *275*, 69–78. <https://doi.org/10.1016/j.agrformet.2019.05.015>
- Dunfield, P., Knowles, R., Dumont, R., & Moore, T. R. (1993). Methane production and consumption in temperate and subarctic peat soils: Response to temperature and pH. *Soil Biology and Biochemistry*, *25*(3), 321–326. [https://doi.org/10.1016/0038-0717\(93\)90130-4](https://doi.org/10.1016/0038-0717(93)90130-4)

- Dunn, A. L., Barford, C. C., Wofsy, S. C., Goulden, M. L., & Daube, B. C. (2007). A long-term record of carbon exchange in a boreal black spruce forest: Means, responses to interannual variability, and decadal trends. *Global Change Biology*, *13*(3), 577–590. <https://doi.org/10.1111/j.1365-2486.2006.01221.x>
- Dyson, K. E., Billett, M. F., Dinsmore, K. J., Harvey, F., Thomson, A. M., Piirainen, S., & Kortelainen, P. (2011). Release of aquatic carbon from two peatland catchments in E. Finland during the spring snowmelt period. *Biogeochemistry*, *103*(1), 125–142. <https://doi.org/10.1007/s10533-010-9452-3>
- ECCC. (2018). *National Inventory Report 1990-2016: Greenhouse Gas Sources and Sinks in Canada*. Environment and Climate Change Canada, Part 1.
- Eppinga, M. B., Rietkerk, M., Wassen, M. J., & Ruiten, P. C. D. (2009). Linking habitat modification to catastrophic shifts and vegetation patterns in bogs. *Plant Ecology*, *200*(1), 53–68. <https://doi.org/10.1007/s11258-007-9309-6>
- Euskirchen, E. S., Edgar, C. W., Turetsky, M. R., Waldrop, M. P., & Harden, J. W. (2014). Differential response of carbon fluxes to climate in three peatland ecosystems that vary in the presence and stability of permafrost. *Journal of Geophysical Research: Biogeosciences*, *119*(8), 2014JG002683. <https://doi.org/10.1002/2014JG002683>
- Evans, C. D., Monteith, D. T., & Cooper, D. M. (2005). Long-term increases in surface water dissolved organic carbon: Observations, possible causes and environmental impacts. *Environmental Pollution*, *137*(1), 55–71. <https://doi.org/10.1016/j.envpol.2004.12.031>
- Evans, C. D., Renou-Wilson, F., & Strack, M. (2016). The role of waterborne carbon in the greenhouse gas balance of drained and re-wetted peatlands. *Aquatic Sciences*, *78*(3), 573–590. <https://doi.org/10.1007/s00027-015-0447-y>
- Flanagan, L. B., & Syed, K. H. (2011). Stimulation of both photosynthesis and respiration in response to warmer and drier conditions in a boreal peatland ecosystem. *Global Change Biology*, *17*(7), 2271–2287. <https://doi.org/10.1111/j.1365-2486.2010.02378.x>
- Fortuniak, K., Pawlak, W., Bednorz, L., Grygoruk, M., Siedlecki, M., & Zieliński, M. (2017). Methane and carbon dioxide fluxes of a temperate mire in Central Europe. *Agricultural and Forest Meteorology*, *232*, 306–318. <https://doi.org/10.1016/j.agrformet.2016.08.023>
- Franz, D., Koebsch, F., Larmanou, E., Augustin, J., & Sachs, T. (2016). High net CO₂ and CH₄ release at a eutrophic shallow lake on a formerly drained fen. *Biogeosciences*, *13*(10),

- 3051–3070. <https://doi.org/10.5194/bg-13-3051-2016>
- Fraser, C. J. D., Roulet, N. T., & Lafleur, M. (2001). Groundwater flow patterns in a large peatland. *Journal of Hydrology*, *246*(1–4), 142–154. [https://doi.org/10.1016/S0022-1694\(01\)00362-6](https://doi.org/10.1016/S0022-1694(01)00362-6)
- Fraser, C. J. D., Roulet, N. T., & Moore, T. R. (2001). Hydrology and dissolved organic carbon biogeochemistry in an ombrotrophic bog. *Hydrological Processes*, *15*(16), 3151–3166. <https://doi.org/10.1002/hyp.322>
- Freeman, C., Evans, C. D., Monteith, D. T., Reynolds, B., & Fenner, N. (2001). Export of organic carbon from peat soils. *Nature*, *412*(6849), 785–785. <https://doi.org/10.1038/35090628>
- Friborg, T., Christensen, T. R., Hansen, B. U., Nordstroem, C., & Soegaard, H. (2000). Trace gas exchange in a high-Arctic valley: 2. Landscape CH₄ fluxes measured and modeled using eddy correlation data. *Global Biogeochemical Cycles*, *14*(3), 715–723. <https://doi.org/10.1029/1999GB001136>
- Friborg, T., Soegaard, H., Christensen, T. R., Lloyd, C. R., & Panikov, N. S. (2003). Siberian wetlands: Where a sink is a source. *Geophysical Research Letters*, *30*(21). <https://doi.org/10.1029/2003GL017797>
- Frolking, S., & Roulet, N. T. (2007). Holocene radiative forcing impact of northern peatland carbon accumulation and methane emissions. *Global Change Biology*, *13*(5), 1079–1088. <https://doi.org/10.1111/j.1365-2486.2007.01339.x>
- Frolking, S., Roulet, N. T., Moore, T. R., Lafleur, P. M., Bubier, J. L., & Crill, P. M. (2002). Modeling seasonal to annual carbon balance of Mer Bleue Bog, Ontario, Canada. *Global Biogeochemical Cycles*, *16*(3), 4–1. <https://doi.org/10.1029/2001GB001457>
- Frolking, S., Roulet, N. T., Moore, T. R., Richard, P. J. H., Lavoie, M., & Muller, S. D. (2001). Modeling northern peatland decomposition and peat accumulation. *Ecosystems*, *4*(5), 479–498. <https://doi.org/10.1007/s10021-001-0105-1>
- Frolking, S., Roulet, N., & Fuglestedt, J. (2006). How northern peatlands influence the Earth's radiative budget: Sustained methane emission versus sustained carbon sequestration. *Journal of Geophysical Research: Biogeosciences*, *111*(G1), G01008. <https://doi.org/10.1029/2005JG000091>
- Frolking, S., Roulet, N., Tuittila, E.-S., Bubier, J., Quillet, A., Talbot, J., & Richard, P. J. (2010).

- A new model of Holocene peatland net primary production, decomposition, water balance, and peat accumulation. *Earth System Dynamics*. <https://doi.org/10.5194/esd-1-1-2010>
- Graf, M. and Rochefort, L. (2016). A conceptual framework for ecosystem restoration applied to industrial peatlands. In: Bonn A, Allot T, Evans M, Joosten H, Stoneman R (eds) *Peatlands Restoration and Ecosystem Services: Sciences, Policy and Practice*. Ecological Reviews of Cambridge University Press, Cambridge, pp 192-212.
- Greenup, A. L., Bradford, M. A., McNamara, N. P., Ineson, P., & Lee, J. A. (2000). The role of *Eriophorum vaginatum* in CH₄ flux from an ombrotrophic peatland. *Plant and Soil*, 227(1–2), 265–272. <https://doi.org/10.1023/A:1026573727311>
- Groenefeld, E. V. G. & Rochefort, L. (2005). *Polytrichum Strictum* as a solution to frost heaving in disturbed ecosystems: a case study with milled peatlands. *Restoration Ecology* 13(1), 74-82. <https://doi.org/10.1111/j.1526-100X.2005.00009.x>
- Hahn, J., Köhler, S., Glatzel, S., & Jurasinski, G. (2015). Methane exchange in a coastal fen in the first year after flooding - A systems shift. *PLOS ONE*, 10(10), e0140657. <https://doi.org/10.1371/journal.pone.0140657>
- Hájek, T., Ballance, S., Limpens, J., Zijlstra, M., & Verhoeven, J. T. A. (2010). Cell-wall polysaccharides play an important role in decay resistance of *Sphagnum* and actively depressed decomposition in vitro. *Biogeochemistry*, 103(1–3), 45–57. <https://doi.org/10.1007/s10533-010-9444-3>
- Hanis, K. L., Tenuta, M., Amiro, B. D., & Papakyriakou, T. N. (2013). Seasonal dynamics of methane emissions from a subarctic fen in the Hudson Bay Lowlands. *Biogeosciences*, 10(7), 4465–4479. <https://doi.org/10.5194/bg-10-4465-2013>
- Helbig, M., Chasmer, L. E., Kljun, N., Quinton, W. L., Treat, C. C., & Sonnentag, O. (2017). The positive net radiative greenhouse gas forcing of increasing methane emissions from a thawing boreal forest-wetland landscape. *Global Change Biology*, 23(6), 2413–2427. <https://doi.org/10.1111/gcb.13520>
- Helfter, C., Campbell, C., Dinsmore, K. J., Drewer, J., Coyle, M., Anderson, M., ... Sutton, M. A. (2015). Drivers of long-term variability in CO₂ net ecosystem exchange in a temperate peatland. *Biogeosciences*, 12(6), 1799–1811. <https://doi.org/10.5194/bg-12-1799-2015>

- Hendriks, D. M. D., Van Huissteden, J., Dolman, A. J., & Van Der Molen, M. K. (2007). The full greenhouse gas balance of an abandoned peat meadow. *Biogeosciences Discussions*, 4(1), 277–316.
- Herbst, M., Friborg, T., Ringgaard, R., & Soegaard, H. (2011). Interpreting the variations in atmospheric methane fluxes observed above a restored wetland. *Agricultural and Forest Meteorology*, 151(7), 841–853. <https://doi.org/10.1016/j.agrformet.2011.02.002>
- Hilbert, D. W., Roulet, N., & Moore, T. (2000). Modelling and analysis of peatlands as dynamical systems. *Journal of Ecology*, 88(2), 230–242. <https://doi.org/10.1046/j.1365-2745.2000.00438.x>
- Hines, M. E., Duddleston, K. N., Rooney-Varga, J. N., Fields, D., & Chanton, J. P. (2008). Uncoupling of acetate degradation from methane formation in Alaskan wetlands: Connections to vegetation distribution. *Global Biogeochemical Cycles*, 22(2), GB2017. <https://doi.org/10.1029/2006GB002903>
- Hogg, E. H. (1993). Decay potential of hummock and hollow sphagnum peats at different depths in a Swedish raised bog. *Oikos*, 66(2), 269–278. <https://doi.org/10.2307/3544814>
- Holden, J. (2005). Peatland hydrology and carbon release: Why small-scale process matters. *Philosophical Transactions of the Royal Society of London A: Mathematical, Physical and Engineering Sciences*, 363(1837), 2891–2913. <https://doi.org/10.1098/rsta.2005.1671>
- Huete, A. R., Liu, H. Q., Batchily, K., & van Leeuwen, W. (1997). A comparison of vegetation indices over a global set of TM images for EOS-MODIS. *Remote Sensing of Environment*, 59(3), 440–451. [https://doi.org/10.1016/S0034-4257\(96\)00112-5](https://doi.org/10.1016/S0034-4257(96)00112-5)
- Huete, A., Didan, K., Miura, T., Rodriguez, E. P., Gao, X., & Ferreira, L. G. (2002). Overview of the radiometric and biophysical performance of the MODIS vegetation indices. *Remote Sensing of Environment*, 83(1), 195–213. [https://doi.org/10.1016/S0034-4257\(02\)00096-2](https://doi.org/10.1016/S0034-4257(02)00096-2)
- Huete, A., Justice, C., & Liu, H. (1994). Development of vegetation and soil indices for MODIS-EOS. *Remote Sensing of Environment*, 49(3), 224–234. [https://doi.org/10.1016/0034-4257\(94\)90018-3](https://doi.org/10.1016/0034-4257(94)90018-3)
- Huttunen, J. T., Alm, J., Liikanen, A., Juutinen, S., Larmola, T., Hammar, T., ... Martikainen, P. J. (2003). Fluxes of methane, carbon dioxide and nitrous oxide in boreal lakes and potential anthropogenic effects on the aquatic greenhouse gas emissions. *Chemosphere*,

- 52(3), 609–621. [https://doi.org/10.1016/S0045-6535\(03\)00243-1](https://doi.org/10.1016/S0045-6535(03)00243-1)
- Illeris, L., Christensen, T. R., & Mastepanov, M. (2004). Moisture Effects on Temperature Sensitivity of CO₂ Exchange in a Subarctic Heath Ecosystem. *Biogeochemistry*, *70*(3), 315–330. <https://doi.org/10.1007/s10533-003-0855-2>
- IPCC. (2014). *2013 Supplement to the 2006 Inter-Governmental Panel on Climate Change Guidelines for National Greenhouse Gas Inventories: Wetlands*. Switzerland: IPCC.
- Jackowicz-Korczyński, M., Christensen, T. R., Bäckstrand, K., Crill, P., Friborg, T., Mastepanov, M., & Ström, L. (2010). Annual cycle of methane emission from a subarctic peatland. *Journal of Geophysical Research: Biogeosciences*, *115*(G2), G02009. <https://doi.org/10.1029/2008JG000913>
- Järveoja, J., Peichl, M., Maddison, M., Soosaar, K., Vellak, K., Karofeld, E., ... 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. <https://doi.org/10.5194/bg-13-2637-2016>
- Joabsson, A., & Christensen, T. R. (2001). Methane emissions from wetlands and their relationship with vascular plants: An Arctic example. *Global Change Biology*, *7*(8), 919–932. <https://doi.org/10.1046/j.1354-1013.2001.00044.x>
- Joabsson, A., Christensen, T. R., & Wallén, B. (1999). Vascular plant controls on methane emissions from northern peatforming wetlands. *Trends in Ecology & Evolution*, *14*(10), 385–388. [https://doi.org/10.1016/S0169-5347\(99\)01649-3](https://doi.org/10.1016/S0169-5347(99)01649-3)
- Joos, F., Roth, R., Fuglestedt, J. S., Peters, G. P., Enting, I. G., von Bloh, W., ... Weaver, A. J. (2013). Carbon dioxide and climate impulse response functions for the computation of greenhouse gas metrics: A multi-model analysis. *Atmos. Chem. Phys.*, *13*(5), 2793–2825. <https://doi.org/10.5194/acp-13-2793-2013>
- Joosten, H. (2009). *The Global Peatland CO₂ Picture: Peatland Status and Drainage Related Emissions in All Countries of the World*. Wetland International, Netherlands.
- Joosten, H., Tapoi-Biström, M. L. & Tol, S. (2012). *Peatlands – Guidance for Climate Change Mitigation Through Conservation, Rehabilitation and Sustainable Use*. FAO and Wetlands International, Rome, Italy.
- Juottonen, H., Hynninen, A., Nieminen, M., Tuomivirta, T. T., Tuittila, E.-S., Nousiainen, H., ... Fritze, H. (2012). Methane-cycling microbial communities and methane emission in

- natural and restored peatlands. *Applied and Environmental Microbiology*, 78(17), 6386–6389. <https://doi.org/10.1128/AEM.00261-12>
- Kalacska, M., Arroyo-Mora, J. P., de Gea, J., Snirer, E., Herzog, C., & Moore, T. R. (2013). Videographic analysis of *Eriophorum Vaginatum* spatial coverage in an ombrotrophic bog. *Remote Sensing*, 5(12), 6501–6512. <https://doi.org/10.3390/rs5126501>
- Kamal, S., & Varma, A. (2008). Peatland Microbiology. In P. D. P. Dion & P. D. C. S. Nautiyal (Eds.), *Microbiology of Extreme Soils* (pp. 177–203). https://doi.org/10.1007/978-3-540-74231-9_9
- Karofeld, E., Müür, M., & Vellak, K. (2016). Factors affecting re-vegetation dynamics of experimentally restored extracted peatland in Estonia. *Environmental Science and Pollution Research*, 23(14), 13706–13717. <https://doi.org/10.1007/s11356-015-5396-4>
- Keller, J. K., & Bridgham, S. D. (2007). Pathways of anaerobic carbon cycling across an ombrotrophic-minerotrophic peatland gradient. *Limnology and Oceanography*, 52(1), 96–107. <https://doi.org/10.4319/lo.2007.52.1.0096>
- Kelly, C. A., Dise, N. B., & Martens, C. S. (1992). Temporal variations in the stable carbon isotopic composition of methane emitted from Minnesota peatlands. *Global Biogeochemical Cycles*, 6(3), 263–269. <https://doi.org/10.1029/92GB01478>
- Killham, K. (1994). *Soil Ecology*. Cambridge University Press.
- Kim, J., Verma, S. B., Billesbach, D. P., & Clement, R. J. (1998). Diel variation in methane emission from a midlatitude prairie wetland: Significance of convective throughflow in *Phragmites australis*. *Journal of Geophysical Research: Atmospheres*, 103(D21), 28029–28039. <https://doi.org/10.1029/98JD02441>
- Kivimäki, S. K., Yli-petäys, M., & Tuittila, E. (2008). Carbon sink function of sedge and Sphagnum patches in a restored cut-away peatland: increased functional diversity leads to higher production. *Journal of Applied Ecology*, 45(3), 921–929. <https://doi.org/10.1111/j.1365-2664.2008.01458.x>
- Kljun, N., Calanca, P., Rotach, M. W., & Schmid, H. P. (2015). A simple two-dimensional parameterisation for Flux Footprint Prediction (FFP). *Geosci. Model Dev.*, 8(11), 3695–3713. <https://doi.org/10.5194/gmd-8-3695-2015>
- Koehler, A.-K., Murphy, K., Kiely, G., & Sottocornola, M. (2009). Seasonal variation of DOC concentration and annual loss of DOC from an Atlantic blanket bog in South Western

- Ireland. *Biogeochemistry*, 95(2–3), 231–242. <https://doi.org/10.1007/s10533-009-9333-9>
- Koehler, A.-K., Sottocornola, M., & Kiely, G. (2011). How strong is the current carbon sequestration of an Atlantic blanket bog? *Global Change Biology*, 17(1), 309–319. <https://doi.org/10.1111/j.1365-2486.2010.02180.x>
- Komulainen, V.-M., Nykänen, H., Martikainen, P. J., & Laine, J. (1998). Short-term effect of restoration on vegetation change and methane emissions from peatlands drained for forestry in southern Finland. *Canadian Journal of Forest Research*, 28(3), 402–411. <https://doi.org/10.1139/x98-011>
- Kotiaho, M., Fritze, H., Merilä, P., Juottonen, H., Leppälä, M., Laine, J., ... Tuittila, E.-S. (2010). Methanogen activity in relation to water table level in two boreal fens. *Biology and Fertility of Soils*, 46(6), 567–575. <https://doi.org/10.1007/s00374-010-0461-0>
- Kuzyakov, Y., & Domanski, G. (2000). Carbon input by plants into the soil. Review. *Journal of Plant Nutrition and Soil Science*, 163(4), 421–431. [https://doi.org/10.1002/1522-2624\(200008\)163:4<421::AID-JPLN421>3.0.CO;2-R](https://doi.org/10.1002/1522-2624(200008)163:4<421::AID-JPLN421>3.0.CO;2-R)
- Laanbroek, H. J. (2010). Methane emission from natural wetlands: Interplay between emergent macrophytes and soil microbial processes. A mini-review. *Annals of Botany*, 105(1), 141–153. <https://doi.org/10.1093/aob/mcp201>
- Lafleur, P. M. (2009). Connecting atmosphere and wetland: Trace gas exchange. *Geography Compass*, 3(2), 560–585. <https://doi.org/10.1111/j.1749-8198.2008.00212.x>
- Lafleur, P. M., Moore, T. R., Roulet, N. T., & Froelking, S. (2005). Ecosystem respiration in a cool temperate bog depends on peat temperature but not water table. *Ecosystems*, 8(6), 619–629. <https://doi.org/10.1007/s10021-003-0131-2>
- Lafleur, P. M., Roulet, N. T., Bubier, J. L., Froelking, S., & Moore, T. R. (2003). Interannual variability in the peatland-atmosphere carbon dioxide exchange at an ombrotrophic bog. *Global Biogeochemical Cycles*, 17(2), 1036. <https://doi.org/10.1029/2002GB001983>
- Lai, D. Y. F. (2009). Methane dynamics in northern peatlands: A review. *Pedosphere*, 19(4), 409–421. [https://doi.org/10.1016/S1002-0160\(09\)00003-4](https://doi.org/10.1016/S1002-0160(09)00003-4)
- Lai, D. Y. F., Moore, T. R., & Roulet, N. T. (2014). Spatial and temporal variations of methane flux measured by autochambers in a temperate ombrotrophic peatland. *Journal of Geophysical Research: Biogeosciences*, 119(5), 2013JG002410. <https://doi.org/10.1002/2013JG002410>

- Lai, D. Y. F., Roulet, N. T., Humphreys, E. R., Moore, T. R., & Dalva, M. (2012). The effect of atmospheric turbulence and chamber deployment period on autochamber CO₂ and CH₄ flux measurements in an ombrotrophic peatland. *Biogeosciences*, *9*(8), 3305–3322. <https://doi.org/10.5194/bg-9-3305-2012>
- Laine, A., Wilson, D., Kiely, G., & Byrne, K. A. (2007). Methane flux dynamics in an Irish lowland blanket bog. *Plant and Soil*, *299*(1–2), 181–193. <https://doi.org/10.1007/s11104-007-9374-6>
- Laine, J., Silvola, J., Tolonen, K., Alm, J., Nykänen, H., Vasander, H., ... Martikainen, P. J. (1996). Effect of Water-Level Drawdown on Global Climatic Warming: Northern Peatlands. *Ambio*, *25*(3), 179–184. Retrieved from JSTOR.
- Lansdown, J. M., Quay, P. D., & King, S. L. (1992). CH₄ production via CO₂ reduction in a temperate bog: A source of ¹³C-depleted CH₄. *Geochimica et Cosmochimica Acta*, *56*(9), 3493–3503. [https://doi.org/10.1016/0016-7037\(92\)90393-W](https://doi.org/10.1016/0016-7037(92)90393-W)
- Lashof, D. A. (2000). The Use of Global Warming Potentials in the Kyoto Protocol. *Climatic Change* *44*, 423–425.
- Lasslop, G., Reichstein, M., Detto, M., Richardson, A. D., & Baldocchi, D. D. (2010). Comment on Vickers et al.: Self-correlation between assimilation and respiration resulting from flux partitioning of eddy-covariance CO₂ fluxes. *Agricultural and Forest Meteorology*, *150*, 312–314.
- Lapham, L., Proctor, L., & Chanton, J. (1999). Using Respiration Rates and Stable Carbon Isotopes to Monitor the Biodegradation of Orimulsion by Marine Benthic Bacteria. *Environmental Science & Technology*, *33*(12), 2035–2039. <https://doi.org/10.1021/es981158a>
- Lavoie, C., Zimmerman, C., & Pellerin, S. (2001). Peatland restoration in southern Quebec (Canada): a paleoecological perspective. *Ecoscience*, *8*, 247–258.
- Lee, S.-C., Christen, A., Black, A. T., Johnson, M. S., Jassal, R. S., Ketler, R., ... Merkens, M. (2017). Annual greenhouse gas budget for a bog ecosystem undergoing restoration by rewetting. *Biogeosciences*, *14*(11), 2799–2814. <https://doi.org/10.5194/bg-14-2799-2017>
- Leifeld, J., & Menichetti, L. (2018). The underappreciated potential of peatlands in global climate change mitigation strategies. *Nature Communications*, *9*(1),

1071. <https://doi.org/10.1038/s41467-018-03406-6>
- Levy, P. E., & Gray, A. (2015). Greenhouse gas balance of a semi-natural peatbog in northern Scotland. *Environmental Research Letters*, *10*(9), 94019. <https://doi.org/10.1088/1748-9326/10/9/094019>
- Li, T., Raivonen, M., Alekseychik, P., Aurela, M., Lohila, A., Zheng, X., ... Zhang, W. (2016). Importance of vegetation classes in modeling CH₄ emissions from boreal and subarctic wetlands in Finland. *Science of The Total Environment*, *572*, 1111–1122. <https://doi.org/10.1016/j.scitotenv.2016.08.020>
- Limpens, J., Berendse, F., Blodau, C., Canadell, J. G., Freeman, C., Holden, J., ... Schaepman-Strub, G. (2008). Peatlands and the carbon cycle: from local processes to global implications – a synthesis. *Biogeosciences*, *5*(5), 1475–1491. <https://doi.org/10.5194/bg-5-1475-2008>
- Limpens, Juul, & Berendse, F. (2003). How litter quality affects mass loss and N loss from decomposing Sphagnum. *Oikos*, *103*(3), 537–547. <https://doi.org/10.1034/j.1600-0706.2003.12707.x>
- Lindroth, A., Lund, M., Nilsson, M., Aurela, M., Christensen, T. R., Laurila, T., ... Vesala, T. (2007). Environmental controls on the CO₂ exchange in north European mires. *Tellus B*, *59*(5), 812–825. <https://doi.org/10.1111/j.1600-0889.2007.00310.x>
- Lohila, A. *et al.* (2010). Forestation of boreal peatlands: Impacts of changing albedo and greenhouse gas fluxes on radiative forcing. *J. Geophys. Res.* *115*, G04011.
- 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*(9), 2420–2435. <https://doi.org/10.1111/j.1365-2486.2009.02083.x>
- Lortie, G. (1983). Les diatomées fossiles de deux tourbières ombrotrophes du Bas-Saint-Laurent, Québec. *Géographie physique et Quaternaire*, *37*(2), 159–177. <https://doi.org/10.7202/032512ar>
- Lovley, D. R., Coates, J. D., Blunt-Harris, E. L., Phillips, E. J. P., & Woodward, J. C. (1996). Humic substances as electron acceptors for microbial respiration. *Nature*, *382*(6590), 445. <https://doi.org/10.1038/382445a0>
- Lucchese, M., Waddington, J. M., Poulin, M., Pouliot, R., Rochefort, L., & Strack, M. (2010). Organic matter accumulation in a restored peatland: Evaluating restoration success.

- Ecological Engineering*, 36(4), 482–488. <https://doi.org/10.1016/j.ecoleng.2009.11.017>
- Lund, M., Bjerke, J. W., Drake, B. G., Engelsen, O., Hansen, G. H., Parmentier, F. J. W., ... Rasse, D. P. (2015). Low impact of dry conditions on the CO₂ exchange of a Northern-Norwegian blanket bog. *Environmental Research Letters*, 10(2), 25004. <https://doi.org/10.1088/1748-9326/10/2/025004>
- Lund, M., Christensen, T. R., Lindroth, A., & Schubert, P. (2012). Effects of drought conditions on the carbon dioxide dynamics in a temperate peatland. *Environmental Research Letters*, 7(4), 45704. <https://doi.org/10.1088/1748-9326/7/4/045704>
- Lund, M., Lafleur, P. M., Roulet, N. T., Lindroth, A., Christensen, T. R., Aurela, M., ... Nilsson, M. B. (2010). Variability in exchange of CO₂ across 12 northern peatland and tundra sites. *Global Change Biology*, 16(9), 2436–2448. <https://doi.org/10.1111/j.1365-2486.2009.02104.x>
- MacDonald, S. (2017). Interannual variability and spatial heterogeneity in net carbon exchange at a restored peatland in Alberta. Unpublished M.Sc. thesis, McGill University, 102 pp.
- Mahecha, M. D., Reichstein, M., Lange, H., Carvalhais, N., Bernhofer, C., Grünwald, T., ... Seufert, G. (2007). Characterizing ecosystem-atmosphere interactions from short to interannual time scales. *Biogeosciences*, 4(5), 743–758.
- Malhotra, A., Roulet, N. T., Wilson, P., Giroux-Bougard, X. & Harris, L. I. (2016). Ecohydrological feedbacks in peatlands: an empirical test of the relationship among vegetation, microtopography and water table. *Ecohydrology*, 9(7), 1346-1357. <https://doi.org/10.1002/eco.1731>
- Maljanen, M., Sigurdsson, B. D., Guðmundsson, J., Óskarsson, H., Huttunen, J. T., & Martikainen, P. J. (2010). Greenhouse gas balances of managed peatlands in the Nordic countries – present knowledge and gaps. *Biogeosciences*, 7(9), 2711–2738. <https://doi.org/10.5194/bg-7-2711-2010>
- Marinier, M., Glatzel, S., & Moore, T. R. (2004). The role of cotton-grass (*Eriophorum vaginatum*) in the exchange of CO₂ and CH₄ at two restored peatlands, eastern Canada. *Écoscience*, 11(2), 141–149.
- Marushchak, M. E., Friberg, T., Biasi, C., Herbst, M., Johansson, T., Kiepe, I., ... Shurpali, N. J. (2016). Methane dynamics in the subarctic tundra: Combining stable isotope analyses, plot- and ecosystem-scale flux measurements. *Biogeosciences*, 13(2), 597–608.

- <https://doi.org/10.5194/bg-13-597-2016>
- Masek, J. G., Vermote, E. F., Saleous, N. E., Wolfe, R., Hall, F. G., Huemmrich, K. F., ... Lim, T.-K. (2006). A Landsat surface reflectance dataset for North America, 1990-2000. *IEEE Geoscience and Remote Sensing Letters*, 3(1), 68–72.
<https://doi.org/10.1109/LGRS.2005.857030>
- Mauder, M., & Foken, T. (2011). Documentation and Instruction Manual of the Eddy-Covariance Software Package TK3. Bayreuth, Germany. Retrieved from <https://epub.uni-bayreuth.de/342/1/ARBERG046.pdf>
- McCarter, C. P. R., & Price, J. S. (2013). The hydrology of the Bois-des-Bel bog peatland restoration: 10 years post-restoration. *Ecological Engineering*, 55, 73–81.
<https://doi.org/10.1016/j.ecoleng.2013.02.003>
- McCarter, C. P. R., & Price, J. S. (2015). The hydrology of the Bois-des-Bel peatland restoration: hydrophysical properties limiting connectivity between regenerated Sphagnum and remnant vacuum harvested peat deposit. *Ecohydrology*, 8(2), 173–187.
<https://doi.org/10.1002/eco.1498>
- McDermitt, D., Burba, G., Xu, L., Anderson, T., Komissarov, A., Riensche, B., ... Hastings, S. (2010). A new low-power, open-path instrument for measuring methane flux by eddy covariance. *Applied Physics B*, 102(2), 391–405. <https://doi.org/10.1007/s00340-010-4307-0>
- McNeil, P., & Waddington, J. M. (2003). Moisture controls on Sphagnum growth and CO₂ exchange on a cutover bog. *Journal of Applied Ecology*, 40(2), 354–367.
<https://doi.org/10.1046/j.1365-2664.2003.00790.x>
- McVeigh, P., Sottocornola, M., Foley, N., Leahy, P., & Kiely, G. (2014). Meteorological and functional response partitioning to explain interannual variability of CO₂ exchange at an Irish Atlantic blanket bog. *Agricultural and Forest Meteorology*, 194, 8–19.
<https://doi.org/10.1016/j.agrformet.2014.01.017>
- Minkinen, K., Laine, J., Nykänen, H., & Martikainen, P. J. (1997). *Importance of drainage ditches in emissions of methane from mires drained for forestry*. 27, 4.
- Moncrieff, J. B., Massheder, J. M., de Bruin, H., Elbers, J., Friborg, T., Heusinkveld, B., ... Verhoef, A. (1997). A system to measure surface fluxes of momentum, sensible heat, water vapour and carbon dioxide. *Journal of Hydrology*, 188–189(Supplement C), 589–

611. [https://doi.org/10.1016/S0022-1694\(96\)03194-0](https://doi.org/10.1016/S0022-1694(96)03194-0)
- Moncrieff, J., Clement, R., Finnigan, J., & Meyers, T. (2004). Averaging, Detrending, and Filtering of Eddy Covariance Time Series. In *Handbook of Micrometeorology* (pp. 7–31). Springer, Dordrecht. Retrieved from https://link.springer.com/chapter/10.1007/1-4020-2265-4_2
- Moore, T. R., & Dalva, M. (2001). Some controls on the release of dissolved organic carbon by plant tissues and soils. *Soil Science*, *166*(1), 38–47.
- Moore, T. R., & Knowles, R. (1989). The Influence of Water Table Levels on Methane and Carbon Dioxide Emissions from Peatland Soils. *Canadian Journal of Soil Science*, *69*(1), 33–38. <https://doi.org/10.4141/cjss89-004>
- Moore, T. R., Roulet, N. T., & Waddington, J. M. (1998). Uncertainty in Predicting the Effect of Climatic Change on the Carbon Cycling of Canadian Peatlands. *Climatic Change*, *40*(2), 229–245. <https://doi.org/10.1023/A:1005408719297>
- Moore, T., & Basiliko, N. (2006). Decomposition in Boreal Peatlands. In R. K. Wieder & D. H. Vitt (Eds.), *Boreal Peatland Ecosystems* (pp. 125–143). https://doi.org/10.1007/978-3-540-31913-9_7
- Moore, Tim R., Bubier, J. L., Frohling, S. E., Lafleur, P. M., & Roulet, N. T. (2002). Plant biomass and production and CO₂ exchange in an ombrotrophic bog. *Journal of Ecology*, *90*(1), 25–36. <https://doi.org/10.1046/j.0022-0477.2001.00633.x>
- Moore, Tim R., Young, A. D., Bubier, J. L., Humphreys, E. R., Lafleur, P. M., & Roulet, N. T. (2011). A Multi-Year Record of Methane Flux at the Mer Bleue Bog, Southern Canada. *Ecosystems*, *14*(4), 646–657. <https://doi.org/10.1007/s10021-011-9435-9>
- Myhre, G., Shindell, D., Bréon, F. M., Collins, W., Fuglestedt, J., Huang, J., ... others (2013). Anthropogenic and Natural Radiative Forcing. In T. F. Stocker, D. Qin, G.-K. Plattner, M. Tignor, S. K. Allen, J. Boschung, A. Nuaels, Y. Xia, V. Bex & P. M. Midgley (Eds.) *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* (pp. 659–740). Cambridge, UK and New York, NY: Cambridge University Press.
- Neubauer, S. C. (2014). On the challenges of modeling the net radiative forcing of wetlands: Reconsidering Mitsch et al. 2013. *Landscape Ecology*, *29*(4), 571–577. <https://doi.org/10.1007/s10980-014-9986-1>

- Neubauer, S. C., & Megonigal, J. P. (2015). Moving Beyond Global Warming Potentials to Quantify the Climatic Role of Ecosystems. *Ecosystems*, 18(6), 1000–1013.
<https://doi.org/10.1007/s10021-015-9879-4>
- Nijp, J. J., Limpens, J., Metselaar, K., Peichl, M., Nilsson, M. B., van der Zee, S. E. A. T. M., & Berendse, F. (2015). Rain events decrease boreal peatland net CO₂ uptake through reduced light availability. *Global Change Biology*, 21(6), 2309–2320.
<https://doi.org/10.1111/gcb.12864>
- Nilsson, M., Sagerfors, J., Buffam, I., Laudon, H., Eriksson, T., Grelle, A., Weslien, P. & Lindroth, A. (2008). Contemporary carbon accumulation in a boreal oligotrophic minerogenic mire – a significant sink after accounting for all C-fluxes. *Global Change Biology*, 14(10), 2317–2332. <https://doi.org/10.1111/j.1365-2486.2008.01654.x>
- Novick, K. A., Ficklin, D. L., Stoy, P. C., Williams, C. A., Bohrer, G., Oishi, A. C., ... Phillips, R. P. (2016). The increasing importance of atmospheric demand for ecosystem water and carbon fluxes. *Nature Climate Change*, 6(11), 1023–1027.
<https://doi.org/10.1038/nclimate3114>
- Nugent, K. A., Strachan, I. B., Strack, M., Roulet, N. T., & Rochefort, L. (2018). Multi-year net ecosystem carbon balance of a restored peatland reveals a return to carbon sink. *Global Change Biology*, 24(12), 5751–5768. <https://doi.org/10.1111/gcb.14449>
- Nugent K. A., Strachan, I. B., Roulet, N. T., Strack, M., Frohling, S. & Helbig, M. Early active restoration of peatlands substantially reduces climate impact. *Accepted in Environmental Research Letters*.
- Nwaishi, F., Petrone, R. M., Macrae, M. L., Price, J. S., Strack, M., & Andersen, R. (2016). Preliminary assessment of greenhouse gas emissions from a constructed fen on post-mining landscape in the Athabasca oil sands region, Alberta, Canada. *Ecological Engineering*, 95(Supplement C), 119–128. <https://doi.org/10.1016/j.ecoleng.2016.06.061>
- Olefeldt, D., & Roulet, N. T. (2012). Effects of permafrost and hydrology on the composition and transport of dissolved organic carbon in a subarctic peatland complex. *Journal of Geophysical Research: Biogeosciences*, 117(G1), G01005.
<https://doi.org/10.1029/2011JG001819>
- Olefeldt, D., Turetsky, M. R., Crill, P. M., & McGuire, A. D. (2013). Environmental and physical controls on northern terrestrial methane emissions across permafrost zones.

- Global Change Biology*, 19(2), 589–603. <https://doi.org/10.1111/gcb.12071>
- Olson, D. M., Griffis, T. J., Noormets, A., Kolka, R., & Chen, J. (2013). Interannual, seasonal, and retrospective analysis of the methane and carbon dioxide budgets of a temperate peatland. *Journal of Geophysical Research: Biogeosciences*, 118(1), 226–238. <https://doi.org/10.1002/jgrg.20031>
- Öquist, M. G., Wallin, M., Seibert, J., Bishop, K., & Laudon, H. (2009). Dissolved Inorganic Carbon Export Across the Soil/Stream Interface and Its Fate in a Boreal Headwater Stream. *Environmental Science & Technology*, 43(19), 7364–7369. <https://doi.org/10.1021/es900416h>
- Page, S. E., Rieley, J. O., & Banks, C. J. (2011). Global and regional importance of the tropical peatland carbon pool. *Global Change Biology*, 17(2), 798–818. <https://doi.org/10.1111/j.1365-2486.2010.02279.x>
- Papale, D., Reichstein, M., Aubinet, M., Canfora, E., Bernhofer, C., Kutsch, W., ... Yakir, D. (2006). Towards a standardized processing of Net Ecosystem Exchange measured with eddy covariance technique: algorithms and uncertainty estimation. *Biogeosciences*, 3(4), 571–583.
- Parish, F., Sirin, A. A., Charman, D. J., Joosten, H., Minaeva, T. Y., & Silvius, M. (2008). *Assessment on Peatlands, Biodiversity and Climate Change*. Global Environmental Centre, Kuala Lumpur, Malaysia and Wetlands International, Wageningen, The Netherlands.
- Parmentier, F. J. W., van Huissteden, J., van der Molen, M. K., Schaepman-Strub, G., Karsanaev, S. A., Maximov, T. C., & Dolman, A. J. (2011). Spatial and temporal dynamics in eddy covariance observations of methane fluxes at a tundra site in northeastern Siberia. *Journal of Geophysical Research: Biogeosciences*, 116(G3), G03016. <https://doi.org/10.1029/2010JG001637>
- Pastor, J., Solin, J., Bridgham, S. D., Updegraff, K., Harth, C., Weishampel, P., & Dewey, B. (2003). Global Warming and the Export of Dissolved Organic Carbon from Boreal Peatlands. *Oikos*, 100(2), 380–386.
- Peichl, M., Öquist, M., Löfvenius, M. O., Ilstedt, U., Sagerfors, J., Achim Grelle, ... Nilsson, M. B. (2014). A 12-year record reveals pre-growing season temperature and water table level threshold effects on the net carbon dioxide exchange in a boreal fen. *Environmental*

- Research Letters*, 9(5), 55006. <https://doi.org/10.1088/1748-9326/9/5/055006>
- Pelletier, L., Garneau, M., & Moore, T. R. (2011). Variation in CO₂ exchange over three summers at microform scale in a boreal bog, Eastmain region, Québec, Canada. *Journal of Geophysical Research: Biogeosciences*, 116(G3), G03019. <https://doi.org/10.1029/2011JG001657>
- Pelletier, L., Moore, T. R., Roulet, N. T., Garneau, M., & Beaulieu-Audy, V. (2007). Methane fluxes from three peatlands in the La Grande Rivière watershed, James Bay lowland, Canada. *Journal of Geophysical Research: Biogeosciences*, 112(G1), G01018. <https://doi.org/10.1029/2006JG000216>
- Petrone, R. M., Waddington, J. M., & Price, J. S. (2003). Ecosystem-scale flux of CO₂ from a restored vacuum harvested peatland. *Wetlands Ecology and Management*, 11(6), 419–432. <https://doi.org/10.1023/B:WETL.0000007192.78408.62>
- Popp, T. J., Chanton, J. P., Whiting, G. J., & Grant, N. (1999). Methane stable isotope distribution at a Carex dominated fen in north central Alberta. *Global Biogeochemical Cycles*, 13(4), 1063–1077. <https://doi.org/10.1029/1999GB900060>
- Poulin, M., Andersen, R., & Rochefort, L. (2013). A New Approach for Tracking Vegetation Change after Restoration: A Case Study with Peatlands. *Restoration Ecology*, 21(3), 363–371. <https://doi.org/10.1111/j.1526-100X.2012.00889.x>
- Poulin, M., Rochefort, L., Pellerin, S., & Thibault, J. (2004). Threats and protection for peatlands in Eastern Canada. *Géocarrefour*, 79(4), 331–344. <https://doi.org/10.4000/geocarrefour.875>
- Pouliot, R., Rochefort, L. & Karofeld, E. (2011). Initiation of microtopography in revegetated cutover peatlands. *Applied Vegetation Science*, 14(2), 158-171. <https://doi.org/10.1111/j.1654-109X.2010.01118.x>
- Prater, J. L., Chanton, J. P., & Whiting, G. J. (2007). Variation in methane production pathways associated with permafrost decomposition in collapse scar bogs of Alberta, Canada. *Global Biogeochemical Cycles*, 21(4), GB4004. <https://doi.org/10.1029/2006GB002866>
- Price, J. S., Branfireun, B. A., Waddington, J. M., & Devito, K. J. (2005). Advances in Canadian wetland hydrology, 1999–2003. *Hydrological Processes*, 19(1), 201–214. <https://doi.org/10.1002/hyp.5774>
- Proctor, C., & He, Y. (2017). Quantifying root extracts and exudates of sedge and shrub in

- relation to root morphology. *Soil Biology and Biochemistry*, 114, 168–180.
<https://doi.org/10.1016/j.soilbio.2017.07.006>
- Pullens, J. W. M., Sottocornola, M., Kiely, G., Toscano, P., & Gianelle, D. (2016). Carbon fluxes of an alpine peatland in Northern Italy. *Agricultural and Forest Meteorology*, 220, 69–82.
<https://doi.org/10.1016/j.agrformet.2016.01.012>
- Ramchunder, S. J., Brown, L. E., & Holden, J. (2012). Catchment-scale peatland restoration benefits stream ecosystem biodiversity. *Journal of Applied Ecology*, 49(1), 182–191.
<https://doi.org/10.1111/j.1365-2664.2011.02075.x>
- Rankin, T., Strachan, I. B., & Strack, M. (2018). Carbon dioxide and methane exchange at a post-extraction, unrestored peatland. *Ecological Engineering*, 122, 241–251
<https://doi.org/10.1016/j.ecoleng.2018.06.021>
- Reichstein, M., Falge, E., Baldocchi, D., Papale, D., Aubinet, M., Berbigier, P., ... Valentini, R. (2005). On the separation of net ecosystem exchange into assimilation and ecosystem respiration: review and improved algorithm. *Global Change Biology*, 11(9), 1424–1439.
<https://doi.org/10.1111/j.1365-2486.2005.001002.x>
- Renou-Wilson, F., Moser, G., Fallon, D., Farrell, C. A., Müller, C., & Wilson, D. (2019). Rewetting degraded peatlands for climate and biodiversity benefits: Results from two raised bogs. *Ecological Engineering*, 127, 547–560.
<https://doi.org/10.1016/j.ecoleng.2018.02.014>
- Renou-Wilson, F., Müller, C., Moser, G., & Wilson, D. (2016). To graze or not to graze? Four years greenhouse gas balances and vegetation composition from a drained and a rewetted organic soil under grassland. *Agriculture, Ecosystems & Environment*, 222, 156–170.
<https://doi.org/10.1016/j.agee.2016.02.011>
- Richardson, A. D., Hollinger, D. Y., Burba, G. G., Davis, K. J., Flanagan, L. B., Katul, G. G., ... Wofsy, S. C. (2006). A multi-site analysis of random error in tower-based measurements of carbon and energy fluxes. *Agricultural and Forest Meteorology*, 136(1–2), 1–18.
<https://doi.org/10.1016/j.agrformet.2006.01.007>
- Rinne, J., Riutta, T., Pihlatie, M., Aurela, M., Haapanala, S., Tuovinen, J.-P., ... Vesala, T. (2007). Annual cycle of methane emission from a boreal fen measured by the eddy covariance technique. *Tellus B*, 59(3), 449–457. <https://doi.org/10.1111/j.1600-0889.2007.00261.x>

- Rinne, J., Tuittila, E.-S., Peltola, O., Li, X., Raivonen, M., Alekseychik, P., ... Vesala, T. (2018). Temporal variation of ecosystem scale methane emission from a boreal fen in relation to temperature, water table position, and carbon dioxide fluxes. *Global Biogeochemical Cycles*, *32*(7), 1087–1106. <https://doi.org/10.1029/2017GB005747>
- Riutta, T., Laine, J., Aurela, M., Rinne, J., Vesala, T., Laurila, T., ... Tuittila, E.-S. (2007). Spatial variation in plant community functions regulates carbon gas dynamics in a boreal fen ecosystem. *Tellus B: Chemical and Physical Meteorology*, *59*(5), 838–852. <https://doi.org/10.1111/j.1600-0889.2007.00302.x>
- Rocheftort, 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*(1–2), 3–20. <https://doi.org/10.1023/A:1022011027946>
- Rocheftort, L., Vitt, D. H., & Bayley, S. E. (1990). Growth, Production, and Decomposition Dynamics of Sphagnum under Natural and Experimentally Acidified Conditions. *Ecology*, *71*(5), 1986–2000. <https://doi.org/10.2307/1937607>
- Romanowicz, E. A., Siegel, D. I., Chanton, J. P., & Glaser, P. H. (1995). Temporal variations in dissolved methane deep in the Lake Agassiz Peatlands, Minnesota. *Global Biogeochemical Cycles*, *9*(2), 197–212. <https://doi.org/10.1029/95GB00634>
- Roulet, N. T. (2000). Peatlands, carbon storage, greenhouse gases, and the Kyoto Protocol: Prospects and significance for Canada. *Wetlands*, *20*(4), 605–615. [https://doi.org/10.1672/0277-5212\(2000\)020\[0605:PCSGGA\]2.0.CO;2](https://doi.org/10.1672/0277-5212(2000)020[0605:PCSGGA]2.0.CO;2)
- 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*(2), 397–411. <https://doi.org/10.1111/j.1365-2486.2006.01292.x>
- Runkle, B. R. K., Sachs, T., Wille, C., Pfeiffer, E.-M., & Kutzbach, L. (2013). Bulk partitioning the growing season net ecosystem exchange of CO₂ in Siberian tundra reveals the seasonality of its carbon sequestration strength. *Biogeosciences*, *10*, 1337–1349.
- Rydin, H., Gunnarsson, U., & Sundberg, S. (2006). The Role of Sphagnum in Peatland Development and Persistence. In R. K. Wieder & D. H. Vitt (Eds.), *Boreal Peatland Ecosystems* (pp. 47–65). https://doi.org/10.1007/978-3-540-31913-9_4
- Salm, J.-O., Maddison, M., Tammik, S., Soosaar, K., Truu, J., & Mander, Ü. (2012). Emissions

- of CO₂, CH₄ and N₂O from undisturbed, drained and mined peatlands in Estonia. *Hydrobiologia*, 692(1), 41–55. <https://doi.org/10.1007/s10750-011-0934-7>
- Salonen, V. (1987). Relationship between the seed rain and the establishment of vegetation in two areas abandoned after peat harvesting. *Ecography*, 10(3), 171–174. <https://doi.org/10.1111/j.1600-0587.1987.tb00755.x>
- Scanlon, T. M., & Kiely, G. (2003). Ecosystem-scale measurements of nitrous oxide fluxes for an intensely grazed, fertilized grassland. *Geophysical Research Letters*, 30(16). <https://doi.org/10.1029/2003GL017454>
- Scharlemann, J. P., Tanner, E. V., Hiederer, R., & Kapos, V. (2014). Global soil carbon: Understanding and managing the largest terrestrial carbon pool. *Carbon Management*, 5(1), 81–91. <https://doi.org/10.4155/cmt.13.77>
- Schoellhamer, D. H. (2001). Singular spectrum analysis for time series with missing data. *Geophysical Research Letters*, 28(16), 3187–3190. <https://doi.org/10.1029/2000GL012698>
- 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(1), 265–279. <https://doi.org/10.1007/s10533-010-9440-7>
- Silvola, J., Alm, J., Ahlholm, U., Nykänen, H., & Martikainen, P. J. (1996). The contribution of plant roots to CO₂ fluxes from organic soils. *Biology and Fertility of Soils*, 23(2), 126–131. <https://doi.org/10.1007/BF00336052>
- Singleton, C. M., McCalley, C. K., Woodcroft, B. J., Boyd, J. A., Evans, P. N., Hodgkins, S. B., ... Tyson, G. W. (2018). Methanotrophy across a natural permafrost thaw environment. *The ISME Journal*, 12(10), 2544–2558. <https://doi.org/10.1038/s41396-018-0065-5>
- Smith, P., Bustamante, M., Ahammad, H., Clark, H., Dong, H., Elsidig, E. A., ... Tubiello, F. N. (2014). Agriculture, Forestry and Other Land Use (AFOLU). In *Climate Change 2014: Mitigation of Climate Change. Contribution of Working Group III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* (pp. 811–922). Cambridge, United Kingdom and New York, NY, USA: Cambridge University Press.
- Sonnentag, O., Hufkens, K., Teshera-Sterne, C., Young, A. M., Friedl, M., Braswell, B. H., ... Richardson, A. D. (2012). Digital repeat photography for phenological research in forest ecosystems. *Agricultural and Forest Meteorology*, 152, 159–177.

- <https://doi.org/10.1016/j.agrformet.2011.09.009>
- Strachan, I. B., Nugent, K. A., Crombie, S., & Bonneville, M.-C. (2015). Carbon dioxide and methane exchange at a cool-temperate freshwater marsh. *Environmental Research Letters*, *10*(6), 065006. <https://doi.org/10.1088/1748-9326/10/6/065006>
- 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*(1), 99–111. <https://doi.org/10.1007/s10533-015-0170-8>
- Strack, M., & Zuback, Y. C. A. (2013). Annual carbon balance of a peatland 10 yr following restoration. *Biogeosciences*, *10*(5), 2885–2896. <https://doi.org/10.5194/bg-10-2885-2013>
- Strack, M., Cagampan, J. P., Hassanpour Fard, G., Keith, A. M., Nugent, K. A., Rankin, T., Robinson, C., Strachan, I.B., Waddington, J.M., & Xu, B. (2016). Controls on plot-scale growing season CO₂ and CH₄ fluxes in restored peatlands: Do they differ from unrestored and natural sites? *Mires and Peat*, *17*, 1–18.
- 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. <https://doi.org/10.1016/j.ecoleng.2013.12.013>
- Strack, M., Kellner, E., & Waddington, J. M. (2005). Dynamics of biogenic gas bubbles in peat and their effects on peatland biogeochemistry. *Global Biogeochemical Cycles*, *19*(1), GB1003. <https://doi.org/10.1029/2004GB002330>
- Strack, M., Waddington, J. M., & Tuittila, E.-S. (2004). Effect of water table drawdown on northern peatland methane dynamics: Implications for climate change. *Global Biogeochemical Cycles*, *18*(4), GB4003. <https://doi.org/10.1029/2003GB002209>
- Strack, M., Tóth, K., Bourbonniere, R., & Waddington, J. M. (2011). Dissolved organic carbon production and runoff quality following peatland extraction and restoration. *Ecological Engineering*, *37*(12), 1998–2008. <https://doi.org/10.1016/j.ecoleng.2011.08.015>
- Strack, Maria, Zuback, Y., McCarter, C., & Price, J. (2015). Changes in dissolved organic carbon quality in soils and discharge 10 years after peatland restoration. *Journal of Hydrology*, *527*, 345–354. <https://doi.org/10.1016/j.jhydrol.2015.04.061>
- Ström, L., & Christensen, T. R. (2007). Below ground carbon turnover and greenhouse gas exchanges in a sub-arctic wetland. *Soil Biology and Biochemistry*, *39*(7), 1689–1698. <https://doi.org/10.1016/j.soilbio.2007.01.019>

- Ström, L., Ekberg, A., Mastepanov, M., & Røjle Christensen, T. (2003). The effect of vascular plants on carbon turnover and methane emissions from a tundra wetland. *Global Change Biology*, 9(8), 1185–1192. <https://doi.org/10.1046/j.1365-2486.2003.00655.x>
- Ström, L., Mastepanov, M., & Christensen, T. R. (2005). Species-specific Effects of Vascular Plants on Carbon Turnover and Methane Emissions from Wetlands. *Biogeochemistry*, 75(1), 65–82. <https://doi.org/10.1007/s10533-004-6124-1>
- Ström, L., Tagesson, T., Mastepanov, M., & Christensen, T. R. (2012). Presence of *Eriophorum scheuchzeri* enhances substrate availability and methane emission in an Arctic wetland. *Soil Biology and Biochemistry*, 45, 61–70. <https://doi.org/10.1016/j.soilbio.2011.09.005>
- Sulman, B. N., Desai, A. R., Saliendra, N. Z., Lafleur, P. M., Flanagan, L. B., Sonnentag, O., ... 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(19), L19702. <https://doi.org/10.1029/2010GL044018>
- Sundh, I., Nilsson, M., Granberg, G., & Svensson, B. H. (1994). Depth distribution of microbial production and oxidation of methane in northern boreal peatlands. *Microbial Ecology*, 27(3), 253–265. <https://doi.org/10.1007/BF00182409>
- Sundh, I., Nilsson, M., Mikkilä, C., Granberg, G., & Svensson, B. H. (2000). Fluxes of methane and carbon dioxide on peat-mining areas in Sweden. *AMBIO: A Journal of the Human Environment*, 29(8), 499–503. <https://doi.org/10.1579/0044-7447-29.8.499>
- Suyker, A. E., Verma, S. B., Clement, R. J., & Billesbach, D. P. (1996). Methane flux in a boreal fen: Season-long measurement by eddy correlation. *Journal of Geophysical Research: Atmospheres*, 101(D22), 28637–28647. <https://doi.org/10.1029/96JD02751>
- Swenson, M. M., Regan, S., Bremmers, D. T. H., Lawless, J., Saunders, M., & Gill, L. W. (2019). Carbon balance of a restored and cutover raised bog: Implications for restoration and comparison to global trends. *Biogeosciences*, 16(3), 713–731. <https://doi.org/10.5194/bg-16-713-2019>
- Tagesson, T., Mölder, M., Mastepanov, M., Sigsgaard, C., Tamstorf, M. P., Lund, M., ... Ström, L. (2012). Land-atmosphere exchange of methane from soil thawing to soil freezing in a high-Arctic wet tundra ecosystem. *Global Change Biology*, 18(6), 1928–1940. <https://doi.org/10.1111/j.1365-2486.2012.02647.x>
- 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: Biogeosciences*, 112(G1), G01014.
<https://doi.org/10.1029/2006JG000210>
- Tuittila, E.-S., Komulainen, V.-M., Vasander, H., & Laine, J. (1999). Restored cut-away peatland as a sink for atmospheric CO₂. *Oecologia*, 120(4), 563–574.
<https://doi.org/10.1007/s004420050891>
- Tuittila, E.-S., Komulainen, V.-M., Vasander, H., Nykänen, H., Martikainen, P. J., & Laine, J. (2000). Methane dynamics of a restored cut-away peatland. *Global Change Biology*, 6(5), 569–581. <https://doi.org/10.1046/j.1365-2486.2000.00341.x>
- Tuittila, E.-S., Vasander, H., & Laine, J. (2004). Sensitivity of C sequestration in reintroduced Sphagnum to water-level variation in a cutaway peatland. *Restoration Ecology*, 12(4), 483–493. <https://doi.org/10.1111/j.1061-2971.2004.00280.x>
- Vanselow-Algan, M., Schmidt, S. R., Greven, M., Fiencke, C., Kutzbach, L., & Pfeiffer, E.-M. (2015). High methane emissions dominated annual greenhouse gas balances 30 years after bog rewetting. *Biogeosciences*, 12(14), 4361–4371. <https://doi.org/10.5194/bg-12-4361-2015>
- Vermote, E., Justice, C., Claverie, M., & Franch, B. (2016). Preliminary analysis of the performance of the Landsat 8/OLI land surface reflectance product. *Remote Sensing of Environment*, 185(Supplement C), 46–56. <https://doi.org/10.1016/j.rse.2016.04.008>
- Vickers, D., & Mahrt, L. (1997). Quality control and flux sampling problems for tower and aircraft data. *Journal of Atmospheric and Oceanic Technology*, 14(3), 512–526.
[https://doi.org/10.1175/1520-0426\(1997\)014<0512:QCAFSP>2.0.CO;2](https://doi.org/10.1175/1520-0426(1997)014<0512:QCAFSP>2.0.CO;2)
- Waddington, J. M., & Day, S. M. (2007). Methane emissions from a peatland following restoration. *Journal of Geophysical Research: Biogeosciences*, 112(G3), G03018.
<https://doi.org/10.1029/2007JG000400>
- Waddington, J. M., & McNeil, P. (2002). Peat oxidation in an abandoned cutover peatland. *Canadian Journal of Soil Science*, 82(3), 279–286. <https://doi.org/10.4141/S01-043>
- Waddington, J. M., & Roulet, N. T. (2000). Carbon balance of a boreal patterned peatland. *Global Change Biology*, 6(1), 87–97. <https://doi.org/10.1046/j.1365-2486.2000.00283.x>
- 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. [https://doi.org/10.1016/S0925-8574\(03\)00025-9](https://doi.org/10.1016/S0925-8574(03)00025-9)
- Waddington, J. M., Lucchese, M. C., & Duval, T. P. (2011). Sphagnum moss moisture retention following the re-vegetation of degraded peatlands. *Ecohydrology*, 4(3), 359–366. <https://doi.org/10.1002/eco.130>
- Waddington, J. M., Roulet, N. T., & Swanson, R. V. (1996). Water table control of CH₄ emission enhancement by vascular plants in boreal peatlands. *Journal of Geophysical Research: Atmospheres*, 101(D17), 22775–22785. <https://doi.org/10.1029/96JD02014>
- Waddington, J. M., Strack, M., & Greenwood, M. J. (2010). Toward 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(G1), G01008. <https://doi.org/10.1029/2009JG001090>
- Waddington, J. M., Tóth, K., & Bourbonniere, R. (2008). Dissolved organic carbon export from a cutover and restored peatland. *Hydrological Processes*, 22(13), 2215–2224. <https://doi.org/10.1002/hyp.6818>
- Walling, D. E., & Webb, B. W. (1985). Estimating the discharge of contaminants to coastal waters by rivers: Some cautionary comments. *Marine Pollution Bulletin*, 16(12), 488–492. [https://doi.org/10.1016/0025-326X\(85\)90382-0](https://doi.org/10.1016/0025-326X(85)90382-0)
- Wang, M. & Moore, T. R. (2014). Carbon, nitrogen, phosphorus, and potassium stoichiometry in an ombrotrophic peatland reflects plant functional type. *Ecosystems*, 17(4), 673–684. <https://doi.org/10.1007/s10021-014-9752-x>
- Wang, M., Wu, J., Lafleur, P. M., Luan, J., Chen, H., & Zhu, X. (2018). Temporal shifts in controls over methane emissions from a boreal bog. *Agricultural and Forest Meteorology*, 262, 120–134. <https://doi.org/10.1016/j.agrformet.2018.07.002>
- Ward, S. E., Ostle, N. J., Oakley, S., Quirk, H., Henrys, P. A., & Bardgett, R. D. (2013). Warming effects on greenhouse gas fluxes in peatlands are modulated by vegetation composition. *Ecology Letters*, 16(10), 1285–1293. <https://doi.org/10.1111/ele.12167>
- Webb, E. K., Pearman, G. I., & Leuning, R. (1980). Correction of flux measurements for density effects due to heat and water vapour transfer. *Quarterly Journal of the Royal Meteorological Society*, 106(447), 85–100. <https://doi.org/10.1002/qj.49710644707>
- Wehr, R., Munger, J. W., McManus, J. B., Nelson, D. D., Zahniser, M. S., Davidson, E. A., ...

- Saleska, S. R. (2016). Seasonality of temperate forest photosynthesis and daytime respiration. *Nature*, 534(7609), 680–683. <https://doi.org/10.1038/nature17966>
- Whalen, S. C. (2005). Biogeochemistry of methane exchange between natural wetlands and the atmosphere. *Environmental Engineering Science*, 22(1), 73–94. <https://doi.org/10.1089/ees.2005.22.73>
- Whiticar, M. J, Faber, E., & Schoell, M. (1986). Biogenic methane formation in marine and freshwater environments: CO₂ reduction vs. acetate fermentation—Isotope evidence. *Geochimica et Cosmochimica Acta*, 50(5), 693–709. [https://doi.org/10.1016/0016-7037\(86\)90346-7](https://doi.org/10.1016/0016-7037(86)90346-7)
- Whiticar, Michael J. (1999). Carbon and hydrogen isotope systematics of bacterial formation and oxidation of methane. *Chemical Geology*, 161(1), 291–314. [https://doi.org/10.1016/S0009-2541\(99\)00092-3](https://doi.org/10.1016/S0009-2541(99)00092-3)
- Wilson, D., Alm, J., Laine, J., Byrne, K. A., Farrell, E. P., & Tuittila, E.-S. (2009). Rewetting of cutaway peatlands: Are we re-creating hot spots of methane emissions? *Restoration Ecology*, 17(6), 796–806. <https://doi.org/10.1111/j.1526-100X.2008.00416.x>
- Wilson, D., Dixon, S. D., Artz, R. R. E., Smith, T. E. L., Evans, C. D., Owen, H. J. F., ... Renou-Wilson, F. (2015). Derivation of greenhouse gas emission factors for peatlands managed for extraction in the Republic of Ireland and the United Kingdom. *Biogeosciences; Katlenburg-Lindau*, 12(18), 5291. <https://doi.org/http://dx.doi.org/10.5194/bg-12-5291-2015>
- Wilson, D., Farrell, C. A., Fallon, D., Moser, G., Müller, C., & Renou-Wilson, F. (2016). Multiyear greenhouse gas balances at a rewetted temperate peatland. *Global Change Biology*, 22(12), 4080–4095. <https://doi.org/10.1111/gcb.13325>
- Wilson, D., Farrell, C., Mueller, C., Hepp, S., & Renou-Wilson, F. (2013). Rewetted industrial cutaway peatlands in western Ireland: a prime location for climate change mitigation? *Mires and Peat*, 11, 1–22.
- Wilson, David, Tuittila, E.-S., Alm, J., Laine, J., Farrell, E. P., & Byrne, K. A. (2007). Carbon dioxide dynamics of a restored maritime peatland. *Ecoscience*, 14(1), 71–80. [https://doi.org/10.2980/1195-6860\(2007\)14\[71:CDDOAR\]2.0.CO;2](https://doi.org/10.2980/1195-6860(2007)14[71:CDDOAR]2.0.CO;2)
- Wilson, L., Wilson, J., Holden, J., Johnstone, I., Armstrong, A., & Morris, M. (2011). Ditch blocking, water chemistry and organic carbon flux: Evidence that blanket bog restoration

- reduces erosion and fluvial carbon loss. *Science of The Total Environment*, 409(11), 2010–2018. <https://doi.org/10.1016/j.scitotenv.2011.02.036>
- Worrall, F., Burt, T. P., Rowson, J. G., Warburton, J., & Adamson, J. K. (2009). The multi-annual carbon budget of a peat-covered catchment. *Science of The Total Environment*, 407(13), 4084–4094. <https://doi.org/10.1016/j.scitotenv.2009.03.008>
- Worrall, F., Reed, M., Warburton, J., & Burt, T. (2003). Carbon budget for a British upland peat catchment. *Science of The Total Environment*, 312(1–3), 133–146. [https://doi.org/10.1016/S0048-9697\(03\)00226-2](https://doi.org/10.1016/S0048-9697(03)00226-2)
- Yavitt, J. B., Williams, C. J., & Wieder, R. K. (1997). Production of methane and carbon dioxide in peatland ecosystems across North America: Effects of temperature, aeration, and organic chemistry of peat. *Geomicrobiology Journal*, 14(4), 299–316. <https://doi.org/10.1080/01490459709378054>
- Yu, Z. C. (2012). Northern peatland carbon stocks and dynamics: A review. *Biogeosciences*, 9(10), 4071–4085. <https://doi.org/10.5194/bg-9-4071-2012>
- Yu, Z., Loisel, J., Brosseau, D. P., Beilman, D. W., & Hunt, S. J. (2010). Global peatland dynamics since the Last Glacial Maximum. *Geophysical Research Letters*, 37(13), L13402. <https://doi.org/10.1029/2010GL043584>

Appendix I

Chapter 3

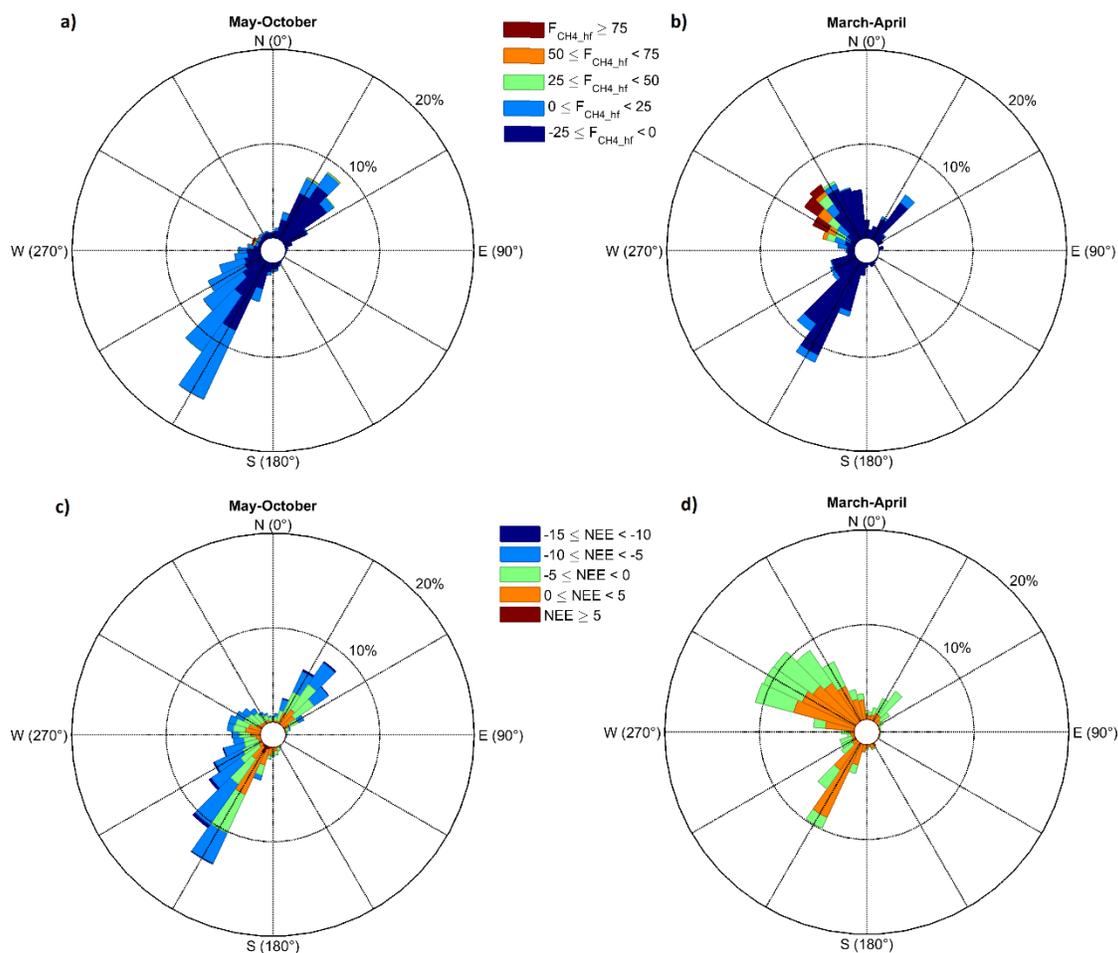


Figure I.1 – The spectral signature of the CH₄ flux footprint is expected to vary at a higher frequency (*e.g.* hours) in relation to rapid changes in footprint composition, with instantaneous effects on flux measurements. The top two wind roses show the relative occurrence of high frequency CH₄ flux signals ($\text{nmol m}^{-2} \text{s}^{-1}$) in different wind directions (30° bins) during the (a) warm season and (b) Spring season. Blue is low uptake to low emission while red is emission greater than $75 \text{ nmol m}^{-2} \text{s}^{-1}$. The frequency and magnitude of NEE ($\mu\text{mol m}^{-2} \text{s}^{-1}$) by wind direction during the (c) warm season and (d) Spring season is shown to illustrate that NEE varies little by direction in comparison.

Table I.1 – Eddy covariance-derived seasonal CH₄ emissions from undisturbed or semi-intact northern peatlands

Region	Site	Ecosystem	Climate	Flux (g C m ⁻²)	Study Period	Years	Reference
NE Poland	Kopytkowo	Minerogenic	Temperate	18.3-22.1	annual	2	Fortuniak et al. (2016)
SE Canada	Mer Bleue	Ombrogenic	Cool-Temp.	1.6-3.1	15 May-30 Sep	2	Brown et al. (2014)
West Canada	-	Minerogenic	Boreal	2.4	24 May-26 Sep	1	Long et al. (2010)
Southern Finland	Siikaneva	Minerogenic	Boreal	11.4	29 Apr-30 Nov	1	Rinne et al. (2007)
Central Canada	-	Minerogenic	Boreal	18.3	19 May-4 Oct	1	Sukyer et al. (1996)
NW Canada	Scotty Creek	Ombrogenic	Boreal	9.7	1 Apr-31 Oct	1	Helbig et al. (2017)
Interior Alaska	Tanana Flats	Ombrogenic	Boreal	3.7	21 Apr-21 Sep	1	Euskirchen et al. (2014)
HBL Canada	Churchill	Minero. (palsa)	Subarctic	5.3	30 May-16 Nov	4	Hanis et al. (2013)
North Sweden	Stordalen	Minero. (palsa)	Subarctic	14.1-16.8	18 Apr-22 Oct	2	Jackowicz-Korczynski et al. (2010)
NE Siberia	Chokurdakh	Minero. (tundra)	High-Arctic	1.9	5 Jul-3 Aug	2	Parmentier et al. (2011)
NE Greenland	Zackenbergl	Minerogenic	High-Arctic	2.8	1 Jun-26 Aug	1	Friberg et al. (2000)
NE Greenland	Rylekaerne	Minero. (tundra)	High-Arctic	6.5-7.6	16 May-28 Oct	2	Tagesson et al. (2012)
Northern Italy	Monte Bondone	Minerogenic	Mountain	3.2	late Dec-late Sep	1	Pullens et al. (2016)

Appendix II

Chapter 5

II.1 Study sites information

The four tables seen below detail the main characteristics of the study sites, what measurements occurred, how the data was managed and the annual flux results.

Table II.1 Main characteristics of the study sites

Site Name	Coordinates	Climate	Ecosystem State/Type	Age at study start (yr)	Vegetation Composition	T (°C)	P (mm)	WTD (m)	References
Bois-des-Bel	47.97 N, 69.43 W	Temperate	Abandoned peat extraction site	19	BP, O	3.5 ± 2.9	964	0.55	Waddington et al., 2010
			Restored peat extraction site	1	BP, S, E, O			0.32	Waddington et al., 2010
Mer Bleue	45.41 N, 75.52 W	Temperate continental	Intact ombrogenic bog	8500	S, ES, E, O	6.4 ± 0.8	943	0.41 ± 0.06	Nugent et al., 2018
Saint-Alexandre	47.73 N, 69.61 W	Temperate	Abandoned peat extraction site	14	BP, E, O	3.5 ± 2.9	964	0.46 ± 0.14	Rankin et al., 2018; this study
Seba Beach Restored	53.46 N, 114.88 W	Boreal continental	Restored peat extraction site	1	S, C, E, O	3.5 ± 1.1	550	0.45 ± 0.12	This study
Seba Beach Unrestored	53.46 N, 114.88 W	Boreal continental	Abandoned peat extraction site	1	BP	3.5 ± 1.1	550	0.66 ± 0.07	This study
Seba Beach Wet	53.46 N, 114.88 W	Boreal continental	Restored peat extraction site	4	O, S, BP, E	3.5 ± 1.1	550	0.34 ± 0.07	This study

Temperature (T) and precipitation (P) are 30-year climate normals (1981-2010; Environment Canada), water table depth (WTD) refers to seasonal averages, with positive values indicating a water table below the surface.

S, *Sphagnum* spp.; ES, Ericaceous shrub spp.; E, *Eriophorum* spp.; C, *Carex* spp.; O, others; BP, bare peat.

Table II.2 Site-specific measurement techniques and instrumentation for CO₂, CH₄ and DOC fluxes

Site name	Timeline	Measurement technique, CO ₂ fluxes	Measurement technique, CH ₄ fluxes	DOC fluxes	References
Bois-des-Bel	1999-2001	-	-	Yes	Waddington et al., 2008
	1999-2002	-	Closed chambers	-	Waddington and Day, 2007
	2000-2001	Eddy covariance LI-7500	-	-	Petrone et al., 2003
Mer Bleue	2014-2016	Eddy covariance LI-7500A	Eddy covariance LI-7700	Yes	Nugent et al., 2018
	1999-2015	Eddy covariance LI-7000	Autochambers LI-6262	Yes	Nugent et al., 2018
Saint-Alexandre	2014-2015	Eddy covariance LI-7500A	Eddy covariance LI-7700	-	Rankin et al., 2018; this study
Seba Beach Restored	2013-2015	-	Closed chambers	-	This study
	2014-2015	Eddy covariance LI-7500A	-	-	This study
	2016	Eddy covariance LI-7500A	Eddy covariance LI-7700	-	This study
Seba Beach Unrestored	2013-2015	-	Closed chambers	-	This study
	2014	Eddy covariance LI-7500A	-	-	This study
Seba Beach Wet	2016	Eddy covariance LI-7500A	Eddy covariance LI-7700	-	This study

Table II.3 Site-specific gap-filling methods for CO₂ and CH₄

Site name	Timeline	Gap-filling CO ₂	Gap-filling CH ₄	References
Bois-des-Bel	1999-2002	-	Weighted average seasonal flux	Waddington and Day, 2007
	2000-2001	Time dependent light and temperature response (e.g. Barr et al., 2004)	-	Petrone et al., 2003
	2014-2016	Marginal distribution sampling method (MDS; Reichstein et al., 2005)	MDS, exponential temperature model	Nugent et al., 2018
Mer Bleue	1999-2015	Time dependent light and temperature response	Linear regression with log 10 flux	Roulet et al., 2007; Lai et al., 2012
Saint-Alexandre	2014-2015	MDS	MDS, exponential temperature model	Refer to Nugent et al., 2018
Seba Beach Restored	2013-2015	-	Weighted average seasonal flux	refer to Strack et al., 2016
	2014-2015	MDS	-	refer to Nugent et al., 2018
	2016	MDS	MDS, exponential temperature model	refer to Nugent et al., 2018
Seba Beach Unrestored	2013-2015	-	Weighted average seasonal flux	refer to Strack et al., 2016
	2014	MDS	-	refer to Nugent et al., 2018
Seba Beach Wet	2016	MDS	MDS, exponential temperature model	refer to Nugent et al., 2018

Table II.4 Annual CO₂, CH₄ and DOC fluxes at the study sites

Site name	Period	Chronosequence	CO ₂ (95% CI) (g C m ⁻² yr ⁻¹)	CH ₄ (95% CI) (g C m ⁻² yr ⁻¹)	DOC (g C m ⁻² yr ⁻¹)
Bois-des-Bel (abandoned section)	1999	UNR	-	0.1	31.7
	2000	UNR	-	0.9	33.7
	2001	UNR	-	0.4	48.6
	2002	UNR	-	1.0	-
Bois-des-Bel (section restored in Fall 1999)	1999	UNR	-	0.0	26.2
	2000	RES-1yr	695 (587-804) ²	0.1	7.9
	2001	RES-1yr	685 (577-794) ²	1.4	10.6
	2002	RES-4yr	-	4.1	-
	2014	RES-15yr	-94 (-102--82)	4.4 (4.3-4.5)	9.2
	2015	RES-15yr	-105 (-111--97)	4.5 (4.3-4.6)	6.6
	2016	RES-15yr	-70 (-76--63)	4.2 (4.1-4.4)	4.8
Mer Bleue	1999-2015	REF (RES-30yr)	-73 ± 40 ¹	6 ± 4 ¹	17 ± 3 ¹
Saint-Alexandre	2014	UNR-15yr	173 (169-177)	0.5 (0.5-0.6)	-
	2015	UNR-15yr	259 (253-274)	0.8 (0.7-0.8)	-
Seba Beach Restored	2013	RES-1yr	-	1.8	-
	2014	RES-1yr	275 (271-279)	0.9	-
	2015	RES-1yr	362 (358-366)	1.5	-
	2016	RES-4yr	225 (220-231)	1.2 (1.1-1.3)	-
	2013	UNR-1yr	-	0.7	-
Seba Beach Unrestored	2014	UNR-1yr	445 (426-460)	0.4	-
	2015	UNR-1yr	-	0.5	-
Seba Beach Wet	2016	RES-4yr	65 (54-72)	7.6 (7.0-8.0)	-

¹ Mean ± SD for the 17-year period

² Annual flux was estimated from the published seasonal flux by adding 1 (± 0.5) g C m⁻² day⁻¹ for the missing period

II.2 Additional model methodology

We simulated the peatland atmospheric flux perturbations as annual net fluxes of CO₂ and CH₄ from peatland initiation to 500 years after peat extraction termination that occurred in 1980 CE. The spin up period, of peatland initiation through to extraction termination, was used to establish an atmospheric concentration perturbation baseline. Peat accumulation at Bois-des-Bel was 3 m over 6985 years (Lavoie et al., 2001) and was represented as a constant CO₂ sequestration rate of 22 g CO₂-C m⁻² yr⁻¹. Peat extraction lasted 10 years, during which 334 g CO₂-C m⁻² yr⁻¹ and 0.5 g CH₄-C m⁻² yr⁻¹ was emitted. The CO₂ flux is based on a 19-yr peat oxidation/erosion rate of 5.7 ± 1.1 mm yr⁻¹ measured at Bois-des-Bel prior to restoration (Waddington and McNeil,

2002). This gas loss during extraction implicitly includes wind erosion and particulate organic carbon (POC) export, the latter of which can represent upward of 65% of total carbon loss at peat extraction sites (excluding extracted peat) (Evans et al., 2016). For this analysis, we assume that any POC exported was oxidized during the year it was lost. The CH₄ flux for the extraction period is a multiplication of ditch cover fraction (0.05) and mean growing season ditch emissions (10.9 g CH₄-C m⁻²) measured in a section of Bois-des-Bel that remains unrestored (Waddington and Day, 2007). While we lack direct measurements from peatlands under extraction, we expect the fluxes to be broadly similar, as no management actions occurred at the site after extraction termination.

II.3 Additional model analysis including nitrous oxide

We neglected N₂O emissions in our main analysis because we had insufficient data from our undisturbed, unrestored and restored post-extraction peatlands to make a defensible estimate of mean annual fluxes. IPCC Tier 1 assumes a N₂O flux of 0.03 g N m⁻² yr⁻¹ when drained and a negligible flux after rewetting (IPCC, 2014). The N₂O lifetime in the atmosphere is 121 years (Myhre et al., 2013), whereby a constant addition to the atmosphere will reach equilibrium after about 500 years. Thus, the climate impact of even a small amount of N₂O is likely non-negligible over the 500-year time frame of our study. To test this, we conducted an additional IPCC Tier 1 simulation with N₂O included. Figure S3.1, which compares the no rewetting scenario with and without N₂O, clearly demonstrates the N₂O emission rates being discussed for post-extraction peatlands have a minimal climate impact relative to CO₂ and CH₄.

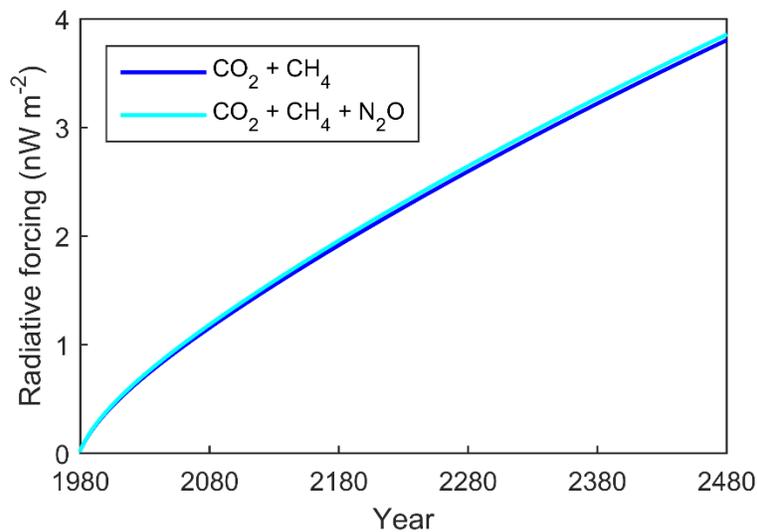


Figure II.1 – Instantaneous net radiative forcing of a post-extraction unrestored peatland using IPCC Tier 1 emission factors with (light blue line) and without (dark blue line) N₂O emission included.

II.4 Comparison of atmospheric perturbation model results to applying the global warming potential metric

In Table S4.1, modelled RF and GWP show both a net warming effect for the Drained/Unrestored scenario. However, RF is increasing with longer timeframes while GWP is decreasing (Table S4.1). The difference is caused by considering a one-time pulse emission for GWP vs. continuous emissions for the modelled RF. Constant net CO₂ emissions for the Drained/Unrestored scenario lead to a steadily increasing positive RF. In contrast, the shorter atmospheric lifetime of CH₄ (compared to CO₂) causes GWP to decrease from the 20- to 100-year timeframe (Table S4.1). If continuous CH₄ emissions would be considered, instantaneous RF would increase and then remain constant after a few decades (Neubauer & Megonigal, 2015). Since a drained/unrestored peatland is a constant source of CO₂ and CH₄, modelled instantaneous RF is the appropriate tool to assess climate impacts.

For the Prompt Rewetted/Restored scenario, GWP is positive for Tier 1 for both timeframes, positive for Tier 2 for the 20-year timeframe and negative for Tier 2 for the 100-year timeframe (Table S4.1). The larger reductions in GWP between the 20- and 100-year timeframe compared to the Drained/Unrestored scenario are due to larger contributions from CH₄ emissions.

For the Tier 2, the Prompt Rewetted/Restored scenario has a cooling effect (i.e. negative RF) for the 100- and 500-year timeframe (Table S4.1). The switch is caused by the development of a continuous net CO₂ sink, which leads to a cooling effect due to the longer atmospheric lifetime of CO₂ compared to CH₄. In this case, using a GWP approach does also identify the cooling effect of prompt rewetting/restoring activities within a century.

Table II.5 Comparing modelled instantaneous net radiative forcing (RF) to applying the global warming potential (GWP) metric. IPCC emission factors (Tier 1) and fluxes at UNR-15yr and RES-15yr (Tier 2) (see Table 1) were used to calculate GWP (no carbon-climate feedbacks: $GWP_{20} = 84$; $GWP_{100} = 28$).

	RF ($nW m^{-2}$)			GWP ($g CO_2e m^{-2} yr^{-1}$)		
	at 20 yr	at 100 yr	at 500 yr	over 20 yr	over 100 yr	over 100 yr
Drained/Unrestored						
Tier 1	0.36 (0.13 - 0.59)	1.15 (0.45 - 1.79)	3.80 (1.53 - 5.81)	1405 (457 - 2207)	1220 (420 - 1874)	
Tier 2	0.18 (0.11 - 0.25)	0.76 (0.43 - 1.08)	2.90 (1.76 - 4.07)	963 (592 - 1341)	926 (570 - 1289)	
20-yr Delay						
Tier 1	0.36 (0.13 - 0.59)	0.46 (-0.07 - 2.29)	0.28 (-0.56 - 2.70)	-	-	-
Tier 2	0.18 (0.11 - 0.25)	0.14 (-0.25 - 0.58)	-0.41 (-1.38 - 0.62)	-	-	-
Prompt						
Tier 1	0.27 (-0.04 - 1.58)	0.32 (-0.17 - 2.06)	0.31 (-0.63 - 2.53)	1027 (-160 - 5190)	339 (-182 - 1862)	
Tier 2	0.03 (-0.09 - 0.10)	-0.09 (-0.46 - 0.21)	-0.57 (-1.52 - 0.33)	190 (85 - 299)	-140 (-229 - -45)	

II.5 Relative climate benefit of peatland restoration actions

Table II.6

The relative climate benefit of peatland restoration actions at 20 years, calculated by defining a reference and calculating the difference in net radiative forcing between the baseline and alternative management action.

	Prompt active restoration	Active restoration	No restoration	Prompt average rewetting	Average rewetting	No rewetting
Prompt active restoration	-	-83%	-83%	-89%	-92%	-92%
Active restoration		-	0%	-32%	-50%	-50%
No restoration			-	-32%	-50%	-50%
Prompt average rewetting				-	-26%	-26%
Average rewetting					-	0%
No rewetting						-

Example: after 20 years, prompt active restoration results in an 83% reduction in RF over no restoration.