UNIVERSITÉ DU QUÉBEC À MONTRÉAL

INTEGRATING BEAVER PONDS AS A COMPONENT OF CARBON EMISSIONS FROM BOREAL INLAND WATERS

MÉMOIRE

PRÉSENTÉ

COMME EXIGENCE PARTIELLE

DE LA MAÎTRISE EN BIOLOGIE

PAR

FACUNDO SMUFER SIRUELA

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UNIVERSITÉ DU QUÉBEC À MONTRÉAL

INTÉGRER LES ÉTANGS DE CASTOR AU BILAN DES ÉMISSIONS DE CARBONE DES EAUX CONTINENTALES BORÉALES

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RÉSUMÉ

Le rétablissement progressif des populations de castors dans le biome boréal d'Amérique du Nord conduit à la prolifération de leurs étangs au sein du réseau aquatique. Des études écosystémiques ont démontré que ces étangs étaient des points chauds pour la production du dioxyde de carbone (CO_2) et du méthane (CH_4). Toutefois, leurs émissions sont rarement intégrées aux estimations des bilans de carbone (C) des eaux continentales du biome boréal, et constituent donc une source d'incertitude potentiellement importante. L'objectif de cette étude était d'intégrer les émissions de C provenant des étangs de castor au bilan des émissions de C de l'ensemble du réseau aquatique. Nous avons réalisé cet exercice à l'échelle d'un bassin versant (13,000 km^2) situé dans la région de l'Abitibi, au Québec, Canada. En utilisant l'imagerie satellitaire à très haute résolution, nous avons estimé l'étendue et le nombre d'étangs de castors dans ce bassin versant, puis extrapolé des taux d'émission de CO_2 et de CH_4, échantillonnés au préalable, au nombre total d'étangs. Selon nos calculs, les étangs de castor représenteraient 7 % du total des émissions de C annuelles du réseau aquatique et seraient approximativement responsables de 6 % et 18 % des émissions annuelles de CO_2 et de CH_4, respectivement. Les informations fournies par cette étude améliorent notre compréhension du rôle des étangs de castor dans le bilan des échanges de C au sein du biome boréal, non seulement à l'heure actuelle, mais aussi dans le cadre de la prédiction de scénarios qui tiendraient compte du réchauffement climatique et de la croissance des populations de castors. Cette étude a également produit un ensemble de données qui pourraient être utilisées dans de nouvelles études hydrologiques, biogéochimiques et écologiques liées à la présence du castor dans le paysage.

Mots clés : Télédétection, étangs de castor, dioxyde de carbone, méthane, carbone.

ABSTRACT

The ongoing recovery of beaver populations across the boreal biome of North America entails an increasing proliferation of beaver ponds in the aquatic networks. Ecosystem-scale studies have demonstrated that beaver ponds are hotspots of CO_2 and CH_4 production. However, beaver pond C emissions have rarely been incorporated into estimates of inland water C budgets. Therefore, this potentially represents a major source of uncertainty for the C budget of the boreal biome. The objective of this study was to integrate C emissions from beaver ponds into a whole-aquatic network assessment. We conducted this exercise in a selected watershed located in the region of Abitibi, Québec, Canada. Using very-high-resolution satellite imagery, we estimated the number and surface extent of beaver ponds within the selected watershed, and then we extrapolated sampled CO_2 and CH_4 emission rates to the total pond surface. Our results show that within the selected watershed (13,000 km^2), there are 10,844 beaver ponds comprising an area of 77 km^2. We estimate that beaver ponds contribute 7% of the total C emissions from the aquatic network and are responsible for about 6% and 18% of the total CO_2 and CH_4 emitted annually, respectively. The information provided by this study increases our overall understanding of the role of beaver ponds in the C balance of the boreal biome not only at present but also for possible future scenarios given climate warming and beaver population growth. This study has also produced a dataset that has the potential to develop further hydrological, biogeochemical, and ecological studies related to the presence of beavers within the landscape.

Key words: Remote sensing, beaver ponds, CO_2, CH_4, carbon.

0. INTRODUCTION

Beaver ponds, a common and distinctive feature of the aquatic network within the boreal biome of North America (Naiman et al., 1986), have been excluded from inland water C budgets. Consequently, this represents a source of uncertainty for the C balance in regions where beavers are present. Beavers are known as ecosystem engineers due to their ability to build dams and create ponds. These ponds are recognized as a hotspot of greenhouse gases (GHG) due to their unique biological and physical characteristics, which set prime conditions for CO_2 and CH_4 production (Cazzolla Gatti et al., 2018; Ford & Naiman, 1988; Lazar et al., 2014; Roulet et al., 1997; Weyhenmeyer, 1999; Yavitt & Fahey, 1994). On the other hand, recent research indicates that the presence of beavers in the landscape may also increase C storage via several mechanisms, such as enhanced deposition of organic-rich sediments by reducing the velocity of stream flow, regular tree cutting, and the generation of meadows (which often replace beaver-formed water bodies) (Wohl 2013, Laurel & Wohl, 2019). The need to incorporate beaver ponds into inland water C budgets becomes important considering that the beaver population is increasing and is not only recovering its original distribution range but is expanding it (Rosell et al., 2005; Tape et al., 2022; Tape et al., 2018; Whitfield et al., 2015). Therefore, there is a clear need for studies to improve the understanding of the role of beaver ponds in inland water C budgets as well as to develop future predictions for the coming years under the current scenario of beaver population recovery.

0.1 Literature review

0.1.1 Population dynamics

It is estimated that the population of *Castor Canadensis* in North America before the arrival of European settlers was 60 to 400 million (Seton, 1925). During the 18th,19th, and part of the 20th century, beaver felt hats were considered a fashionable symbol on the European continent. The popularity of beaver felt hats in Europe drove the demand and the need to import large quantities of beaver fur from North America, where the beaver populations were healthy and unexploited (Hawkins, 2014). The high demand for beaver fur for more than two centuries eventually led to overexploitation and the near extirpation of beaver populations (Baker & Hill, 2003). The overhunting not only removed the animals from the landscape but also their habitats (Johnston, 2017). During the 20th century, the public became concerned about declining beaver populations, which led to regulations for trapping and hunting activities. Moreover, in recent decades, conservation programs through re-introduction and management have stimulated population growth. For North America, Naiman et al. (1988) estimated a beaver population ranging between 6-12 million, increasing exponentially and recovering part of their original distribution range. Even if much of their historical habitat has changed due to anthropogenic alterations, beavers are expected to regain their presence across the continent (Naiman et al., 1991). In addition, recent studies have suggested that climate change is causing beavers to colonize new territories that were previously less suitable, as is the case of the arctic tundra in North America (Jones et al., 2020; Tape et al., 2022; Tape et al., 2018). However, it is debated if this is due to habitat improvement or whether beavers were present in the tundra before the fur trade, and thus the current colonization could be a reoccupation of their former distribution range.

0.1.2 Beaver distribution range within Québec

In the analysis of abundance and spatial distribution (Jarema et al., 2009) describe the beaver density across the province of Québec as a logistic envelope pattern, with high density in the southwest portion of the province, a sharp decline towards 49°N, and a long tail of low density that extends to 58°N corresponding to their northern range limit (Figure 0.1). The factors that explain beaver density along the landscape are mainly related to food availability and the quality of aquatic habitats (Pinto et al., 2009; Slough & Sadleir, 1977; St-Pierre et al., 2017). Concerning the quality of the aquatic habitat, factors such as water level, river width, bank material, height, and slope are important criteria (Pinto et al., 2009).

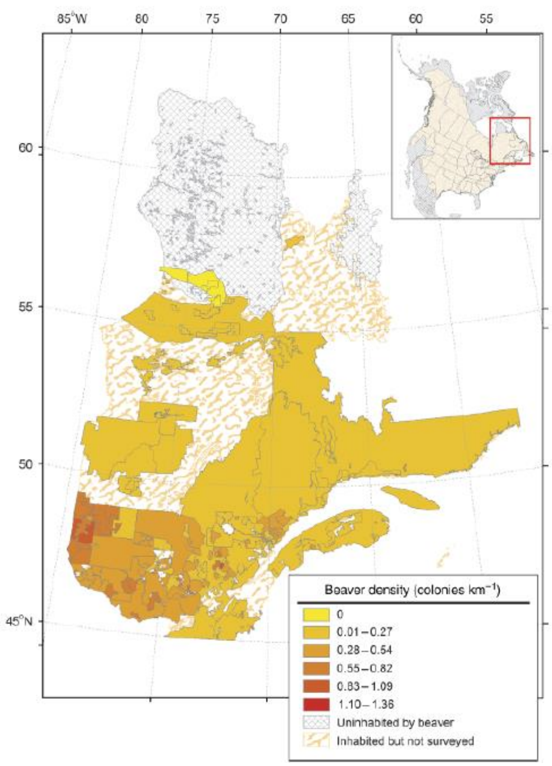

Figure 0.1. Average numbers of active beaver complexes per km^2 across the province of Québec, Canada. Densities were derived from 161 helicopter surveys conducted between 1976 and 2004. From Jarema et al. (2009).

0.1.3 Beaver colonies

Beaver colonies are the fundamental units of the beaver population and are usually composed of 3 to 8 related individuals (Novak, 1977). Colonies are widely used to estimate beaver population density, expressed by the number of colonies per unit of area or stream length (Broschart et al., 1989; Pinto et al., 2009). The aquatic habitat occupied by each colony typically comprises a cluster of one or more ponds. Hereafter, we refer to these clusters of ponds as beaver complexes, and ponds as the open water bodies generated by beaver activity. These are used for protection from predators, to store food for the winter season, or for easy access to food (Novak, 1977). In North America, the number of ponds per beaver complex is estimated to be between 2-5 (Butler & Malanson, 1995, 2005). But beavers do not always establish colonies through dam building and instead, they may occupy dens on river banks or build lodges in lakes.

0.1.4 Beaver ponds

In the boreal biome, beavers commonly build their complex on low-order streams, lake outlets, or wetlands. As a result, one or several connected ponds are formed, greatly increasing the extent of the original water body. The morphometry of these water bodies depends on the topography of the area where the dam is located (Butler & Malanson, 2005; Johnston & Naiman, 1987). Johnston and Naiman (1987) have shown that in narrow upland valleys, beaver ponds generally cover a small area and tend to be deep, whereas, in regions of flat topography, the ponds tend to have a big surface with shallow depths. However, the maximum depth of beaver ponds usually is not more than 4 meters. In North America, beaver ponds are reported to be as large as 300.000 m^2, although the average size seldom exceeds 10,000-20,000 m^2 (Whitfield et al., 2015).

0.1.5 Beaver ponds and CO_2 and CH_4 emissions

Like most boreal lakes (Duarte & Prairie, 2005; Huttunen et al., 2006; Rasilo et al., 2015), beaver ponds are supersaturated in CO_2 and CH_4. The effect of ecosystem respiration in exceeding primary production, lateral inputs of organic and inorganic C from flooded soils, and the limited opportunity for CH_4 oxidation due to shallow depth support the oversaturation pattern of CO_2 and CH_4 (Huttunen et al., 2002; Lazar et al., 2014; Roulet et al., 1997). Although beaver ponds are clearly sources of CO_2 and CH_4 to the atmosphere, there exists a high variability in the C-gas emissions reported from these systems (Table 0.1).

Table 0.1 Average CO_2 diffusive, CH_4, diffusive and ebullitive fluxes reported in previous studies conducted in North America. The number in parenthesis indicates median values.

Study	*f*CO_2 (mg C m^{-2} d^{-1})	*f*CH_4 (mg C m^{-2} d^{-1})	*Ebu*CH_4 (mg C m^{-2} d^{-1})	Season	Region
Lazar et al. (2014)	1173 (912)	157 (87)	NA	April-November	Rhode Island, NY, United States
Yavitt et al. (1992); Yavitt & Fahey (1994)	2366	225	NA	May-October	Adirondack, NY United States
Roulet et al. (1997)	NA	84	NA	May - September	Manitoba, Canada
Dove et al. (1999)	NA	104 (45)	63 (24)	May - September	Manitoba, Canada
Weyhenmeyer (1999)	NA	11	17	June – October	Ontario, Canada
Ford & Naiman (1988)	NA	20	NA	May - October	Québec, Canada
Bubier et al. (1993)	NA	217	NA	May - October	Ontario, Canada
Naiman et al. (1991)	NA	58	NA	May – October	Minnesota, United States

0.2 Problem statement

Global or regional integration of beaver ponds into inland water C budgets requires an understanding of the rates and dynamics of C-related biogeochemical processes mediated by these water bodies, as well as an accurate inventory of their spatial distribution and extent within the landscape. As described previously, several studies have reported CO_2 and CH_4 emissions from North American beaver ponds. However, most of those studies have focused on individual systems, and only a few studies have assessed CH_4 and CO_2 simultaneously. To our knowledge, so far, no study has explored large-scale patterns of CO_2 and CH_4 emission from beaver ponds, considering the heterogeneity related to the shape, size, and age, features that are expected to drive the variability of C dynamics among these systems (Catalán et al., 2016; Johnston & Naiman, 1987; Klotz, 2013; Wright, 2009). With the sparse data available, deriving rules to extrapolate CO_2 and CH_4 emissions of beaver ponds to regional or large-scale C budgets remains challenging. Uncertainty increases when it comes to calculating the total area covered by beaver ponds within the landscape. This is mainly due to the dynamic nature of these systems, where beaver habitat development goes through stages of dam construction, abandonment, and recolonization (Johnston, 2014; Johnston & Naiman, 1987; Naiman et al., 1986; Vehkaoja et al., 2015). Further, compared to human-built impoundments, beaver dams are more ephemeral as they are frequently damaged or even destroyed during high-flow events, which makes their inclusion on maps difficult (Butler & Malanson, 2005). The few large-scale studies of beaver habitat coverage for North America (Butler & Malanson, 2005; Whitfield et al., 2015) were based on the average population numbers. However, the use of remote sensing data is currently leading to more accurate results, and this approach could represent the best alternative to improve our understanding of the location and spatial distribution of beaver ponds in the landscape. Collectively, these two knowledge gaps highlighted here lead to high uncertainty in the estimation of C emissions from beaver ponds at local or regional scales, resulting in an underestimation or overestimation of the role of these habitats in inland water C-GHG budgets.

0.3 Thesis objectives

The overall objective of this study was to incorporate beaver ponds into a whole-network assessment of aquatic C emissions for a selected watershed located in boreal Québec, Canada. To this end, we set three specific objectives: I) To quantify the number and the total area of beaver ponds for the selected watershed through large-scale geospatial analysis. II) To develop an upscaling approach that captures the intrinsic variability for the three major pathways of C emissions to the atmosphere from beaver ponds, accounting for diffusive CO_2, CH_4 ebullition, and diffusive fluxes. III) To integrate C-gas emissions from beaver ponds along with the emissions from streams, rivers, and lakes that were calculated for the same watershed by a previous study. Overall, this study yields an improved scientific understanding of the role of beaver ponds in the C-GHG dynamics of inland waters at a regional scale, as well as a framework to incorporate these fluxes that can be applied at larger scales. Ultimately with this study, we expect to reduce the uncertainty around the C balance within regions where beavers are present.

1. CHAPITRE I

INTEGRATING BEAVER PONDS INTO THE CARBON EMISSION BUDGET OF BOREAL INLAND WATERS: A CASE STUDY AT THE WATERSHED SCALE

1.1 Abstract

The rebound of beaver populations across the boreal biome of North America and the proliferation of beaver ponds highlights the need to address the role of these systems in regional inland water C budgets. In this study, we combined a detailed geospatial analysis with measured CO_2 and CH_4 diffusive and ebullitive emissions rates to estimate beaver pond total C emissions and then incorporated these into a whole-aquatic network assessment. We carried out this study in a selected watershed (13,105 km^2) located in the region of Abitibi, Québec, Canada. Our results show that beaver ponds covered 77 km^2 representing 9% of the total aquatic surface area in the watershed. We estimate that beaver ponds contributed 7% of the total C emissions from the aquatic network, which is roughly proportional to the area that they occupy relative to the total aquatic surface area. Their impact is much more pronounced on the estimates of total aquatic CH_4 emissions, where their contribution is about 18% of the total CH_4 emitted by the aquatic network. We project that for the same watershed, beaver pond CO_2 and CH_4 emissions may increase significantly by 2055 (about 12% and 48%, respectively) due to a combination of expanding beaver habitat and increasing temperatures. Overall, this study highlights the role of beaver ponds not only in current aquatic CH_4 emissions for the boreal biome but also as a positive feedback loop for climate change with significant radiative forcing potential given a scenario of climate warming and beaver population growth.

1.2 Introduction

It is well known that inland waters play a substantial role in the C cycle and annually emit significant amounts of CO_2 and CH_4 to the atmosphere (Bastviken et al., 2011; Cole et al., 2007; Tranvik et al., 2009). A recent study (Rosentreter et al., 2021) has shown that aquatic ecosystems are responsible for about 53% of global CH_4 emissions, and considering that CH_4 has a warming potential 34 times higher than CO_2 (Myhre et al., 2014), inland waters may be playing a major role in controlling the Earth's climate. Despite considerable research efforts focusing on the global estimates of C fluxes and transformations in inland waters, aquatic C emissions, particularly CH_4 fluxes, remain poorly constrained. This is mainly hindered by the relatively small number of observations and the exclusion of certain types of freshwater ecosystems from current assessments (Battin et al., 2009; Downing et al., 2006; Verpoorter et al., 2014). Accurate estimates of C fluxes from inland waters are important to understand the global C balance as well as to predict future scenarios of climate change. There is therefore a need for integrative studies considering the whole ensemble of inland water types, their spatial distribution, and their associated C gas dynamics. Furthermore, knowledge of how the extent of inland waters ecosystems and their C emissions will vary over time is central for predicting the contribution of inland waters to the C balance in future scenarios.

The overall contribution of any ecosystem type to the inland water C emissions budget is a product of the areal extent and the intensity of C-related biogeochemical processes in those ecosystems (Downing, 2010). In the boreal biome of North America, beaver ponds are an important component of the landscape. Estimates of the percent coverage by beaver habitat in specific areas range from < 1% to 10% (Naiman et al., 1991). During the last decades, the beaver population has been increasing steadily, driven by declines in trapping and predation, resource management, and reintroduction programs that have stimulated the population's recovery from near extinction at the end of the

20th century (Rosell et al., 2005; Whitfield et al., 2015). Considering different climate change scenarios, population models suggest that the beaver population will not only increase but also expand its range in northern latitudes (Jarema et al., 2009). In this regard, a recent study Jones et al. (2020) has reported that beavers have started to colonize or re-colonize the low arctic tundra in some areas of North America. Consequently, the number and area of beaver ponds throughout the landscape are expected to increase across the boreal and tundra biomes over the coming decades. Moreover, it has been suggested that beaver ponds are a hotspot for CO_2 and CH_4 emissions (Cazzolla Gatti et al., 2018; Dove et al., 1999; Ecke et al., 2017; Ford & Naiman, 1988; Lazar et al., 2014; Roulet et al., 1997; Weyhenmeyer, 1999; Yavitt & Fahey, 1994). Some studies (Downing, 2010; Holgerson & Raymond, 2016) suggest that many C-related biogeochemical processes are more intense and complex in ponds and small lakes than in larger lakes. The average size and depth of beaver ponds rarely exceed 10,000-20,000 m^2 and 3 m, respectively. (Whitfield et al., 2015), making them fall within the recent functional definition of ponds made by (Richardson et al., 2022). Regardless of their size, beaver ponds have specific dynamics and conditions that favor intense rates of C-related biogeochemical processes. Flooded soils, translocation of vegetation by beaver activity, water retention as the result of dam construction, and loadings of terrestrial organic and inorganic C from the surrounding flooded areas provide conditions that enhance microbial activity, stimulate respiration rates (CO_2 production), and methanogenesis under oxygen-depleted conditions. However, despite the recognition of these systems as important sites for CO_2 and CH_4 production, beaver pond C emissions have rarely been incorporated into assessments of inland water C emissions.

The exclusion of beaver ponds from inland waters C assessments is partly a consequence of the small number of observations reported in the literature, coupled with the uncertainty related to their number, areal extent, and spatial distribution within the landscape. There are a few studies that have reported CO_2 and CH_4 emissions from beaver ponds (Bubier et al., 1993; Dove et al., 1999; Lazar et al., 2014; Roulet et al., 1997; Weyhenmeyer, 1999; Yavitt & Fahey, 1994), yet most of these studies have focused on individual systems at small-scale, and only a few have assessed CH_4 and CO_2 simultaneously. Therefore, with the existing sparse data, any extrapolation of the contribution of beaver ponds to regional or large-scale GHG budgets remains challenging. Additional uncertainties arise when it comes to estimating the total area covered by beaver ponds within the landscape. Butler and Malanson (1995, 2005); and Whitfield et al. (2015) have reported large-scale data on beaver pond numbers and coverage for North America, but these studies were based on average population numbers. Transposing population numbers to pond numbers and area requires certain assumptions that may lead to biased estimates. In contrast, studies for North America that have used aerial photography (Cunningham et al., 2006; Johnston & Naiman, 1990; Pearl et al., 2015) or satellite imagery (Fairfax & Small, 2018; Jones et al., 2020; Swift & Kennedy, 2021; Tape et al., 2018) to map beaver ponds have yielded more accurate outcomes. Therefore, such approaches could provide more robust geospatial data of beaver ponds and thus reduce uncertainty for incorporating this system into inland water C budgets.

The objective of this study was to estimate the C emissions from beaver ponds and to integrate these into an assessment of total aquatic C emissions of a large boreal watershed. We carried out this exercise in a watershed that comprises an area of 13,105 km^2, located in the Abitibi region of boreal Québec, Canada. We combined ecoforestry maps with very high-resolution satellite imagery (3 m) within a platform for large-scale geospatial analysis to estimate the number and the total area covered by beaver ponds within the selected watershed. We assembled the largest dataset to date on beaver pond C-gas emissions by combining 41 sampled ponds from Abitibi and 10 from Saguenay, both regions located in boreal Québec. We then extrapolated those C-gas emissions to the total area of ponds derived from the geospatial analysis within our selected watershed. Our upscaling exercise accounts for CO_2 diffusion and CH_4 ebullitive and diffusive fluxes. Finally, we integrated the C-gas emission from beaver ponds with the collective emissions from streams, rivers, and lakes that were calculated for the same watershed by a previous study (Casas-Ruiz et al., 2021).

1.3 Methods

1.3.1 General approach

This study was based on a detailed geospatial analysis that provided an accurate representation of the beaver pond network within the selected watershed, minimizing the level of uncertainty around their number and area extent. Previous studies on the spatial coverage of beaver habitat. (Butler & Malanson, 1995, 2005; Whitfield et al., 2015) have been based on average population numbers. Here, in contrast, we have used very high-resolution remote sensing products that vastly improve the accuracy when it comes to identifying and mapping water bodies. We then coupled the outcome of the geospatial analysis with a system-specific approach that captures the intrinsic variability for the three major pathways of C-emissions to the atmosphere from beaver ponds: diffusive CO_2, CH_4 ebullition, and diffusive fluxes. In order to accomplish this, we used a combination of high-resolution meteorological data and empirical models based on in situ measurements from two different regions of boreal Québec. The variability in C-gas emissions across beaver ponds might be related to common drivers that apply to other boreal lentic water bodies, but also due to intrinsic characteristics of these systems, boreal beaver ponds may have distinct biogeochemical patterns. For example, recent upscaling studies (DelSontro et al., 2018; Holgerson & Raymond, 2016; Rosentreter et al., 2021) have upscaled CO_2 and CH_4 emissions based on lake size classes, whereas in this study we have not found any allometric relationship that allows to predict CO_2 or CH_4 emissions based on pond morphometry. Therefore, the approach based on waterbody size class cannot be extrapolated to beaver ponds. Instead, we upscaled CO_2 emissions from a lognormal distribution around the mean and the standard deviation of the sampled data from the set of measurements made in the sampled ponds. Methane diffusive fluxes were upscaled based on the positive log-linear relationship between CH_4 diffusive rates and water temperature. To do so, we added a high-resolution climate layer that allowed us to extract the average monthly atmospheric temperature values for all the ponds within the selected area. By doing this, we incorporated the seasonal effect of temperature that has been shown to strongly influence CH_4 dynamics (DelSontro et al., 2016; Yvon-Durocher et al., 2014) and that is present in our systems as well. For CH_4 ebullitive fluxes, we used the multivariate regression model described in DelSontro et al. (2016, equation 4), which includes temperature and total phosphorus, as well as the interaction between both variables. This model includes the effect of temperature and system productivity, which have been shown to be the two strongest predictors for CH_4 ebullitive fluxes in lentic water bodies (Deemer & Holgerson, 2021; DelSontro et al., 2016).

1.3.2 Study area

A 13,105 km^2 watershed was selected within the Abitibi region of Québec, Canada. Abitibi differs from other boreal regions of Québec in that it is a marginal landform created by the retreat of the Laurentian ice sheet, which formed a large plain of glacio-fluvial sediments rich in till and clay and organic deposits (Veillette et al., 2008), and is thus characterized by its flat ground and rich clay soils. Abitibi is one of the regions with the highest density of beaver colonies per km^2 within the province of Québec (Jarema, 2008; St-Pierre et al., 2017). Therefore, low-order streams (1 to 4) are intensively affected by beaver dams, which strongly influence the configuration of the aquatic network and the hydrological regime.

1.3.3 Satellite images

PlanetScope Analytic Ortho Scene product is orthorectified, multispectral data from the satellite constellation of Planet Labs (https://www.planet.com/). PlanetScope imagery has a 3 m spatial resolution with four bands, blue (Band 1, 455–515 nm), green (Band 2, 500–590 nm), red (Band 3, 590–670 nm) and near infrared (Band 4, 780–860 nm). Recent studies (Cooley et al., 2017; Traganos et al., 2017) have shown that the orthorectified product is suitable for analytic and image processing such as land cover classifications. For this study, we used 155 cloud-free PlanetScope orthorectified scenes taken between July and October of 2017 over the study area. PlanetScope images were manually checked for clouds using the cloud index provided by the product developer, images with a cloud percentage higher than 1% were discarded.

1.3.4 Beaver habitat polygons

Beaver habitat polygons were extracted from the 4th edition of Forest Inventory Maps, produced by the Québec Ministry of Natural Resources and Wildlife https://mffp.gouv.qc.ca/les-forets/inventaire-ecoforestier/. The aim of the Québec Forest inventory is the identification of forest stands, in which four main categories of land are defined: productive stands, non-forest lands, unproductive forests and water bodies. Within the last category, beaver habitats are represented by polygons of a minimum mapping size of 0.01 km^2. Because Abitibi is a mining district and we observed that beavers also construct dams at tailing ponds outlets, we removed all beaver habitat polygons located in mining areas. The final beaver habitat dataset included a total number of 4,757 polygons for the study watershed.

1.3.5 Beaver ponds water extraction

To extract the water bodies (i.e., beaver ponds) from the beaver habitat polygons, a binary classification was used. To do so, we delivered the PlanetScope scenes to Google Earth Engine (Gorelick et al., 2017), where we clipped the images by the beaver habitat polygons. Within the beaver habitat polygons, using median pixel values we calculated a Normalized Difference Water Index (NDWI), defined as the differences between the green and near infrared band, divided by the sum of green and near-infrared (Band 2-Band 4 for PlanetScope) (McFeeters, 1996). The NDWI yields an index that ranges between -1 and 1, where open-water pixels approach 1 and terrestrial pixels -1 (Figure 1.1). To set the threshold for water pixels, the Otsu adaptive threshold was used, where the optimal threshold is identified by minimizing the inter-class variance and maximizing the intra-class variance (Otsu, 1979). Finally, the water pixels were transformed into a vector layer and exported as a shape file. The resulting shape file was then processed in ArcMap (Version 11.5) to fill out the gaps within the polygons with a maximum size of 200 m^2. All the beaver pond polygons smaller than 500 m^2 were discarded.

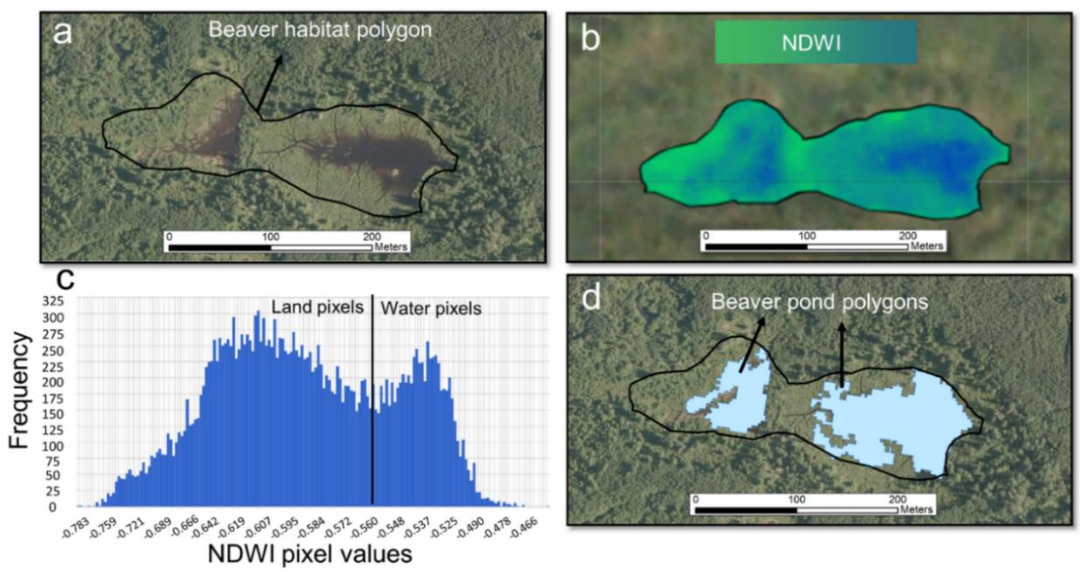

Figure 1.1. Example of the open water classification workflow. Panel a) shows a beaver habitat polygon extracted from the ecoforestry maps, the background is a Foret Ouverte (https://www.foretouverte.gouv.qc.ca/) aerial photo from the summer 2016, spatial resolution 30 cm, (b) shows the NDWI calculated on a Planet Scope Scene from the summer 2017, spatial resolution 3 m, c) bimodal pixel distribution with the threshold used for segmentation between water and land pixels, d) final output of beaver pond polygons on the same background as panel (a).

1.3.6 Accuracy Assessment

The classification error was quantified by computing a confusion matrix based on object-based image analysis (OBIA). The beaver habitat polygons extracted from the ecoforestry maps were defined as our object unit. As reference data, we connected ArcGIS to the complete database of orthophotos from the Foret Ouverte via WMTS (https://www.foretouverte.gouv.qc.ca/). This high-resolution dataset consists of a mosaic of aerial photos taken between 2002- 2020, with a spatial resolution of 20 to 30 cm that covers almost the entire territory south of the 52nd parallel of the Québec public forest domain. For the selected area, the orthophotos were taken between 2016 and 2017, which reduced the temporal differences between the reference data and the satellite images used for the binary classification. To quantify the classification error, we randomly sampled 57 polygons for each category, land, and open water bodies (i.e., beaver ponds). Within each of the polygons, we sampled a fixed-area plot of 9x9 m (81 m^2) and labeled it as land or water bodies, avoiding sampling at the boundaries. Finally, we computed an area-based confusion matrix by comparing the area matches between the reference data with the classified layer to calculate the corresponding accuracy metrics for each category.

1.3.7 In situ sampled data

Beaver ponds were sampled between 2010 and 2011 in two different regions of Québec: Abitibi (48.07 – 48.94°N, 79.47 – 78.65°W) and Saguenay (47.79 – 48.77°N, 72.13 – 70.65°W) (Figure S.1.6). The data collected in the Saguenay region have been presented in DelSontro et al. (2016), whereas the data collected in Abitibi have not been published, but the sampling methodology is common to both sets. In brief, sites were selected to cover the broadest diversity of ponds, with wide gradients of shape, size, type of flooded soils, and trophic status. Most of the sampled ponds had shallow depths between 1 and 3 m. In Abitibi, 41 beaver ponds were sampled during the ice-free season. A selection of these ponds was sampled at least four times, from May to November. In Saguenay, 10 ponds were sampled three times (June, July, and September) (DelSontro et al., 2016).

1.3.8 Diffusive gas fluxes

The CO_2 and CH_4 fluxes at the air-water interface were measured at each site using the floating chamber method following Vachon et al. (2010). The chamber was covered with aluminum foil to reduce sun heating and had an internal thermometer to monitor temperature changes. To measure the CO_2 flux, the chamber was connected to an infrared CO_2 analyzer (EGM-4, PP-Systems) in a closed re-circulating loop, and CO_2 partial pressure in the chamber space was recorded every minute for a total of 10 min. To measure the CH_4 flux, gas samples from the chamber space were withdrawn with a syringe through a sampling valve immediately after deployment, and again after 10, 20, and 30 min. The collected gas was injected into 30 ml vials containing saturated saline solution. In the laboratory, the gas of the vials was injected into a gas chromatograph (GC-8A/GC-2014, Shimadzu, Kyoto, Japan) equipped with an FID (flame ionization detector) to determine its CH_4 concentration. Diffusive CO_2 and CH_4 fluxes were determined using the following equation:

$$Flux = \frac{(s\ x\ Vch)}{(Vm\ x\ A)}\ x\ 1.44$$

where s (µatm min^{-1}) is the slope of the rate of gas accumulation in the chamber with time, Vch (L) is the volume of the chamber, Vm (L atm mol^{-1}) is the molar volume of the gas at ambient temperature, A (m^2) is the surface area of the chamber, and 1.44 is a unit conversion factor to obtain a flux in mmol gas m^{-2} d^{-1} (1 d = 1440 min). Meteorological parameters such as: wind speed (m/s), air temperature (T in °C) and humidity (%), barometric pressure (hPa) were measured before, between and after the floating chambers measurements with a NK Kestrel 4000 pocket weather tracker.

1.3.9 Ebullitive CH_4 flux estimates

Ebullitive CH_4 fluxes were measured in the 10 beaver ponds in the region of Saguenay, Québec, Canada, during three field campaigns, June-July, August, and October 2011. A detailed description of the sampling procedure of those ponds appears in (DelSontro et al., 2016). Ebullitive CH_4 fluxes (mmol $m^{-2}d^{-1}$) were measured with two bubbles gas traps per pond, which consisted of an inverted plastic funnel of 63.5 cm of diameter suspended at 0.5 m under the water surface. In order to store the accumulated gas, a graduated 1 L glass bottle was screwed to the neck of the funnel. The glass bottles were covered with foil to avoid light penetration and solar heating. The gas was withdrawn from the bottle every 4 days or until the accumulation of a gas volume was greater than 250 ml. The bottle containing the gas was carefully removed underwater from the funnel and tapped with a cap equipped with two stopcocks. Nanopure water was injected in the bottle with the purpose to retrieve the gas through the second port. The gas samples were then injected in 30 ml vial filled with oversaturated saline solution. The leftover water in the bottle was measured with a graduated cylinder (subtracting the nanopure water volume added) in order to evaluate the volume of gas that was collected. In the laboratory, the gas composition (CO_2 and CH_4) was determined by gas chromatographic analysis (Shimadzu GC-8A). At each sampling point, surface water and sediment temperature were measured with a digital thermometer (AquaCalClineFinfer) and the depth of the water column was also measured with a portable depth meter echo sounder (SM-5) near each funnel.

1.3.10 Other parameters

In situ water temperature (T in °C), conductivity (in µs cm-1), dissolved oxygen (DO in mg L^{-1} and %) and pH were measured using a YSI environmental monitoring probe (Model 600XLM) equipped with a rapid pulse DO probe. This probe was calibrated for DO (%) on each site. DO (%) values were corrected for in situ barometric pressure.

For measurements YSI probe was placed below 0.2 m from the surface. Surface water samples were collected from the same site at the same depth to measure concentrations of DOC, chlorophyll a (Chl a), TP and TN. DOC concentration was measured using an Aurora 1030W TOC Analyzer from 0.45 µm filtered samples after persulfate digestion. Chlorophyll a was determined spectrophotometrically on Whatman GF/F filtered samples following sonication and pigment extraction with hot (90%) ethanol (Nusch 1980). Total phosphorus was analyzed spectrophotometrically using the colorimetric molybdenum blue method after persulfate digestion (Wetzel and Likens 1991). Total nitrogen was measured on an Alpkem FlowSolution IV autoanalyzer as nitrate following alkaline persulfate digestion.

1.3.11 Upscaling beaver pond CO_2 diffusive emissions

There were no clear relationships between CO_2 fluxes and any of the environmental or morphometric variables that we recorded, including temperature, so we could not develop empirical models that could be used for upscaling CO_2. Hence, for each pond in the watershed derived from the geospatial analysis, we randomly selected a daily emission rate (mg C m^{-2} d^{-1}) based on the lognormal distribution of the measured data (Figure S.1.1). The annual CO_2 efflux (Eg_{CO2} mg C yr^{-1}) for each pond was then calculated using the following equation.

$$EG_{CO2}=E_{RCO2}*A*365_{ice}$$

Where $E_{R\ CO2}$ (mg C m^{-2} d^{-1}) is the emission rate. A (m^2) is the pond size in m^2 and 365_{ice} (days) is the duration of the ice-free season, which for the selected region was assumed to be of 184 days, based on monthly average temperatures above 0°C.

1.3.12 Upscaling beaver pond CH_4 diffusive emissions

Methane diffusive rates were modeled for each month of the ice-free season based on the positive log-linear relationship between CH_4 diffusive rates and water temperature (Table S.1.2). The monthly average air temperature for each pond was extracted from World Clime (https://www.worldclim.org), with a spatial resolution of 1 km^2. Here we assumed that the monthly mean air temperature is equal to the monthly average water temperature, which is reasonable for these shallow, well-mixed ponds. The monthly CH_4 diffusive flux (Em_{CH4} mg C m^{-1}) was calculated using the following equation:

$$Em_{CH4}=E_{RCH4}*A*M_d$$

Where E_{RCH4} (mg C m^{-2} d^{-1}) is the emission rate derived from the model. A (m^2) is the pond size in m^2, and M_d (days) is the specific number of days for the given month. The annual CH_4 was calculated as the sum of monthly emissions of the ice-free season, here assumed to be from May to October.

1.3.13 Upscaling beaver pond CH_4 ebullitive emissions

Monthly ebullitive CH_4 fluxes were estimated following equation 4 in (DelSontro et al., 2016)**,** using sediment temperature and total phosphorus as independent variables. In boreal lentic systems methane ebullition tends to occur in locations where the water depth is 3 meters or less (DelSontro et al., 2016)**.** Beaver ponds rarely exceed 3 meters, thus, in this study we have assumed that ebullition occurs throughout the entire pond area. For each pond, we have assumed that the sediment temperature is the same as the surface water temperature and the latter is the same as the monthly mean air temperature. Total phosphorus (TP) was randomly assigned to each pond by iteratively sampling a probability distribution function derived from the measured TP concentrations in the ponds from Abitibi and Saguenay (*N=113)* (Figure S.1.2). The monthly CH_4 ebullitive flux was calculated following the same equation as for CH_4 ebullitive fluxes, and the annual CH_4 ebullitive emissions were calculated as the sum of monthly emissions of the ice-free season.

1.3.14 CO_2 and CH_4 emissions during spring thaw

During winter, ponds accumulate CO_2 and CH_4 that are emitted during the ice-out period. Campeau et al. (2014) reported that ice-out emissions from boreal streams in this region, many of which are dammed by beavers, contribute on average 21% of annual C emissions, whereas Denfeld et al. (2018) have shown that for boreal lakes the ice-melt period represents 17% and 27% of the annual CO_2 and CH_4 emissions, respectively. So far, no study to our knowledge has captured the CO_2 or CH_4 emissions during the spring thaw in beaver ponds. Therefore, to account for the C evasion during this ice-off period, we assumed that it represents 21% of the total annual C gas emissions.

1.3.15 Uncertainty analysis

We calculated the uncertainty of each C-gas species flux using a Monte Carlo Simulation of 10,000 iterations. The median of these 10,000 iterations was used as a statistically balanced estimate of the C-gas annual emissions, and the 5^{th} and 95^{th} percentiles as a measure of its uncertainty. For the empirical model of CH_4 diffusion, we generated a gaussian distribution of the slope coefficient (intercept was not statistically significant) based on its standard error, in which we randomly selected a value for each iteration. Since the error of the regression coefficients was not available for ebullitive CH_4 emissions, we applied a prediction error of 50% as a conservative measure of uncertainty.

1.3.16 Integrated total aquatic C emission

The C emissions of the ensemble of lakes (> 5,000 m^2), rivers, and streams had been previously estimated by (Casas-Ruiz et al., 2021) for the selected watershed. To integrate the emissions of beaver ponds into this previous analysis and to avoid double accounting, we removed the stream segments that spatially overlapped the beaver pond polygons and re-calculated the emissions for the entire fluvial network following the method described in (Casas-Ruiz et al., 2021). We then added the emissions associated with the beaver ponds. The total aquatic C emissions were calculated as the sum of the annual diffusive and ebullitive emissions of CO_2 and CH_4. All emission values reported are the median and 95% confidence interval of 10,000 Monte Carlo simulations.

1.3.17 Statistical analyses

Linear regression models were used to assess the relationship between CH_4 emissions and temperature and TP, using the *lm* function in R. The assumptions for general linear regression models were checked by examination of tests and diagnostic plots of the residuals and are met in all cases. All statistical tests were considered statistically significant at $p < 0.05$. All data processing, Monte Carlo simulations, statistics, and figures were done in R 3.5.1 (R Core Team, 2019).

1.4 Results

1.4.1 Geospatial analysis and accuracy assessment

Within the selected watershed, we identified 10,844 beaver ponds that comprised a total area of 77 km^2 and a density of 0.82 ponds per watershed km^2. The size of these water bodies ranged from 500 m^2, which was the defined minimum mapping size, to 245,087 m^2, with a median of 2,340 m^2. Beaver pond size followed a positively skewed distribution, with 75% of the ponds having a surface area of less than 10,000 m^2 (Figure

1.2.C). Beaver habitats, consisting of both terrestrial and aquatic components, comprised a total area of 229 km^2, with a median size of 6,091 m^2. The average water fraction, calculated by dividing the total area of beaver ponds by the total area of beaver habitat polygons was 0.33. The six metrics used to evaluate the accuracy of the water extraction are shown in Table 1.1. All these metrics are above the range of the minimum acceptable precision value as an index of classification accuracy (Congalton & Green, 2019).

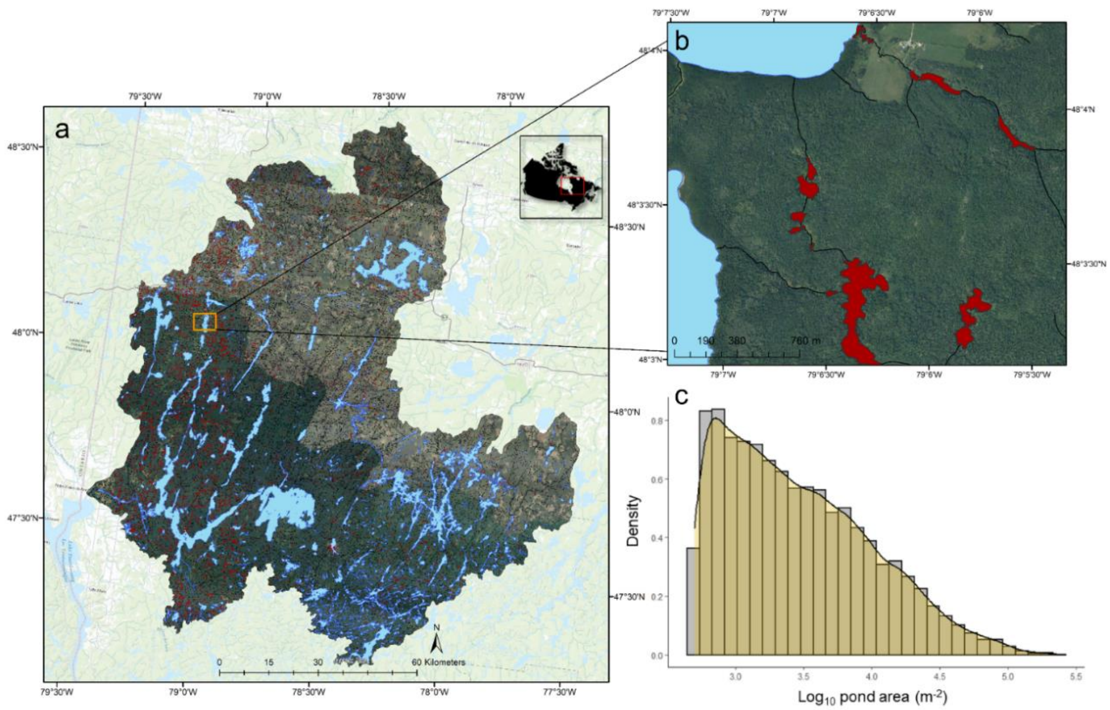

Figure 1.2 a) Location of the selected watershed, with lakes, rivers, and beaver ponds delimited by polygons. b) Mosaic showing the aquatic network configuration, beaver ponds (red polygons), lakes > 5,000 m^2 (blue polygons) and rivers (black lines). c) Size distribution of the beaver pond polygons extracted from the geospatial analysis.

Table1.1 Summary of accuracy metrics for beaver ponds water classification.

Error Metric	Value
Overall accuracy	0.92
Water User's Accuracy	0.93
Land User's Accuracy	0.90
Water Producer's Accuracy	0.91
Land Producer's Accuracy	0.94
Kappa	0.85

1.4.2 Aquatic Network configuration

The aquatic network of the study watershed comprises a total surface area of 877 km^2, with lakes accounting for 87%, beaver ponds for 9%, and streams and rivers for 5%. In comparison to Casas Ruiz et al. (2021), our analysis indicates that beaver ponds have expanded the aquatic network surface area by about 10% (from 800 km^2 to 877 km^2) and have replaced 7% (1,263 km) of the total fluvial network length. Second- and third-order streams were the components of the fluvial network most affected by beavers, with 11.5% and 13% of the total length replaced by ponds (Figure 1.3). Streams of orders 1, 4, and 5 had 4%, 7%, and 2% of fluvial length replaced, respectively (Figure 1.3).

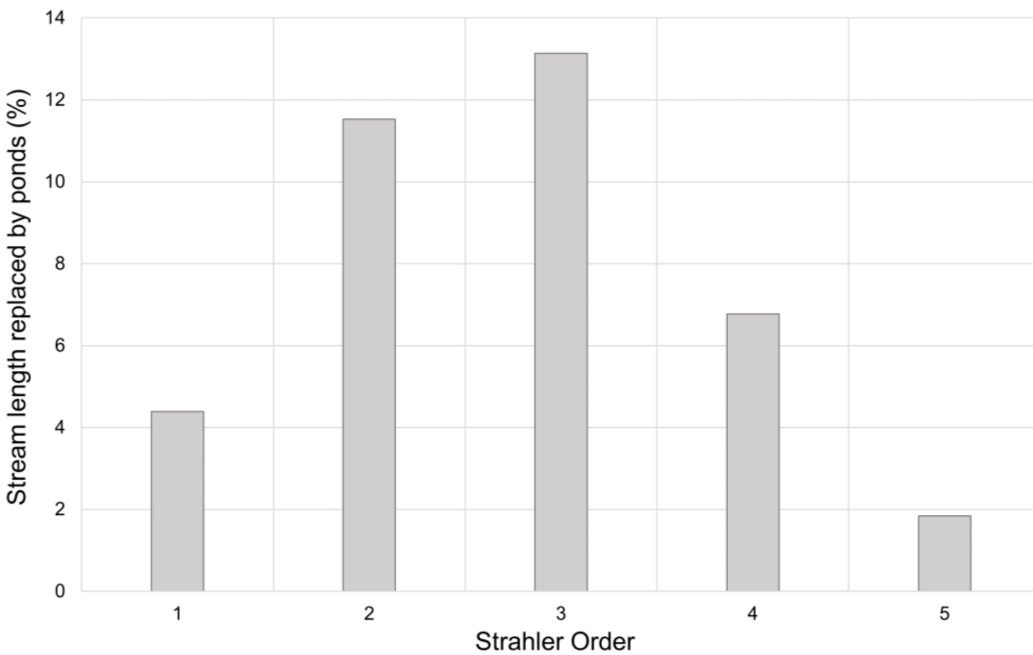

Figure 1.3. Bar plots showing the percentage of the total stream length replaced by beaver ponds for each stream order.

1.4.3 Characteristics of the sampled beaver ponds

Diffusive CO_2 and CH_4 emission rates were highly variable across the sampled ponds in Abitibi and Saguenay. Diffusive CO_2 emission rates varied by two orders of magnitude for the Abitibi ponds (median 618, min-max 19 - 3,226. mg C m^{-2} d^{-1}) and by one order of magnitude for those in Saguenay (median 527, min-max 337 - 2,350 mg C m^{-2} d^{-1}). The measured CO_2 emissions during the growing season (May-October) did not vary significantly between the two regions (Kruskal-Wallis test, P = 0.23) (Figure 4). Diffusive CH_4 emissions rates ranged by four orders of magnitude across the regions (median 44, min-max 0.4 - 3,755 mg C m^{-2} d^{-1}) for Abitibi and (median 40 min-max, 0.4 - 1,001 mg C m^{-2} d^{-1}) for Saguenay. There were no statistical differences between the CH_4 emissions rates measured in both regions (Kruskal–Wallis, P = 0.30)

(Figure 1.4). Ebullitive CH_4 fluxes were sampled only in ponds from Saguenay (median 41, min-max 0.7 – 305 mg C m^{-2} d^{-1}), and previously reported by (DelSontro et al., 2016). Water temperatures measured throughout the growing season did not vary between Abitibi and Saguenay (Kruskal–Wallis, P = 0.51). In contrast, there were regional differences in the pH measured in the ponds of Abitibi and Saguenay (Kruskal–Wallis, P = <0.001), with a median of 7.2 for Abitibi and 6.8 for Saguenay. Both TN and TP concentrations were highest in Abitibi (median 0.8, mg/L and median 61.3 ug/L, respectively). Similarly, DOC and chlorophyll concentrations were highest in Abitibi, (median 19.9 mg/L and median 6.6 mg/L, respectively). Dissolved oxygen concentrations and percentage of saturation were highly variable across-ponds, but overall, there were no regional differences (Kruskal–Wallis, P = 0.35) and (Kruskal–Wallis, P = 0.32) respectively.

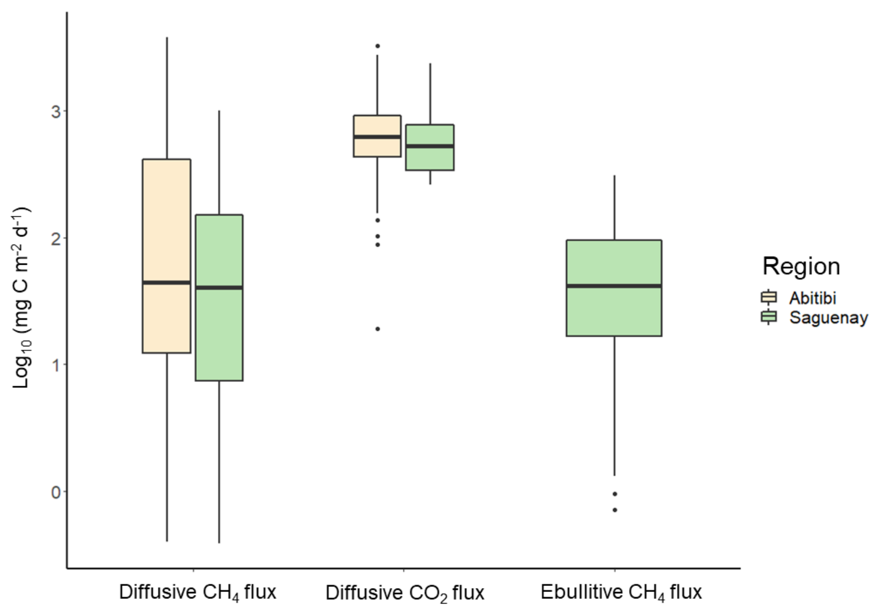

Figure 1.4. Sampled CH_4, diffusive fluxes and CO_2 diffusive fluxes (mg C m^{-2} d^{-1}) in the two different study regions, Abitibi (ivory) and Saguenay (green). Boxplots extend from 25th percentile to 75th percentile and the whiskers start from the edge of the box and extend to the furthest data point that is within 1.5 times the interquartile range. The horizontal bar in the box shows the median values.

1.4.4 Contribution of beaver ponds to whole-network C emissions

We estimate that the beaver ponds in our study watershed emit a total of 14,080 tons C y^{-1} to the atmosphere (sum of the median values, plus an additional 21% to account for the spring thaw). The beaver pond C emission budget is dominated by CO_2 diffusion, which represents 91% of the total C emissions. Methane ebullitive and diffusive fluxes represent 5% and 4%, respectively (Figure 1.5-A). Integrating beaver ponds into the whole network C emission budget carried out by Casas-Ruiz et al. (2021) results in a total aquatic emission of 198,200 tons C y^{-1}, with lakes contributing 63% of these emissions, streams 30% and beaver ponds 7% (Figure 1.5-A). The contribution of beaver ponds to CO_2 and CH_4 emissions was 6% and 18% of total annual aquatic network emissions, respectively. Moreover, beaver ponds contribute approximately 9% to the radiative balance (as C-CO_2 equivalent emissions) of the aquatic network, streams and rivers 39%, and lakes 52%. (Figure 1.5-B). The ratio of CH_4 to CO_2 emissions was highest in beaver ponds (0.10), followed by streams (0.07), and lowest for lakes (0.01) (Figure 1.6).

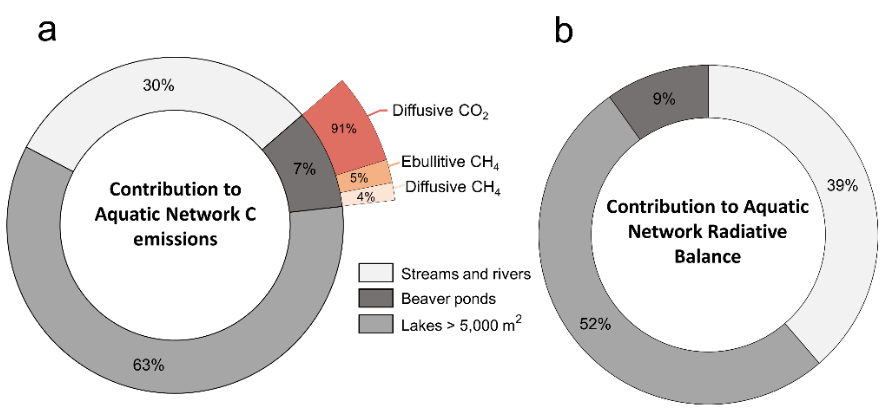

Figure 1.5. a) Pie chart of the percentage of each component of the aquatic network to the total aquatic C-emission budget. The outside ring indicates the percentage of each C-gas species contribution. Panel b) indicates the contribution of each system to the aquatic network radiative balance as (C-CO_2 equivalents emissions).

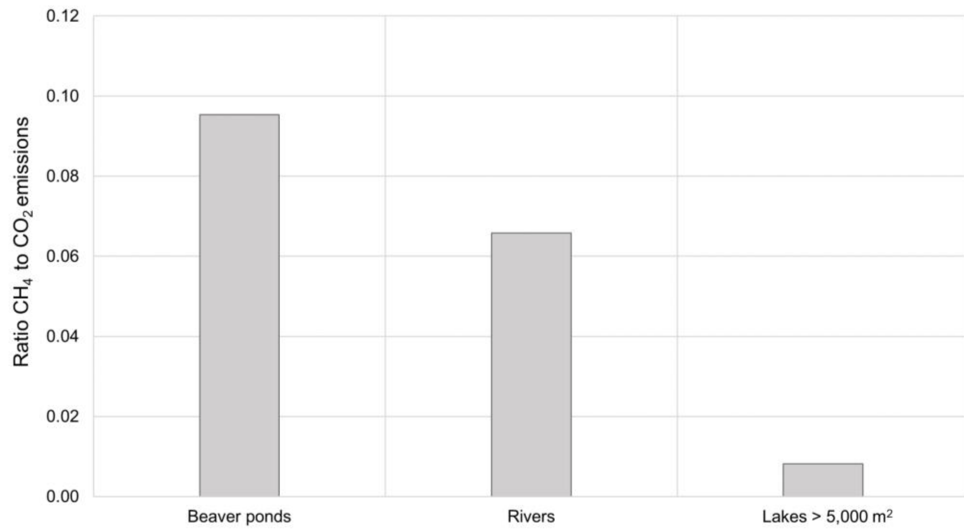

Figure 1.6. Ratios between CH_4 and CO_2 fluxes. The X axis indicates the different system types.

1.5 Discussion

1.5.1 Geospatial analysis

Our results indicate that PlanetScope imagery is suitable for water extraction of small, heterogeneous water bodies such as beaver ponds. The high temporal and spatial resolution of Planet Labs imagery enabled the assembly of a cloud-free image collection that covered the entire selected area. The combination of the high-resolution imagery, the binary classification based on the band ratio index NDWI, and the Otsu with a pixel selection method was shown to perform well for a system such as beaver ponds that often displays pronounced color differences, even between nearby ponds. Other studies (Cooley et al., 2017; Olthof et al., 2015) have used a non-binary approach to classify water bodies in floodplain environments where inundated vegetation and mixed land/water pixels are common. Such approach involves estimating the percent of each inundated pixel, and is useful in areas where many pixels contain inundated vegetation (Cooley et al., 2017; Olthof et al., 2015). Considering that the beaver habitat presents complex boundaries between the aquatic and terrestrial interface (Figure 1.1), further comparisons between both methods are due.

In this study, we used PlanetScope images only to classify and extract water pixels from the polygons and not to delineate or identify the beaver habitat within the landscape, which was already delineated by the ecoforestry maps. From visual inspection and in comparison to previous studies carried out in the same region, we conclude that we may have underestimated the number and total area of beaver ponds. For this same region of Abitibi, (Jarema et al., 2009) reported a beaver complex density between 0.83 -1.09 km^2, whereas (St-Pierre et al., 2017) a density of 0.42 - 0.62 beaver complexes per km^2. According to (Butler & Malanson, 2005) the number of ponds per complex across North America ranges from 2 to 5. Assuming an average of 3.5 ponds per complex, our results show a consistently lower density in comparison to those reports, and we acknowledge this may be due to specific methodological limitations. One such limitation is the minimum mapping size of the beaver habitat polygons extracted from the ecoforestry maps. Individual ponds, or beaver complexes of less than 0.01 km^2 were not included in the ecoforestry maps, so we could not capture those in our analysis. Another important limitation is related to temporal decoupling between the beaver habitat polygons and the date of the satellite imagery used for the ensemble of the image collection. The beaver habitat polygons were delineated from aerial photos taken between 2002-2010, whereas the satellites images were taken between July to October of 2016. Given that beaver ponds are not permanent and can have an ephemeral presence in the landscape, as they are frequently damaged, abandoned or even destroyed during high-flow events (Johnston, 2014; Johnston & Naiman, 1987; Naiman et al., 1986), we have found several occurrences of polygons defined as beaver habitat, that were currently dry or just enclosed vegetation. Nevertheless, despite the mentioned methodological limitations, this study constitutes the first direct large-scale assessment of the number, extent, and spatial distribution of beaver ponds in this region. Our results represent a valuable source of data not only to incorporate beaver ponds into regional estimates of inland water C emissions but also for developing hydrological, biogeochemical, and ecological watershed-scale studies related to the presence of beaver habitats in the landscape.

1.5.2 Aquatic network configuration

Our results show that the surface area covered by beaver ponds is not negligible and makes up a substantial fraction of the entire aquatic network, even if most of these water bodies are smaller than 0.01 km^2. The size distribution of ponds follows the same pattern as the global distribution of lentic water bodies reported by other studies (Downing et al., 2006; Messager et al., 2016; Verpoorter et al., 2014), with a decrease in abundance as pond size increases. For North America, beaver ponds are reported to be as large as 300,000 m^2, with an average size that rarely exceeds 10,000-20,000 m^2 (Whitfield et al., 2015). It would be interesting to further explore whether the pattern of pond size distribution is an intrinsic property of the watershed. The morphometry of the ponds depends on the topography of the landscape where the dam is located. In narrow upland valleys, ponds generally cover a small surface area and tend to be deeper, whereas in regions with flat topography, ponds tend to have a larger surface area with shallower depths (Johnston & Naiman, 1987). Hence, the water fraction within the system is expected to be high in those habitats located on narrow valleys, due to the abrupt boundary between the pond and upland, with steeper transitions between the pond and the surrounding dry habitat. In contrast, those beaver habitats located in flat areas have extensive floodplains, a larger zonation of wetland vegetation and thus a lower fraction of water. This becomes relevant when considering that transition vegetated zones tend to act as C sinks (Johnston, 2014; Wohl, 2013), whereas the open water fraction is a consistently net source of C gases to the atmosphere. In this regard, landscape properties such as topography that may influence the ratio between the open water and terrestrial components of beaver habitats could drive their role as net sources or sinks of C within the landscape.

Our geospatial analysis indicates that most beaver ponds were located on first, second, third, and fourth order streams. These results agree with previously reported patterns of beaver damming preferences for low-order streams (Gurnell, 1998; Naiman et al., 1988; Rosell et al., 2005). Surprisingly, although the study area is one of the regions in the province of Québec with the highest density of beaver colonies, beaver dams have replaced only 7% of the total river network and a maximum of 13% of the total length for streams up to order 3. This may suggest that the beaver population within the selected watershed still has suitable habitat to colonize, and this would undoubtedly be the case for other less densely populated regions of Québec. The dams made by beavers fundamentally alter the hydrology and configuration of the aquatic network. On one hand, they act as a physical barrier that creates a fluvial discontinuity, increasing the extent of the flooded area, water level, and water residence time, as well as decreasing the velocity of the water flow (Butler & Malanson, 1995; Naiman et al., 1986; Nyssen et al., 2011). On the other hand, the presence of beaver dams increases the overall water surface and modifies the relative area of fluvial to lentic systems. Low-order streams dominate stream length in boreal watersheds, but account for only a small proportion of the total stream network area (Hutchins et al., 2020). Therefore, even if beaver ponds replaced a large proportion of the fluvial network, the effect on the total fluvial area would be relatively minor.

1.5.3 Measured CO_2 and CH_4 emissions

All beaver ponds were consistently net sources of CO_2 and CH_4 to the atmosphere during the sampled period. Diffusive CO_2 emissions measured in the ponds of Abitibi, (mean 780 mg C m^{-2} d^{-1}) and Saguenay (mean 721 mg C m^{-2} d^{-1}) were within the lower range of published values for North American beaver ponds, (average values 2,365, 1,697 and 1173 mg C m^{-2} d^{-1}, respectively, (Lazar et al., 2014; Roulet et al., 1997; Yavitt & Fahey, 1994). In contrast, average CH_4 diffusive emissions measured in Abitibi (436 mg C m^{-2} d^{-1}) and Saguenay (150 mg C m^{-2} d^{-1}) were in the upper range for average reported values, (ranging from 11 to 225 mg C m^{-2} d^{-1} (Dove et al., 1999; Ford & Naiman, 1988; Lazar et al., 2014; Weyhenmeyer, 1999; Yavitt & Fahey, 1994). Moreover, CH_4 ebullitive fluxes measured in Saguenay (mean 150 mg C m^{-2} d^{-1}) were also in the upper range for North American beaver ponds, (mean 63 and 17 mg C m^{-2} d^{-1}, (Dove et al., 1999; Weyhenmeyer, 1999). Most of the studies mentioned previously reported only mean values, and most of them focused on individual ponds with several samplings throughout the growing season.

Streams order 0 to 4 of the same region had similar mean daily CO_2 (600 mg C m^{-2} d^{-1}) and CH_4 (174 mg C m^{-2} d^{-1}) fluxes to those reported in this study. This comparison becomes relevant when considering that beaver activity mostly replaces segments of small streams by ponds. Natural lakes with similar morphometric characteristics to those of the beaver ponds presented here (< 3 meters depth and between 0.01 to 0.1 km^2) had higher average CO_2 daily fluxes, but lower CH_4 fluxes, (1335 mg C m^{-2} d^{-1} and 60 mg C m^{-2} d^{-1}) respectively. The average daily CO_2 and CH_4 fluxes from lakes and streams mentioned here were extracted from the database of the Industrial Research Chair in Carbon Biogeochemistry in Boreal Aquatic systems (CarBBAS Chair) and previously reported in other studies (Campeau et al., 2014**,** Rasilo et al., 2015).

The global dataset from Holgerson and Raymond (2016) reported an average daily CO_2 diffusive flux of 255 (mg C m^{-2} d^{-1}) and CH_4 7.80 (mg C m^{-2} d^{-1}) for ponds size within 0.001-0.01 km^2 and for ponds that range between 0.01 to 0.1 km^2 an average of 259 (mg C m^{-2} d^{-1}) and 3.36 (mg C m^{-2} d^{-1}) for CO_2 and CH_4 respectively. Meanwhile, Peacock et al. (2021) reported average daily emissions rates of 37 (mg C m^{-2} d^{-1}) for CH_4 and 431 (mg C m^{-2} d^{-1}) for CO_2 for artificial ponds. Together, the CO_2 and CH_4 emissions rates from beaver ponds reported in this study are within the upper range of those observed in studies of small natural and artificial lentic aquatic systems across different climate regions and trophic states.

1.5.4 Total beaver pond C emissions

Our upscaling exercise suggests that CO_2 diffusive flux is the dominant pathway of C emissions from beaver ponds at the watershed scale, followed by CH_4 ebullition and CH_4 diffusive fluxes. The pattern of CO_2 dominating the overall C pool that is emitted to the atmosphere has been reported in previous studies for other boreal aquatic systems such as lakes (Huttunen et al., 2003; Rasilo et al., 2015) and streams (Campeau et al., 2014; Crawford et al., 2014). Methane ebullition accounts for 56% of the total beaver pond CH_4 emissions, whereas diffusive CH_4 fluxes account for the remaining 44%. These results are comparable to reports of beaver ponds from Manitoba (Dove et al., 1999) and Ontario (Weyhenmeyer, 1999), where CH_4 ebullition accounted for 56 and 65% of the total CH_4 emissions, respectively. Our results are also congruent with previous observations that ebullition in small lakes and ponds can be of the same order or even significantly higher than diffusive fluxes, particularly in shallow systems (Bastviken et al., 2004). Ebullition is a depth-dependent process, with higher fluxes typically found in shallow areas. Beaver ponds rarely exceed 3 meters in depth, and thus the entire surface is potentially an active zone for ebullition, whereas in larger lakes, ebullition is generally limited to the littoral area **(**Bastviken et al., 2004; DelSontro et al., 2016). Furthermore, shallow water columns also imply higher sediment temperatures and lower hydrostatic pressure, variables that have been shown to influence CH_4 ebullition dynamics (Bastviken et al., 2011; DelSontro et al., 2016). As the contribution of ebullition to total CH_4 emissions is critically dependent on the fraction of the lake surface area occupied by the littoral zone (DelSontro et al., 2016), and considering that for beaver ponds the total surface area acts as an active ebullition zone, it is not unexpected that ebullition dominates the contribution to total CH_4 emissions.

Our results show that CH_4 is the main contributor to the radiative balance of beaver ponds (here only accounting for C-GHG). Expressed in metrics of CO_2-EQ, the total annual CH_4 fluxes represent 12,551 tons C-CO_2EQ y^{-1}, compared to CO_2 fluxes of 10,620 tons C y^{-1}. Collectively, CH_4 emissions represent 54% of the annual radiative balance, and CO_2 diffusive emissions contribute the 46% remaining. This is in good agreement with estimates by Lazar et al. (2014) for beaver ponds, where CH_4 diffusive fluxes comprised about 60% of the radiative balance. We link the high contribution of CH_4 to the annual radiative balance with specific physical and biological characteristics of beaver ponds. The low flow regime, water retention and the abundance of organic C within the ponds generate conditions for substantial anaerobic metabolism (Naiman et al., 1986; Roulet et al., 1997; Yavitt et al., 1990). Anoxic conditions and methanogenesis in beaver ponds develop in the surrounding flooded soils or in the benthic zone, where oxygen demand is high and oxygen diffusion is limited (Lazar et al., 2014; Naiman et al., 1986; Roulet et al., 1997). Furthermore, shallow depth, which is a common feature of beaver ponds, could also explain the relatively high diffusive CH_4 emission pattern. Shallow depth reduces the opportunity for CH_4 oxidation throughout the water column, as well as bubble dissolution, increasing the probability that CH_4 produced in the anoxic zones reaches the atmosphere (Bastviken et al., 2004; Juutinen et al., 2009; Kankaala et al., 2013).

1.5.5 Integrating beaver pond emissions into the aquatic network C budget

By comparing our results with those of Casas-Ruiz et al. (2021) we were able to assess how incorporating beaver ponds may influence our estimates of C gas emissions from these boreal aquatic networks. This influence originates from two phenomena that occur with the incorporation of beaver ponds, the substitution of a system for another with different C-gas emissions dynamics (i.e., stream for pond) and the overall increase in the total water surface area of the aquatic network. The comparison of the total C-emissions originally calculated by Casas-Ruiz et al. (2021) with our recalculated total emissions that include beaver ponds suggests that the inclusion of beaver ponds in the assessment of total aquatic C emissions increases the estimate by about 4.5%. In other words, this means that Casas-Ruiz et al. (2021) underestimated total aquatic C emissions by 4,5 % due to the lack of inclusion of beaver ponds. This may appear in principle as a relatively modest adjustment and results from the fact that total aquatic C emissions are dominated by CO_2 fluxes, and beaver ponds do not necessarily contribute disproportionately to these. Total aquatic CO_2 emissions increase by only 3% when beaver ponds are considered, whereas their inclusion results in a much more pronounced increase of CH_4 emissions. Estimates of total aquatic CH_4 emissions previously made for this watershed (4,809 tons C y^{-1}, Casas-Ruiz et al., 2021) increase by 19%, to 5,719 tons C y^{-1} when beaver ponds are integrated into the aquatic network, highlighting the major role that these ponds may play in regional C-GHG budgets, primarily via its CH_4 emissions.

1.5.6 Future scenario of beaver pond C-GHG emissions

The contribution of beaver ponds to regional or global aquatic C-GHG budgets is not static but rather is expected to vary as a function of beaver colonies density and future temperature changes (Naiman et al., 1991; Whitfield et al., 2015). We have shown that the contribution of beaver ponds to total aquatic C emissions is roughly proportional to their areal coverage, whereas their contribution to total CH_4 emissions is substantially larger. These contributions will likely shift as beaver populations expand throughout the boreal biome and with it, beaver aquatic habitats. In addition, the projected increase in temperature in this northern landscape is also expected to influence aquatic C-GHG dynamics, particularly CH_4 production, as it is a temperature-dependent process. It is therefore important to assess how C-GHG emissions from beaver ponds may evolve under scenarios of both rising temperatures and beaver population expansion. Based on climate circulation models Jarema et al. (2009) made beaver population projections for the year 2055 in the same region as our study. Using their climate and beaver density projections we derived a first order estimate of beaver pond CO_2 and CH_4 emissions within the selected watershed for the year 2055. To approach this, we selected an intermediate scenario, Figure 4 Jarema et al (2099), of a 1.01°C average annual temperature rise, and a projected 18% increase in the beaver population. Assuming that the increase in the beaver population will lead to a proportional increase in the number of ponds, we extrapolated our pond size distribution to this new scenario. Then we recalculated the C-GHG emissions from beaver ponds using the shifted monthly temperatures with the same approach that we used to calculate the present emissions. This exercise suggests that by 2055 total beaver pond CO_2 emissions may increase by 12%, whereas CH_4 emissions by up to 48% compared to our present estimates. As mean temperature rises and beaver populations increase and expand, the proportion of CH_4 to total beaver ponds C emissions will also increase, driven by a differential effect of temperature on both C-gases. This exercise once again highlights the role of beaver ponds in mediating CH_4 emissions, but also as a positive feedback loop to climate change with a significant radiative forcing potential.

1.5.7 Considerations about the uncertainty and extrapolation of CO_2 and CH_4

Several challenges and uncertainties are associated with estimating C-GHG emissions from beaver ponds at the watershed scale. Although our study was based on a detailed geospatial analysis, and this represents one of the first direct assessments of beaver ponds water extraction at a scale above 10.000 km^2, we are still underestimating the pond number and their total areal extent. The limitations related to geospatial analysis were discussed previously, and it is therefore important to consider that this is still a clear source of uncertainty for our C-GHG emission estimates. The accuracy of our extrapolated CO_2 and CH_4 emissions is also limited by methodological constraints. The CO_2 and CH_4 diffusive flux data that we used to upscale the emissions are derived from a limited number of ponds (*N=51*) and from a single or few sampling locations within each pond. Hence, the spatial variability for each C-gas within each pond is not accurately captured in our dataset and could not be accounted for in our upscaling exercise. Furthermore, most of our CO_2 and CH_4 emission data was collected from late spring to early fall. Thus, our sampled scheme might not cover the full transition period between seasons, when important processes such as macrophyte die-off, or spring thaw occur. Nonetheless, we have accounted for some key aspects of seasonality by incorporating high-resolution monthly average temperature data for the diffusive and ebullitive CH_4 models as well as by accounting for the outgassing of accumulated CO_2 and CH_4 under the ice. Our annual total C emission calculation could be improved with an accurate assessment of CO_2 and CH_4 winter dynamics specific to beaver ponds. Another aspect to consider is that our upscaling does not account for plant-mediated fluxes. Where macrophytes or emergent plants cover a significant portion of the surface, which is often the case in beaver ponds, this pathway may account for a large fraction of the CH_4 delivered to the atmosphere (Desrosiers et al., 2022). Therefore, the CH_4 flux from beaver ponds with plants was underestimated by our measurements. Finally, a key aspect of any bottom-up upscaling involves adequately extrapolating the measured emissions to the ensemble of surface area of the study system, and this involves identifying predictors and developing empirical models that can be used to propagate these fluxes effectively. Beaver ponds are notoriously diverse and heterogeneous in terms of morphometry and environmental features. Consequently, C-gas fluxes vary greatly among ponds within the same region, yet, as opposed to lakes and rivers, identifying the drivers, and deriving empirical models of these gas fluxes that can be used for upscaling has proven elusive. In the case of CO_2 fluxes, and in the absence of any clear environmental driver, our upscaling approach was based on propagating the observed distribution of fluxes around the median, and this results in a realistic yet conservative extrapolation. Methane fluxes, on the other hand, were upscaled based on statistically significant but weak empirical relationships with temperature and phosphorous, which again yield realistic but rather stunted distributions of fluxes. Overall, the emission estimates that we report here for the ensemble of beaver ponds within this boreal watershed are very conservative and represent a baseline that will likely be adjusted upwards as more data and information become available. In this sense, we consider that our upscaled emission estimates could be improved by identifying additional drivers that may explain a higher proportion of the variability in C-GHG fluxes across ponds and thus improve the performance of upscaling exercises. In this regard, more work is still needed to identify the drivers underlying variability in emissions across ponds, and given the complex and heterogenous nature of beaver ponds, these may have distinct biogeochemical patterns compared to other boreal aquatic systems.

1.6 Conclusions

This study provides a baseline of the contribution of beaver ponds to the aquatic network C emissions at a watershed scale. We carried out this study in one of the regions with the highest beaver density within boreal Québec (Jarema et al., 2009) and probably also one of the regions with the highest beaver density in North America at present. Because beaver populations are rapidly expanding throughout the boreal and temperate regions of North America, the results presented here might reflect scenarios that will be widespread in the future. Overall, our results show that beaver ponds account for 9% of the aquatic surface area in this watershed, and their contribution to total aquatic C emissions is roughly proportional to the percentage of aquatic area that they occupy. Yet their contribution to total CH_4 emissions is substantially larger, representing about 18% of the total methane that is emitted by the aquatic network. This is particularly important considering future scenarios of rising temperatures and beaver population growth, as these two variables will potentially lead to a disproportionately higher contribution of beaver ponds to the radiative balance of the aquatic network. Finally, it is also relevant to consider that the beaver habitat is a system with both a terrestrial and an aquatic component. Therefore, further assessments of the importance of the terrestrial component as a C sink are necessary to understand better the actual role of these systems in the C balance of the boreal biome.

ANNEXE A

SUPPORT INFORMATION

Table S1.1. Limnological variables for the Abitibi and Saguenay sampled ponds during the growing season. Mean, median* and quantiles (1^{st}, 3^{rd}).

Variable	Abitibi	Saguenay
Latitude (°N)	48 - 50	47- 48
Longitude (°W)	78.7 – 79.7	70.5 – 71.5
Area (m^2)	11,879 - 5,000* (1,000 - 13,875)	10,217- 4,000* (12,50 - 10,000)
Water temp (C)	18 - 19* (16 - 22)	18 - 16* (13 - 22)
pH	7.1 - 7.2* (6.8- 7.4)	6.5 – 6.6* (6.5 – 7.0)
Oxygen (mg/L)	6 - 6* (5-8)	6 - 7* (6 - 8)
DO (%)	72 - 71* (51- 93)	72 - 78* (64 - 90)
Chl *a* (µg/L)	14 - 6* (5 - 14)	4 - 3* (2 - 6)
TP (µg/L)	74 - 61* (39- 95)	30 - 26* (20 - 34)
TN (mg/L)	0.9 - 0.8* (0.6 -1.1)	0.4 - 0.3* (0.2 - 0.5)
DOC (mg/L)	24 - 20* (16 - 26)	11 -10* (9 - 13)
CO_2 (mg C m^{-2} d^{-1})	780 - 618* (431 - 907)	721 – 527* (337 - 762)
Dif CH_4(mg C m^{-2} d^{-1})	436 - 44* (12 - 412)	150 - 40* (7 - 151)
Ebu CH_4 (mg C m^{-2} d^{-1})	NA	70 - 41* (16 - 95)

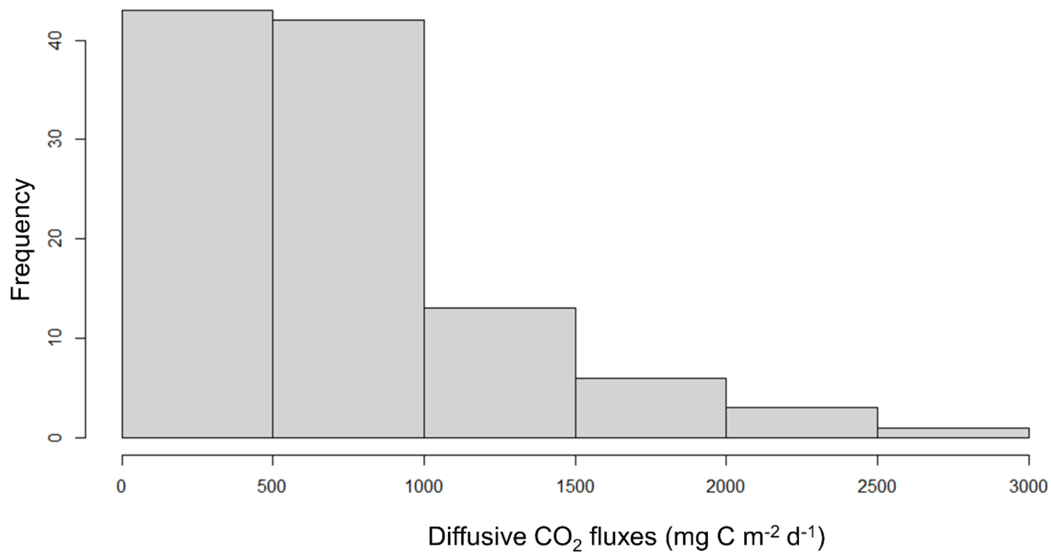

Figure S1.1. Distribution of CO_2 diffusive emissions (mg C m^{-2} d^{-1}) sampled in Abitibi and Saguenay (n=110). Median = 579.84, (380.55 - 881.32) 1st and 3rd. quantiles.

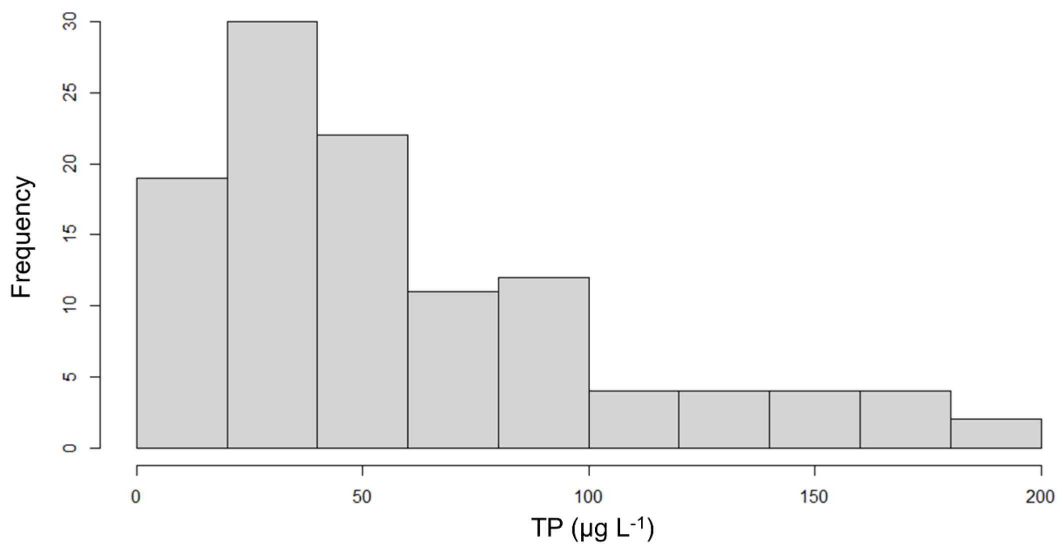

Figure S1.2. Distribution of total phosphorus concentrations of 112 observations sampled in Abitibi and Saguenay (ug L). Median = 46.5 4, (23.7 - 82.6) 1st and 3rd. quantiles.

Table S1.2. Models used to upscale diffusive and ebullitive CH_4 fluxes. The CH_4 ebullitive model corresponds to equation 4 from (DelSontro et al., 2016).

Emission	Equation	*P*	R^2	*n*
Methane Diffusion	$\log_{10}$(diffusive CH_4 flux) = $0.106 \cdot T_{water} - 0.238$	< 0.001	0.34	108
Methane Ebullition	$\log_{10}$(ebullitive CH_4 flux) = $1.04 \log_{10} TP + 0.06\, T_{sed} + 0.14\, (\log_{10} TP - 1.26)\, (T_{sed} - 16.67)$	< 0.001	0.52	102

Table S1.3. Modeled monthly CH_4 diffusive emissions, table shows mean, median*, and in parentheses minimum and maximum values.

Monthly emissions factor	CH_4 diffusive flux (mg C m^{-2} d^{-1})
May	10 - 9* (7- 13)
June	39- 40* (32 - 53)
July	82 - 80* (65 - 108)
August	60 - 61* (47- 78)
September	18 - 17* (13 - 22)
October	3- 4* (3- 5)

Table. S1.4. Modeled monthly CH_4 ebullitive emissions, table shows mean, median*, and in parentheses minimum and maximum values.

Month	CH_4 ebullitive flux (mg C m^{-2} d^{-1})
May	9 - 8* (5- 14)
June	40 - 36* (4 - 155)
July	99 - 75* (3 - 572)
August	68 - 55* (3 - 324)
September	17 - 16* (6 - 35)
October	4 - 3* (0.8 - 16)

Table.S1.5. Pearson correlation coefficients (r) and corresponding p-values between diffusive CO_2, CH_4 emission and environmental variables. (r-values with $p < 0.05$ printed in bold).

	$Log_{10}CO_2$ diffusive		$Log_{10}CH_4$ diffusive	
Variables	r	p-value	r	p-value
Log_{10}TP (µg/L)	0.15	0.10	0.25	**0.01**
Log_{10} TN (µg/L)	0.21	**0.02**	0.34	**<0.005**
Log_{10}Area (m^2)	-0.0052	0.95	0.15	0.12
Log_{10}DOC (mg/L)	0.15	0.10	0.0016	0.98
Water temp.(°C)	0.19	**0.03**	0.34	**<0.005**
CHl a (µg/L)	0.22	0.11	0.35	**<0.005**

Table.S1.6. Pearson correlation coefficients (r) and corresponding p-values between CH_4 ebullition and environmental variables. (r-values with $p < 0.05$ printed in bold).

Variables	$Log_{10}CH_4$ ebullition	
	r	p-value
Log_{10}TP (µg/L)	0.11	0.57
Sediment Temp. (°C)	0.68	**<0.005**
Log_{10} TN (µg/L)	0.20	0.38
Log_{10}DOC (mg/L)	0.13	0.52
CHl a (µg/L)	0.31	0.15

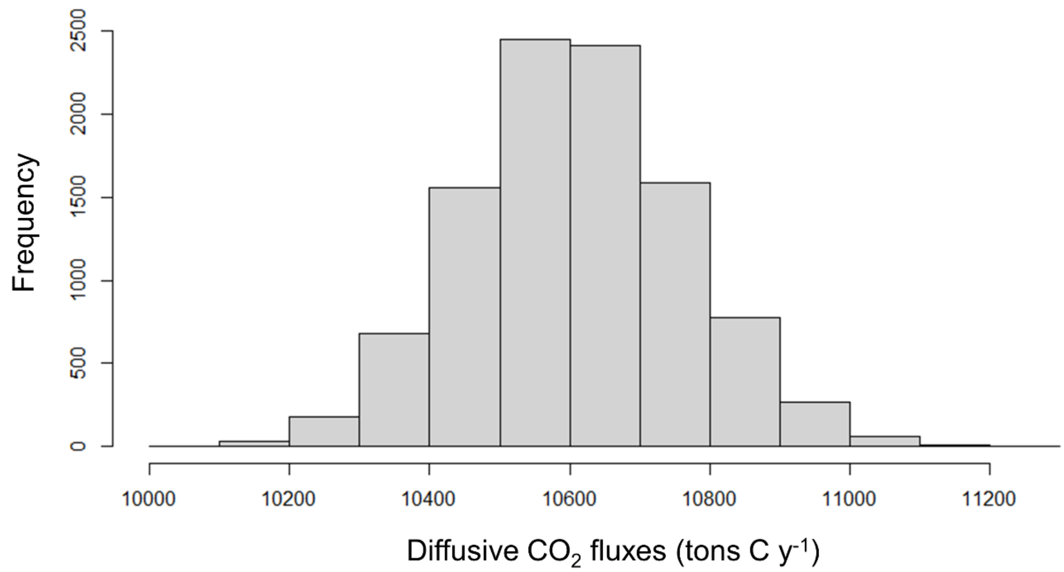

Figure S1.3. Probability distribution function of the 10,000 Monte Carlo simulations for the annual diffusive CO_2 fluxes (tons C y^{-1}). Median = 10,610, (10,311 – 10,920) 5^{th} and 95^{th} percentiles

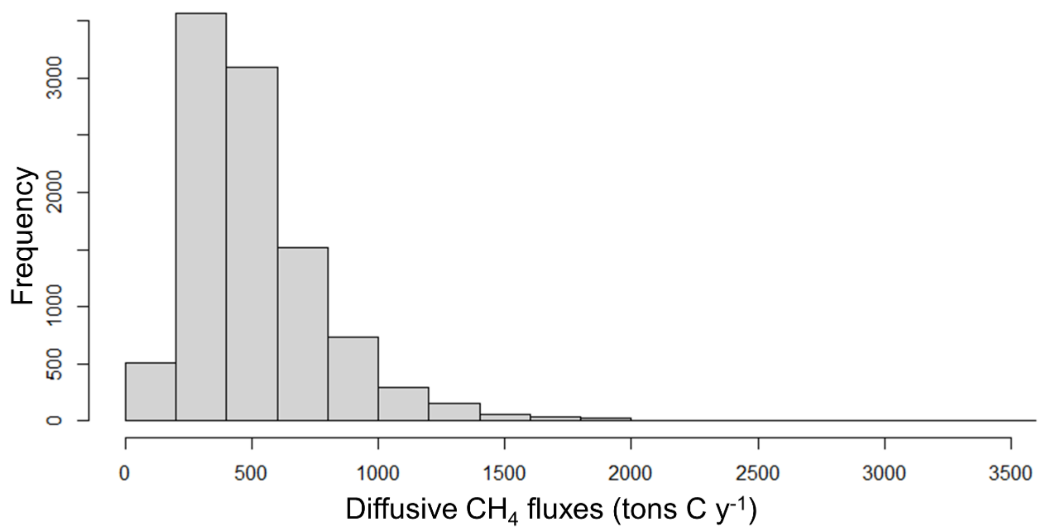

Figure S1.4. Probability distribution function of the 10,000 Monte Carlo simulations for the annual CH_4 diffusive fluxes (tons C y^{-1}). Median = 450, (171 – 1233) 5th and 95th percentiles.

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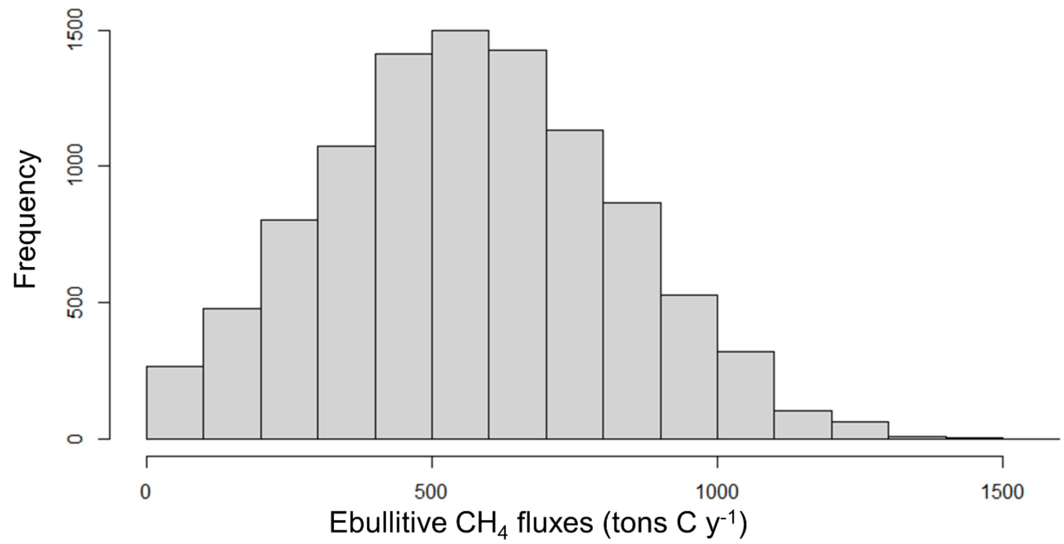

Figure S1.5. Probability distribution function of the 10,000 Monte Carlo simulations for the annual CH_4 ebullitive fluxes (tons C y^{-1}). Median = 564, (95 – 1075) 5^{th} and 95^{th} percentiles.

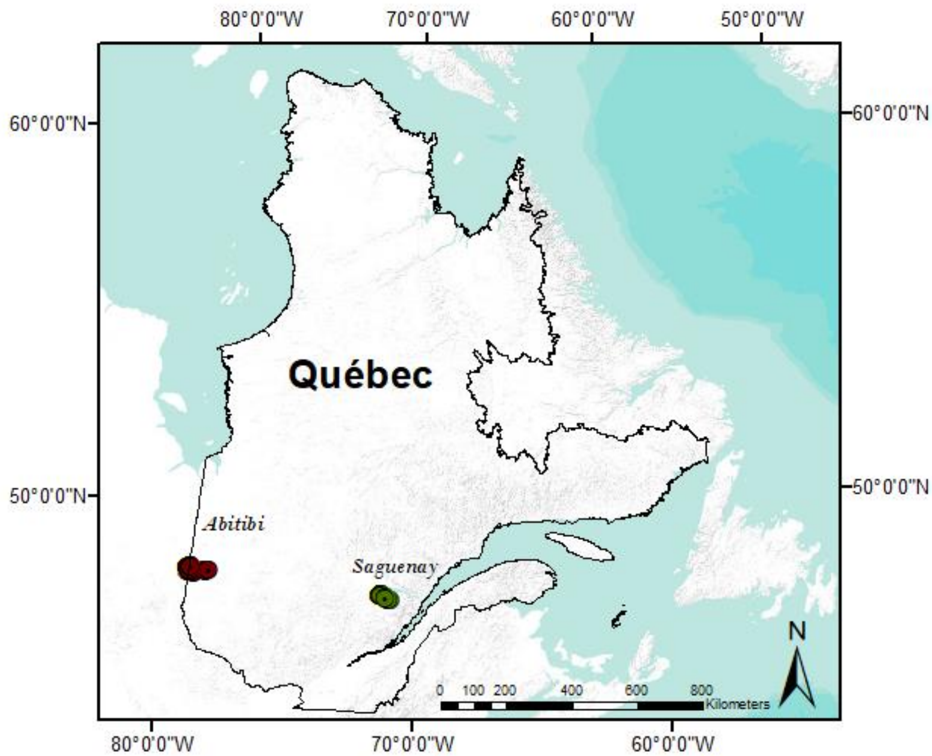

Figure S1.6. Map showing the location of the sampled ponds within the two selected regions, Abitibi (red dots) and Saguenay (green dots), Québec, Canada.

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