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Above and belowground carbon stocks among organic soil wetland types, accounting for peat bathymetry

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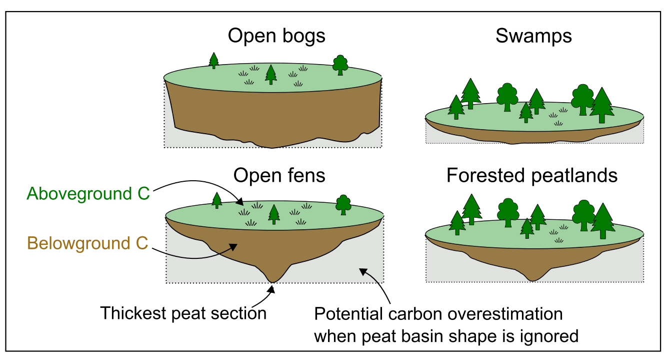
HIGHLIGHTS

- Conservation planning requires to identify C stock variability among wetland types.
- Bathymetry of peat basins is often omitted, likely leading to overestimates.
- 57 sites (four wetland types) were sampled for above and belowground C stocks.
- C is predominantly stored belowground, and accounting for bathymetry is essential.
- Forested peatlands and swamps act as the dominant C stocks at the study region scale

GRAPHICAL ABSTRACT



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ABSTRACT

Wetlands are widely recognized for their carbon (C) sequestration capacity and importance at mitigating climate change. Yet, to best inform regional conservation planning, the variability of C stocks among wetland types and between above and belowground compartments requires further investigation. Additionally, the bathymetry of peat basins has often been ignored, with soil C stock calculations mostly relying on the thickest peat section, potentially leading to overestimates. Here, we sampled vegetation and soil of 57 wetlands of southeastern Canada to characterize the variability of above and belowground organic C stocks among four wetland types: open bogs, open fens, swamps, and forested peatlands. We also compared carbon stock estimation approaches considering peat bathymetry or not. Results showed that peat thickness, and thus soil organic C (SOC), varied substantially within sites due to peat basin shapes. Omitting bathymetry led to site-scale SOC overestimates of about 20–38 % on average, depending on the approach used, with wide variability among sites (overestimates up

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to 200 %). Belowground C stocks varied among wetland types with mean values of 132, 101, 19, and 44 kg C m^{-2} for bogs, fens, swamps, and forested peatlands, respectively. Aboveground C was nearly zero in open bogs and fens but reached ~30 % of total C stock in swamps and ~ 15 % in forested peatlands. C stocks in tree roots and shrubs were negligible. Despite the lower C density (per m^2) of swamps and forested peatlands, these ecosystems represented the dominant C stocks at the regional scale due to their abundance in the landscape. Overall, the four wetland types stored an estimated 2–7 times more C than forest per unit area. Evaluating differences in C stocks according to wetland type, while integrating peat bathymetry in calculations, can significantly improve regional wetland conservation planning.

1. Introduction

Freshwater wetlands, particularly those with a peat deposit, are significant carbon (C) reservoirs and are key in regulating climate as well as supporting many other ecosystem services (Zedler and Kercher, 2005; Mitsch and Gosselink, 2015; Gardner and Finlayson, 2018). While C stocks contained in the woody biomass of wetlands can reach levels similar to those in upland forests (Zoltai and Martikainen, 1996; Lavoie et al., 2005), C accumulation in their soils is estimated to greatly exceed that of forested ecosystems (Poulter et al., 2021b). The water-saturated, low-oxygen soil conditions of wetlands impede biomass decomposition, leading to the accumulation of C-rich soil deposits over millennia, making them one of the most prominent carbon sinks in terrestrial ecosystems (Zoltai and Martikainen, 1996; Lavoie et al., 2005). Despite the valuable role wetlands play in addressing the ongoing climate crisis, human activities continue to cause their loss and degradation at alarming rates worldwide (Davidson, 2014; Dixon et al., 2016; Nahlik and Fennessy, 2016; Fluet-Chouinard et al., 2023). To reach global and national targets for C sequestration, climate change experts have emphasized the essential role of nature-based solutions (Griscom et al., 2017; Seddon et al., 2021), such that wetland conservation has become central in global conventions on mitigation and adaptation strategies (Intergovernmental Panel on Climate, 2014, CBD Secretariat, 2022). However, as recently reported, C stock estimates can still present significant uncertainties since peat bathymetry is often not included in calculations (Loisel et al., 2017), and contributions of below and aboveground compartments to total C stock vary substantially among wetland types at the regional scale (Poulter et al., 2021a). As decisions on land management are mainly made at this scale, a more comprehensive understanding of C stock variability within and among wetland types is essential to best guide conservation planning.

Many factors contribute to the variability of C stocks among peat-forming wetlands. For instance, the forest cover greatly influences where and how C is stored. Indeed, while shrubs and trees mainly sequester C in the aboveground compartment, they also partially control C accumulation in underlying soils through their influence on hydrological processes and litter composition (Simard et al., 2007). Therefore, forested peatlands generally accumulate less peat than open ombrotrophic (bog) and minerotrophic (fen) peatlands primarily due to better soil aeration and enhanced carbon oxidation facilitated by tree roots (Blodau et al., 2004; Bhatti et al., 2006; Magnan et al., 2020). The variability of C stocks among some wetland types has been previously reported (Bernal and Mitsch, 2012; Nahlik and Fennessy, 2016; Magnan et al., 2020), yet most estimates focused on boreal or tropical peatlands, leaving the temperate region understudied (Poulter et al., 2021a). Despite growing evidence across different biomes that the belowground compartment of wetlands has a higher storage capacity than the aboveground one (Magnan et al., 2020; Beaulne et al., 2021; Meng et al., 2021; Poulter et al., 2021a), further scrutiny of this comparison is needed to refine regional-scale C stock estimates and enhance our understanding of wetland C dynamics.

C stock density (per unit area) also varies greatly within individual wetlands because of the complex bathymetry of peat basins (Beilman et al., 2008; Buffam et al., 2010; Fyfe et al., 2014). Studies have suggested that relying solely on data from single peat cores, typically taken near the center of wetlands or at their thickest peat section, and ignoring within-site heterogeneity, is likely to overestimate soil organic C (SOC) (Van Bellen et al., 2011; Yu, 2012; Fyfe et al., 2014; Pluchon et al., 2014; Loisel et al., 2017). For example, in three bogs of eastern Canada, Van Bellen et al. (2011) reported overestimates in the range of 23 % to 61 %, while Loisel et al. (2014) reported an overestimate of 30–40 % for a bog in Sweden. In parallel, most studies have reported SOC values for top peat layers only (< 1 m), thus likely underestimating stocks by more than two-fold since accumulations can reach several meters in certain contexts and C density usually increases with depth, (Tarnocai, 2009; Chimner et al., 2014; Fyfe et al., 2014; Sothe et al., 2022). Although full characterization of peat bathymetry along with complete SOC profiles might represent the ideal way to increase the accuracy of SOC estimates, this is not always feasible due to time-resource constraints. Therefore, time-efficient approaches to evaluating actual belowground C stocks of wetlands, considering peat basin shapes, are necessary to ensure informed land management decisions.

This study aims to characterize the variability in C stocks among and within dominant types of freshwater wetlands of southeastern Canada. More specifically, we aimed to (1) compare peat decomposition and SOC profile among wetland types, (2) investigate peat thickness and SOC heterogeneity within sites and compare approaches to estimate SOC at the site scale, (3) compare above and belowground C stocks across wetland types, and (4) examine how our results apply to the entire study region. We hypothesized that SOC would increase with peat depth and that accounting for peat basin shapes would significantly affect carbon stock estimates. We further hypothesized that the belowground compartment would dominate the total C stock, even in swamps typically not recognized for their peat component. To address these objectives, we collected soil cores in 57 wetlands that encompassed the four dominant wetland types of the study region (bogs, fens, swamps, and forested peatlands), measured peat thickness at multiple locations within each site and calculated the amount of organic C contained in peat, shrubs and trees, including roots.

2. Material and methods

2.1. Study area and sampling sites

The study was conducted in the Greater Quebec City region (~1050 km^2, ~582,000 inhabitants), Qc, Canada, consisting mainly of natural habitats: forests (51 %), wetlands (7 %), and aquatic habitats (3 %). Agriculture occupies 9 % of the area, while other anthropogenic land-cover types reach ~30 %. The regional climate is humid continental, with warm summers and severe winters with strong seasonality. The mean annual temperature is ~4 °C, with average maximums near 19 °C in July and − 11 °C in January (https://climate.weather.gc.ca). The mean annual total precipitation is ~1200 mm, of which ~25 % falls as snow. Among the freshwater wetlands considered in this study, there are 38 bogs, 79 fens, 1636 swamps, and 430 forested peatlands, covering a total of 4964 ha (Beaulieu et al., 2014; Table 1). These represent 86 % of all wetland area within the study region, where shallow waters, marshes and wet prairies (not included in this study) occupy 5 %, 8 % and 1 %, respectively. This nomenclature follows the Quebec wetland classification system (Buteau et al., 1994) that was used by Ducks Unlimited

Table 1
Summary statistics of the four dominant wetland types found in the study area.

Wetland type	Site area (ha)				Number	Total area (ha)
	Median	Mean	Min	Max		
Bogs	1.2	1.9	0.1668	7.9	38	73
Fens	0.7	2.2	0.0013	31.8	79	176
Swamps	0.6	1.7	0.0004	117.0	1636	2763
Forested peatlands	1.1	4.5	0.0014	201.7	430	1953
Total	–	–	–	–	2183	4964

Canada (DUC) to map wetlands in southern Québec (Beaulieu et al., 2014). It separates forested and open wetlands using the cover of woody species taller than 4 m (open wetland <25 % ≤ forested wetlands), as well as organic-soil and mineral-soil wetlands using the thickness of the peat deposit (mineral-soil <30 cm ≤ organic-soil). Consequently, bogs and fens are open wetlands on organic soils, dominated respectively by ericaceous plants and sphagnum mosses in bogs, and by graminoids and brown mosses in fens. Swamps and forested peatlands, on the other hand, are forested wetlands found on mineral and organic soils, respectively (though swamps can occasionally accumulate peat). It should be noted that the wetland maps produced by DUC are based on tele-detection and photointerpretation using multiple products. Data on depth of peat deposit is not available for southern Québec, and this criterion is not used in their photo-based classification, leading to some potential errors in distinguishing between swamps and forested peatlands. While wetlands could have been reclassified following our field measurements using average peat depth values, we decided to keep each site within its original category to reflect the actual variability that can be found within each type under this classification. We selected 57 sites for sampling, considering both accessibility and balanced representation of the four wetland types. We also selected sites with minimal to no human impact using a land development index (LDI) within a buffer of 100 m around each site (See SI for details). This led to the sampling of 9 bogs, 14 fens, 14 swamps, and 20 forested peatlands (Fig. 1). All studied swamps had >30 % soil organic matter content (see results). Thus, we refer to all wetlands considered in this study as organic-soil wetlands (Joosten and Clarke, 2002).

2.2. *Woody above and belowground biomass*

In each site, we estimated the aboveground C stock density (kg C m^{-2}) of trees and shrubs in two 400 m^2 plots (20 × 20 m). One plot was located where the thickest peat deposit was found, and the other at a midpoint between the latter and the wetland margin. We ensured that the plant communities at both sampling sites were representative of the dominant plant community of the site. In each plot, we first evaluated the diameter at breast height (DBH; 1.3 m) of all trees taller than 4 m, classifying them into eleven categories: [2–5[cm; [5–10[cm; [10–15[cm; [15–20[cm; [20–25[cm; [25–30[cm; [30–35[cm; [35–40[cm; [40–45[cm; [45–50[cm; [50–55[cm. For shrubs, we evaluated the coverage of each species in each plot, reporting the vertical projection of foliar area.

We estimated the aboveground tree and shrub biomass using allometric equations. For trees, we first estimated the height of each individual tree based on linear regressions using a dataset of species-specific DBH and height values for all trees found in southern Quebec (Gonzalez, 1990). Then, tree biomass was calculated from our eleven DBH categories and estimated heights using Ung et al. (2013) allometric equations developed for each species. Stem, bark, branches, and foliage were included in biomass estimates. For shrubs, we estimated the volume of each species by multiplying its % cover by its species-specific mean height as reported in Rouleau and Brouillet (2002). We then used 3D models from Flade et al. (2020) to convert each species volume into biomass. We used the coefficients of the nonlinear least square regression models (NLS), as these showed the best R-squared values. When equations were not available for a specific shrub species, we used the model of the closest species based on phylogeny.

To convert tree and shrub biomass into C content (kg), we used a conversion factor of 0.498 for soft wood species and 0.521 for hard wood species (Birdsey, 1992). We then estimated total aboveground C per plot by summing stocks of trees and shrubs. For belowground woody C, we only estimated content in tree roots, and based this on ratios of below:

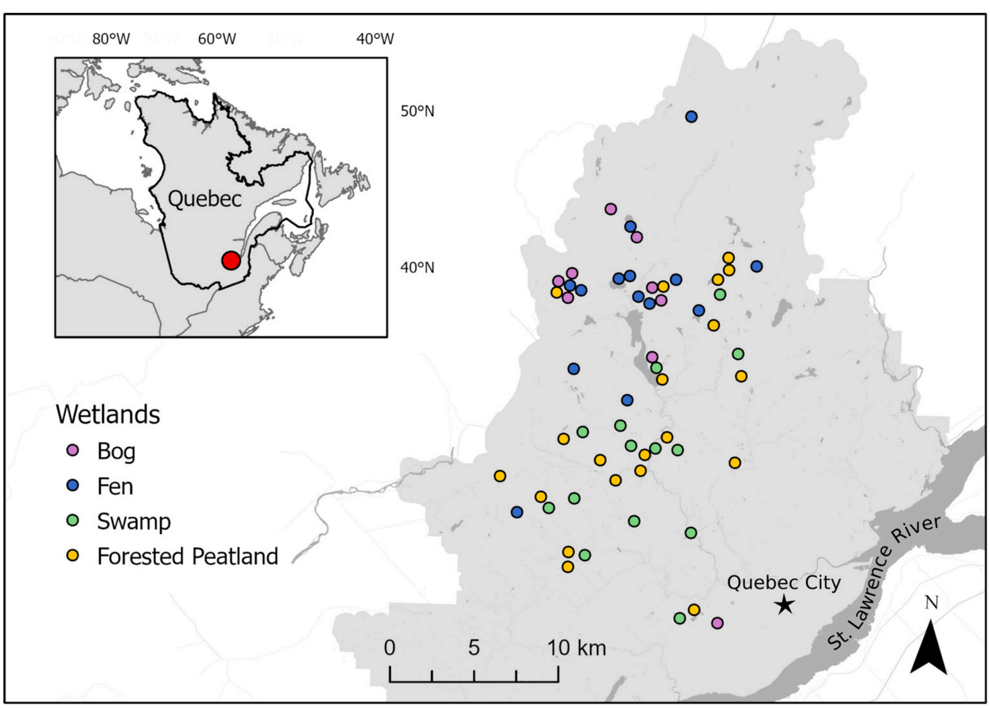

Fig. 1. Study area (light grey), comprising the Greater Quebec City region and the St. Charles River Basin (the area's main hydrologic system), where 57 wetlands were sampled.

aboveground biomass specific to soft (17 %) and hard (15.5 %) wood species (Birdsey, 1992). For statistical analyses, we used the mean value of the two plots in each wetland and reported C stock densities in units of kg C m^{-2}.

2.3. Profiles of soil decomposition and soil organic carbon

We characterized soil organic C (SOC) contained in peat (in kg C m^{-2}) at the center of each 400 m^2 plot used for quantifying woody biomass, based on von Post humification H values (von Post, 1922; Grover and Baldock, 2013), following the well-established methodology of Stanek and Silc (1977). More precisely, we extruded peat samples until the underlying mineral layer was reached. For the upper 1 m, we used a one-piece auger (15 × 5 cm), collected samples at depths of 10 cm, 30 cm, 50 cm, and 100 cm, and measured the von Post humification H value for each. For thicker deposits, we used a Russian borer (50 × 5 cm) to collect samples every additional 50 cm and at the interface of peat and mineral soil.

We estimated peat C content based on our von Post H values using relationships observed in the literature between H values, bulk density (Bd), organic matter (OM) content, and C content. The relationships between H values and Bd are quite consistent among studies (Boelter, 1969; Silc and Stanek, 1977; Krüger et al., 2021). We used the equation of Silc and Stanek (1977). Then, to estimate OM content, we first conducted regressions between Bd and OM content using the dataset of Loisel et al. (2014), which consists of 127 northern peatlands. The relationships observed based on this dataset varied greatly between bogs and fens, such that we fitted a separate model for each (Fig. S1). For fens, the relationship also varied according to peat composition (i.e., peat dominated by sphagnum, woody compounds, brown moss, herbaceous plant debris or humified peat). Two groups emerged, one with sphagnum, herbaceous and woody peat types, and another with brown moss and humified peat types. Because our sites showed a minimal amount of brown moss (see Table S1), we excluded these data points while fitting the models. We also excluded permafrost peatlands since none of our sites were in such northern conditions. Models for bogs (Eq. (1)) and fens (Eq. (2); Fig. S1) were fitted with nonlinear least square, using the Stats package in R (R Core Team, 2020). We tested logarithmic and exponential relationships, and retained the latter as it resulted in better model fits. The resulting models relating Bd to OM content were consistent with those of other studies (Hossain et al., 2015; Krüger et al., 2021).

$$\boldsymbol{OM}(\boldsymbol{bog}) = \mathbf{102}\ exp(-\mathbf{0.80}\ \boldsymbol{BD}) \tag{1}$$

$$\boldsymbol{OM}\ (\boldsymbol{fen}) = \mathbf{106}\ exp(-\mathbf{2.98}\ \boldsymbol{BD}) \tag{2}$$

We then estimated OM content in each of our samples using these models and our Bd estimates. We used our fen model (Eq. (2)) for forested peatlands and swamps because these wetland types showed decomposition profiles more like those of fens than bogs (see results below). This similarity likely arose from the prevalence of herbaceous plants in the understory of forested peatlands and swamps (see Table S1), as herbaceous residues decompose more rapidly compared to the *Sphagnum* biomass dominant in bogs (Barreto and Lindo, 2018). The presence of roots and oxygen may also explain the greater degree of peat decomposition observed in top layers of fens, swamps and forested peatlands (Belyea, 1996; Nordström et al., 2022).

Finally, based on our OM estimates, we calculated SOC in each sample, assuming a 50 % C content (Perie and Ouimet, 2008; Loisel et al., 2014). For statistical analyses, we used the mean value of the two quadrats in each wetland.

2.4. Accounting for soil thickness variability in soil organic carbon estimates

2.4.1. Peat thickness variability within sites

We measured peat thickness of all 57 sites at three locations along a transect; i) at the margin, here identified as where plants and soils became characteristic of wetland conditions, following (Lachance et al., 2021), ii) near the center (according to georeferenced maps), and iii) at the midpoint between these two locations. Peat thickness was measured using probes and extension rods. Two to three measurements were taken at each location, depending on wetland size, leading to a total of 396 measurements across all 57 wetlands. Since we used metal rods that did not extract soil samples, we acknowledge that lake-bottom sediments or mineral layers may also be included in our measurements. To test whether peat thickness varied between margins, centers and midpoints, for each wetland type, we log-transformed thickness data for normality assumption, and conducted pairwise *t*-tests, using the rstatix package in R (R Core Team, 2020).

2.4.2. Soil organic carbon density

To evaluate how SOC estimates can vary within each site, depending on location (margin, midpoint, center), we modeled SOC profiles at each point where we measured thickness. To do this, we first fitted models based on our peat core data, relating SOC values to peat thickness (114 cores and 532 samples along profiles) with an exponential decay function, using the stats package in R (R Core Team, 2020). We did this for each wetland type separately but grouped swamps and forested peatlands since they had similar SOC profiles. We then used these models to estimate SOC profiles at each point of thickness measurement (396 points in total) and reported these per location and wetland type. To compare SOC estimates, we log-transformed all values for normality assumption and conducted pairwise t-tests.

2.4.3. Aggregating SOC values per site: Comparison of approaches

Most studies use the mean of peat thickness measurements to estimate SOC density (kg C m^{-2}) at the site-scale. However, because the maximum thickness likely occurs over an area that is proportionally smaller than the thinner surrounding peat, using a simple mean thickness value may result in an overestimation of SOC. We thus applied an area-weighted mean thickness approach. First, for sites in which the thickest peat section was located at the center (the dominant configuration observed in our sites), we used a hypothetical circular shape and computed areal proportions from the three equal parts of the radius (r), leading to values of 56 %, 33 %, and 11 % for the outer, middle, and center sections, respectively (Fig. S2). In any case where the thickest part was located at the margin or at midpoint, we attributed the areal proportions accordingly: 11 % to the thickest part, 33 % to the middle part and 56 % to the thinnest part. The area-weighted mean peat thickness was calculated per site by multiplying thickness values with these location-specific weighting factors (areal proportions). For each site, we compared SOC estimates based on the 'area-weighted mean thickness approach' with estimates either observed at wetlands' thickest section or based on a 'simple' mean thickness approach.

2.5. Upscaling carbon stocks at the regional scale

To evaluate C stock at the scale of the entire study area and examine its distribution among wetland types, we upscaled our results, obtained at the 57 sampled sites, to the whole region. To do this, we first calculated total C stock per site by multiplying C density values in organic soil, roots, and aboveground C by the area of each wetland and then fitted linear regressions, per wetland type, between total C stock and wetland area, using log-transformed values for normality assumption (Fig. S3; $R^2 = 0.38$ for bogs, $R^2 = 0.82$ for fens and forested peatlands, and $R^2 = 0.89$ for swamps). We used these models to estimate C stock in all wetlands of the region, categorized into the four studied types, based on their area and type.

3. Results

3.1. Variability in peat decomposition among sites, wetland types, and along profiles

We observed a general profile of increasingly decomposed peat towards deeper layers, yet with a wide variability among samples, particularly in the top two meters (Fig. 2a). This variability was related to the different wetland types (Fig. 2b). Bogs showed less decomposed peat in the upper sections of the profiles than the three other types. However, at deeper layers (~250 cm depth), all types appeared to reach similar levels of decomposition around H values of 8. One bog and two fens had thicker deposits, near 700 cm, where the degree of decomposition was higher for the bog (H value of 10) than for the fens (H value of 8). Peat in the surface layers (<30 cm) was generally less decomposed in forested peatlands (H value of ~4) compared to swamps, where the decomposition levels were also more variable (H value of ~4 to 8). By converting the profiles of H values into profiles of soil organic C (SOC), we observed that most SOC was stored in layers below a depth of 1 m (Fig. 2c). Indeed, although OM% was lower at greater depths, the higher bulk density at these depths led to higher SOC values (Fig. S4). Profiles of SOC differed per wetland type, as shown by the distinct model fits (Fig. 2c).

3.2. Peat thickness and soil organic carbon at different locations within each site

Peat thickness varied among sites of each wetland type, with more variability in bogs and fens than in swamps and forested peatlands (Fig. 3a). Mean thickness at centers reached ~270 cm in open bogs and fens, with a standard deviation (SD) of ~200 cm, while it reached 34 cm (SD = 33) and 100 cm (SD = 83) in swamps and forested peatlands, respectively. For swamps, three sites indicated a mean thickness at center slightly >30 cm, and one site distinctly stood out as a forested peatland, with peat thickness reaching 150 cm. Peat thickness also varied within each individual site, with margins generally thinner than centers, and to a lesser degree than midpoints, suggesting bowl shapes for most basins. This was particularly pronounced for fens, with peat ~2.5 thicker at centers, and ~1.9 thicker at midpoints than at margins on average (with sites showing factors as high as 6.3 for center-margin difference; Figs. 3a; S5a). In comparison, the difference between centers and margins was ~1.75 on average in forested peatlands (maximum of 4.5), and ~1.4 in swamps and bogs (max of 3.4 and 2.6, respectively). These differences were significant for all wetland types ($p < .05$) except for swamps, where the midpoint had generally the thickest peat (significant difference with margins; $p = .02$). Bogs showed the least variation among locations, indicating flatter basins than the other wetland types. SOC estimates mirrored the proportional differences and levels of statistical significance between locations observed for peat thickness

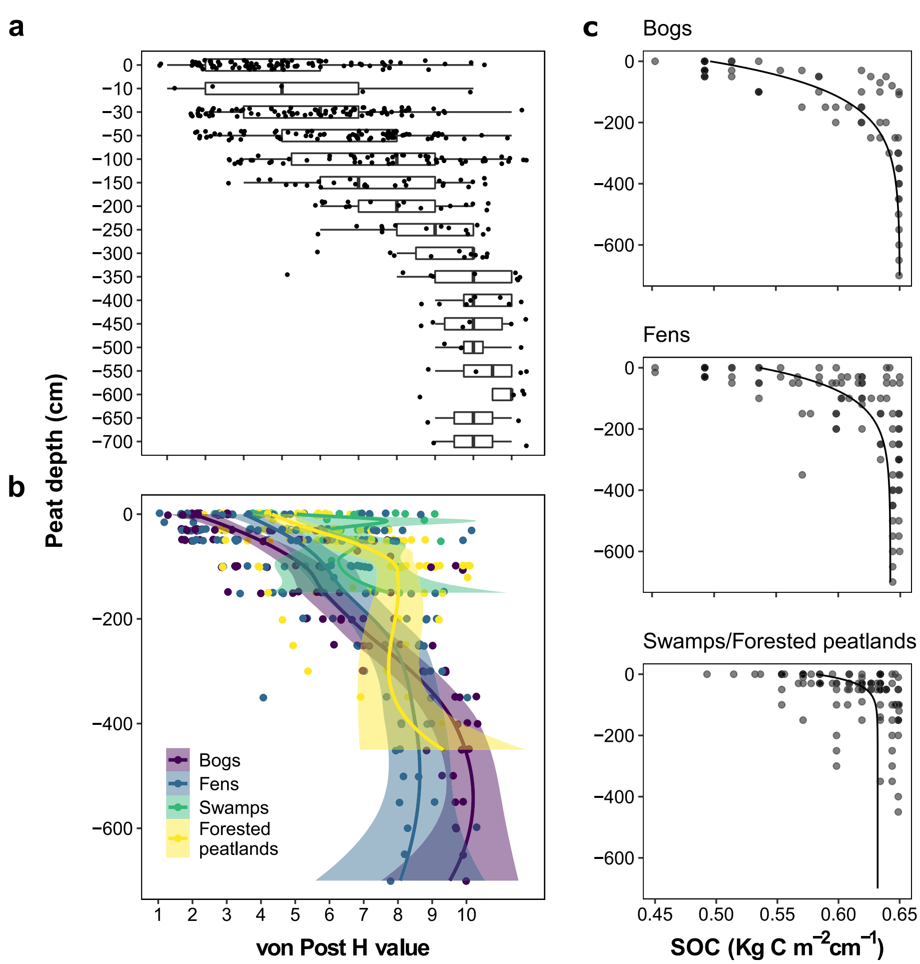

Fig. 2. Profiles of von Post H values **a)** for all sites together, and **b)** per wetland type, and **c)** profiles of soil organic carbon (SOC) per wetland type, estimated based on H values and coefficients from the literature (see methods). In a), boxes represent the inter-quartile range (IQR) and whiskers extend to the highest and lowest value no further than 1.5*IQR. In b), colored trends were fitted with locally weighted scatterplot smoothing (loess) to help with visual representation of differences among wetland types. Exponential decay models between SOC and peat depth were fitted for each group: $SOC_{bogs} = 0.65–0.15^{(depth /103)}$; $SOC_{fens} = 0.64–0.10^{(depth /82.5)}$; $SOC_{Swamps\ and\ Forested\ peatlands} = 0.63–0.15^{(depth /23)}$.

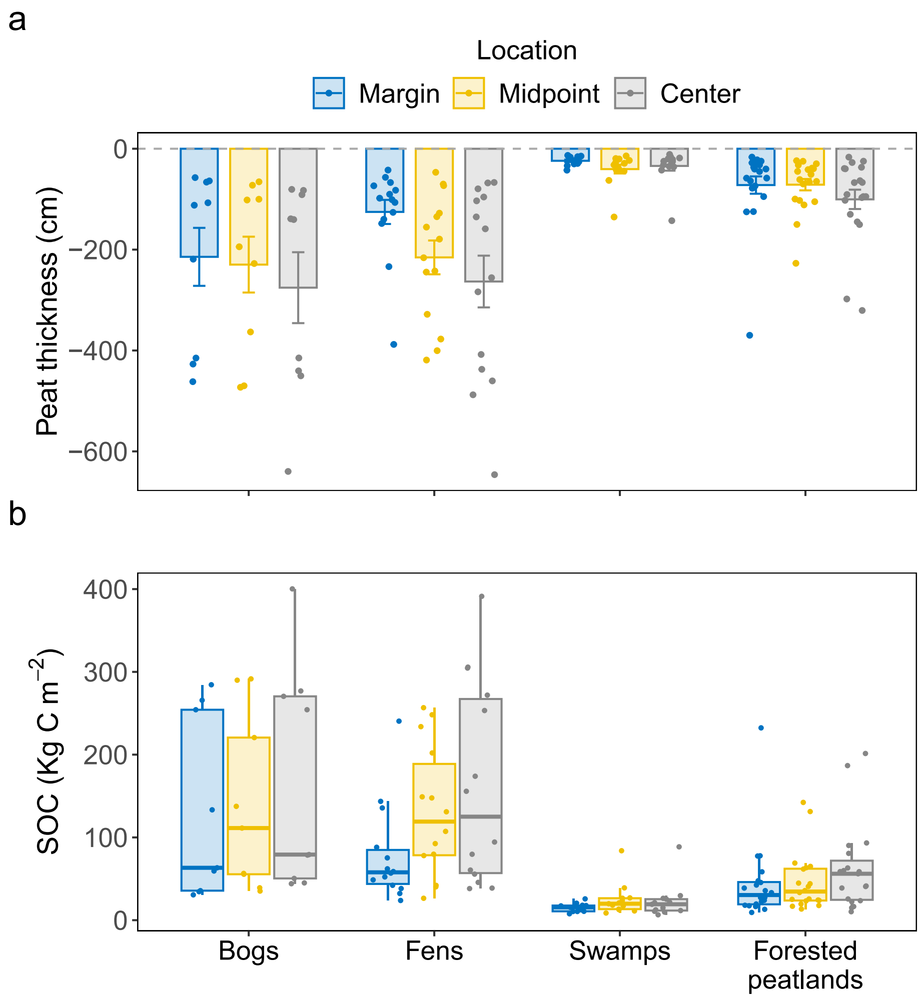

Fig. 3. Within-site heterogeneity of **a)** peat thickness and **b)** soil organic carbon (SOC), shown per wetland type. In a), bars represent the mean values per location and type, and whiskers the standard error. In b), boxes represent the inter-quartile range (IQR) of estimates, middle lines show median values, and whiskers extend to the highest or lowest value no further than 1.5*IQR. SOC values were modeled at each location where peat thickness was measured, based on profiles of SOC observed from peat core data (see methods). Each datapoint represents the mean value, per location and per site, of the three to four replicates of peat thickness (and thus of modeled SOC estimates) measured at each location.

(Fig. 3b; Fig. S5b). Mean SOC values at centers were 192 kg C m^{-2}, 200 kg C m^{-2}, 38 kg C m^{-2}, and 98 kg C m^{-2} for open bogs, open fens, swamps and forested peatlands, respectively. Although the thickest peat section was predominantly found at the center, several wetlands had their thickest deposits, and consequently the highest SOC accumulation, at the margin or midpoint (two bogs, two fens, three swamps, and six forested peatlands; Fig. S5a).

3.3. Aggregating SOC values at the site scale

SOC values at the site scale differed widely depending on the aggregation approach (Fig. 4). When comparing the approach based on the thickest section only with the area-weighted mean thickness approach, which accounted for the bathymetry of the peat basin, we found that the former consistently resulted in higher SOC estimates. The mean percentage difference per type was 28 % for bogs, 53 % for fens, 16 % for swamps, and 46 % for forested peatlands (Fig. 4a). Values varied widely among sites within each wetland type, ranging from −1 % to 77 % in bogs, −46 % to 190 % in fens, −18 % to 70 % in swamps, and – 40 % to 200 % in forested peatlands. Moreover, the ‘simple’ mean thickness approach also consistently led to higher SOC estimates than the area-weighted mean thickness approach, (by 11 %, 25 %, 13 % and 21 % on average for bogs, fens, swamps, and forested peatlands, respectively; Fig. 4b). Again, differences between these two approaches varied widely among sites, ranging from 1 % to 24 % in bogs, 2 % to 86 % in fens, 3 % to 40 % in swamps, and 3 % to 77 % in forested peatlands.

3.4. Aboveground vs. belowground carbon

C was predominantly stored in peat in all wetland types (Fig. 5). Roots stored a negligible amount of C, with nearly null values for bogs and fens, and mean values of ~1.5 kg C m^{-2} in swamps and forested peatlands (5 % and 3 % of total C density, respectively, and 7.5 % and 3 % of the belowground compartment). The aboveground compartment also stored a negligible amount of C in bogs and fens yet reached ~8 kg C m^{-2} in swamps and forested peatlands on average, representing ~30 % and ~15 % of their total C density, respectively. This aboveground pool varied considerably among sites, with values ranging from ~4 to ~10 kg C m^{-2} in swamps and forested peatlands. Within-site variability (between quadrats) of aboveground C density was minimal (Fig. S6), and although shrubs represented a significant proportion of aboveground C store in bogs and fens (Fig. S7), their contribution to total organic C stocks was negligible in all wetland types (<0.1 %). Using the area-weighted mean thickness approach for the peat compartment, mean total C density per wetland type reached 133, 102, 27, and 52 kg C m^{-2} for bogs, fens, swamps, and forested peatlands, respectively.

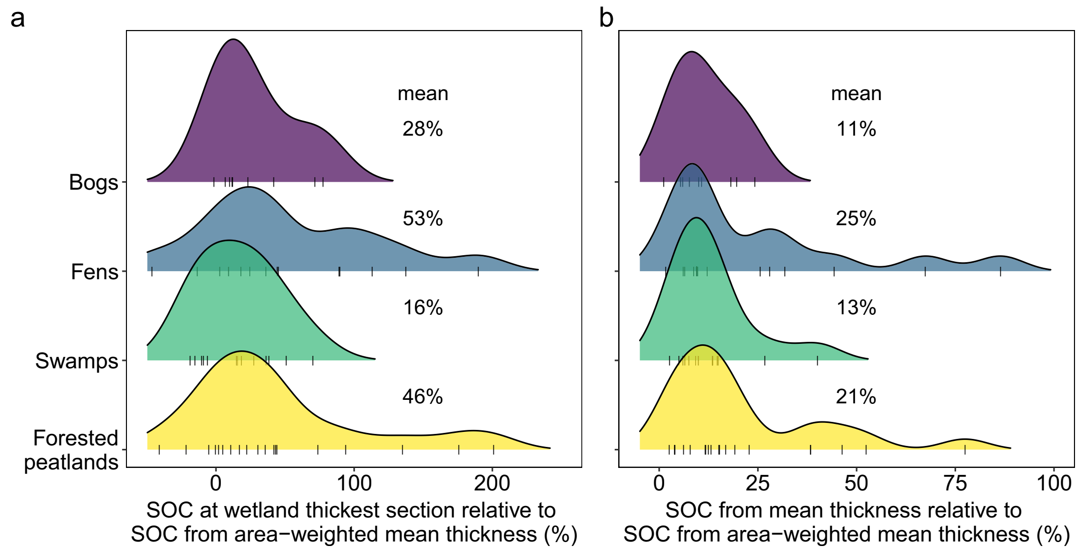

Fig. 4. Density plots of the site-by-site difference (%) in SOC values estimated using **(a)** the wetlands' thickest section relative to the area-weighted mean thickness, and **(b)** the mean thickness relative to the area-weighted mean thickness, per wetland type. Small black lines at the bottom of each distribution represent values for each individual site. Mean differences per wetland type are also indicated. Under the mean thickness approach, peat thickness measurements within a site had equal weight when calculating SOC. Under the area-weighted mean thickness approach, each measurement was weighted according to the hypothetical area it represented within the wetland, thus accounting for peat bathymetry (see methods for details).

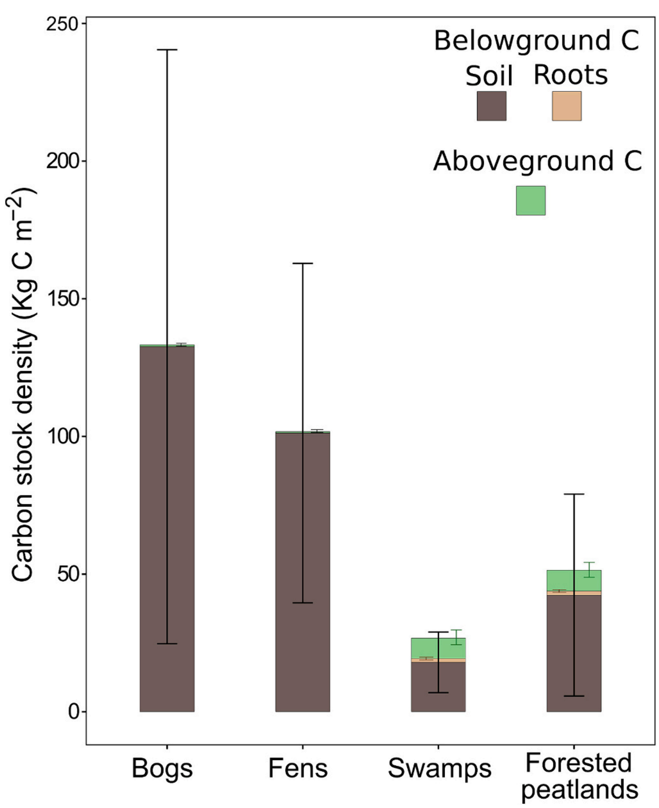

Fig. 5. Comparison of organic carbon stock density (kg C m^{-2}) between aboveground and belowground compartments, and among wetland types. Bars represent mean values per wetland type, with error bars showing the standard deviation. Soil organic carbon estimates accounted for the bathymetry of peat basins using the area-weighted mean thickness approach (see methods for details).

3.5. *Upscaling carbon stocks at the regional scale*

Although swamps and forested peatlands had lower C density on an areal basis than bogs and fens (Fig. 5), they represented the predominant sites for C storage at the study region scale, due to their high abundance (Table 2). Bogs and fens accounted for only 4 % and 10 % of the total organic C stocks in wetlands at the scale of the study region, respectively, while the contribution of swamps reached 38 % and that of forested peatlands was 49 %. Together, these four types of wetlands were estimated to store 1834 kT C within the region (95 % confidence intervals of 1167–3083 kT C).

4. Discussion

This study showed that C stock density varies among wetland types. Peat was consistently the predominant carbon storage component (between 70 % to ~100 %), compared to roots and aboveground biomass. We showed that peat thickness varied significantly at the site-scale and that considering the bathymetry of peat basins is essential for increasing the accuracy of C stock estimates. Relying on maximum thickness alone to evaluate peat C stock led to estimates 38 % higher on average than when accounting for bathymetry, with sites reaching overestimates of up to 200 %. Using mean thickness minimized this tendency, yet still led to values 19 % higher on average than when accounting for bathymetry via the area-weighted mean thickness approach. Finally, we showed that while bogs and fens can store more carbon than swamps or forested peatlands on an areal basis, the latter types represented the main C stocks at the scale of the study region because of their high abundance in

Table 2
Upscaled estimates of wetland total C stocks at the study region level, with 95 % confidence intervals (CI). Estimates were upscaled based on relationships observed in sampled wetlands between C stock and site area (Fig. S3).

Wetland type	Total C stock (kT C)	
	Mean (95 % CI)	
Bogs	73	(24–263)
Fens	181	(101–337)
Swamps	688	(480–1012)
Forested peatlands	892	(562–1471)

the landscape.

4.1. Variability in C density estimates

Our estimates of C contained in the aboveground woody biomass of swamps and forested peatlands are comparable to those recently reported for forests in our study region (Sothe et al., 2022; 6–8 kg C m^{-2} for aboveground biomass and 1.3 kg C m^{-2} for roots). Lower values (1.5–5 kg C m^{-2}) were also reported for forested peatlands in the province of Quebec (Magnan et al., 2020). However, these are likely influenced by the authors' exclusive focus on bogs in higher latitudes compared to ours, two factors known to limit productivity (Thormann and Bayley, 1997; Bubier et al., 1999). In the case of SOC, our mean estimates are also well aligned with those of previous studies, showing larger deposits in non-forested than in forested wetland sites (Mäkilä and Goslar, 2008; Beaulne et al., 2021). However, our estimates varied widely among sites of each wetland type, as well as between plots within the same site (particularly for fens; Fig. S6). This variability can be explained by multiple factors. Hydrology and geomorphology are perhaps the main drivers of peatland formation processes and peat accumulation rates, with terrestrialization (lake in-filling) potentially leading to deeper peat deposits than paludification (lateral expansion of peat over mineral soil; Bauer et al., 2003; Rydin et al., 2013). Others have also reported the influence of peat composition on C stocks, with '*Sphagnum* peat' having lower C content than 'non-*Sphagnum* peat' (Loisel et al., 2014, 2017), a distinction we accounted for in this study (Fig. S1). Distinguishing the nature of peat composition is particularly useful when estimating C stocks, since it is easier to determine during a field campaign than the geomorphology and/or formation process of a site.

4.2. Importance of peat bathymetry

Although our sampling design (transects from margin to center) only partially addresses the problem of peat thickness variability within sites, our protocol captured enough variability to enable comparison of approaches for estimating SOC at the site-scale. Large overestimates based on the thickest section only (compared to estimates of the area-weighted mean thickness approach) were observed for sites that showed wide variability in peat thickness. The topography underneath peat deposits was more homogeneous in bogs and swamps in general (flatter peat basins) than that below fens and forested peatlands, explaining the smaller overestimates observed in these ecosystems. Our mean overestimate of 38 %, with fens and forested peatlands reaching overestimations of up to 200 %, align with the few previous studies that have considered peat bathymetry in their C stock estimates. For example, while Van Bellen et al. (2011) and Loisel et al. (2014) reported overestimates in the range of 23 to 61 % for northern bogs, another study, based on 28 sites in southeastern Canada, including bogs, fens, and forested peatlands, also showed overestimations reaching ~200 % (Major, 2020). Such large overestimates can be explained by sites with highly heterogeneous peat basins, with the thickest peat sections representing only a small areal proportion of the site. These results are of great importance since large scale C stock estimates rely on averaged values from wetland C stock studies, which most often consist of a limited amount of peat cores often collected at wetlands' center or in their thickest section for paleoecological purposes (Loisel et al., 2017).

Although the complete characterization of peat bathymetry is likely the ideal way to address the issue of overestimation, it is hardly feasible for large scale regional assessments. While methods such as ground penetrating radars (Carless et al., 2021) may facilitate such analyses, partial thickness sampling and mean thickness estimates are still often used as a compromise for approximating peat bathymetry in C stock calculations. Yet, as shown here, this strategy may still overestimate SOC by 19 % on average (with values ranging from 1 % to 86 % among sites) by giving a disproportionate weight to wetlands' thickest section. We acknowledge that the area-weighted mean thickness approach used here only approximates the actual peat bathymetry, and caution is warranted in interpreting the reported overestimation. Nevertheless, this approach yielded SOC estimates similar to those of previous studies that characterized peat bathymetry in more detail, particularly Major (2020).

4.3. Upscaling C stocks at regional levels and importance for decision making

The larger C stocks in the belowground wetland compartments compared to aboveground ones could be easily attributed to peat accumulation over millennia, whereas forests develop over mere decades. However, even when comparing these two compartments on the same timescale, Beaulne et al. (2021) reported higher rates of C sequestration by peat compared to overlying tree biomass by a factor of more than two. From this perspective, peatlands may not only represent valuable 'immobilized' C reservoirs, but also highly efficient ecosystems for mitigating climate change through high C sequestration rates.

Additionally, our study underscores the disproportionate C sequestration role of wetlands' belowground compartments per unit area compared to surrounding forests. Using our aboveground C stock estimates of swamps and forested peatlands as a proxy for forest biomass C storage capacity (comparable to values reported by Sothe et al. (2022) for forests in our study region), and estimating SOC density in forested soils at 8 kg m^{-2} based on Bhatti et al. (2006) for the Canadian boreal zone, we estimated that forests within our study region may store ~8400 kT C (half aboveground half belowground). Based on our mean estimate, the four wetland types considered in this study store 1834 kT of carbon (95 % confidence interval: 1167–3083 kT). Despite covering only 12 % of the wetland-forest area in our study region (excluding the three other wetland types; see methods), they contribute 18 % (confidence interval: 12 % to 27 %) to the total organic C pool in the area. This estimate aligns closely with the average 32 % recently reported for Canada as a whole by Sothe et al. (2022), noting that this higher value of wetland contribution includes peatland hotspots like the Hudson Plains Ecozone.

Forested peatlands, and swamps in particular, revealed their unrecognized importance in storing carbon at the regional scale mainly due to their high abundance, a result also observed in previous studies focused on North American ecosystems (Ott and Chimner, 2016; Byun et al., 2018; Davidson et al., 2022). Swamps may have been considered 'less valuable', partially because of their lower C stock per unit area and sometimes small size, leading to their destruction for urban or agricultural development (Van Meter and Basu, 2015; Poulin et al., 2016; Davidson et al., 2022). The difficulty in mapping these wetlands due to canopy cover and their lower prevalence of rare species also likely contributed to their fragmentation and loss. But interestingly, such wetlands have also been shown to be particularly efficient at regulating river flows, thus mitigating floods and drought events, which are expected to increase in frequency and severity with climate change (Fossey et al., 2016; Ameli and Creed, 2019; Goyette et al., 2022). While regulatory programs mandating compensation for lost ecological functions through wetland restoration do exist, studies have demonstrated that these functions can take decades to reestablish, especially in small depressional wetlands like swamps (Moreno-Mateos et al., 2015). This underscores the asset these ecosystems represent for climate change mitigation efforts, and emphasizes the necessity for enhancing their protection (Schuster et al., 2024). Moreover, it has been shown that protecting a diversity of wetlands is necessary to support multiple ecosystem functions and services since these vary significantly by wetland type (Loiselle et al., 2023). Particularly within resource extraction contexts such as forestry, further research is needed to assess the most effective management practices to minimize impacts on other ecosystem services.

5. Conclusions

Human activities continue to cause the degradation of most wetland types worldwide. Drainage of peatlands for agriculture, forestry, peat extraction, and grazing have together been identified as the primary causes of wetlands loss and degradation in the last 300 years, and these multiple drivers are expected to be amplified in the future (Loisel et al., 2021; Fluet-Chouinard et al., 2023). This degradation is thought to turn peatlands from sinks to sources of CO_2 and other greenhouse gases (Leifeld and Menichetti, 2018), such that halting and reversing this wetland decline is becoming essential (Griscom et al., 2017; Drever et al., 2021). To guide conservation planning, time efficient approaches are needed to best evaluate C stock variability within and among wetlands at the regional scale. Our study presents a simple methodology for doing so. Estimating SOC based on the degree of peat humification is a straightforward and effective field approach, and characterizing complete SOC profiles may be required since SOC density varies with peat depth. Importantly, our work has contributed to advancing this field by emphasizing the importance of accounting for peat bathymetry at the site-level as a prerequisite for obtaining more accurate SOC estimates. Additionally, we have shown that the soil compartment can store significantly more C than the aboveground compartment, even in swamps. Given the varying proportional contributions from above and belowground compartments among different wetland types, and the disparate timescales involved in C stock build-up, integrating this information into land management planning is essential for decision makers.

CRediT authorship contribution statement

Jean-Olivier Goyette: Conceptualization, Data curation, Formal analysis, Methodology, Visualization, Writing – original draft, Writing – review & editing. **Audréanne Loiselle:** Data curation, Formal analysis, Writing – original draft, Writing – review & editing. **Poliana Mendes:** Writing – original draft, Writing – review & editing. **Jérôme Cimon-Morin:** Conceptualization, Methodology, Writing – original draft, Writing – review & editing. **Stéphanie Pellerin:** Writing – original draft, Writing – review & editing. **Monique Poulin:** Conceptualization, Funding acquisition, Writing – original draft, Writing – review & editing, Methodology. **Jérôme Dupras:** Funding acquisition, Writing – original draft, Writing – review & editing.

Declaration of Generative AI and AI-assisted technologies in the writing process

During the preparation of this work the authors used ChatGPT to help refine a few complex sentences in English. After using this tool, the authors reviewed and edited the content as needed and take full responsibility for the content of the publication.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

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Data availability

Data will be made available on request.

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Appendix A. Supplementary data

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