



Contrasting sediment carbon storage and turnover in vegetated littoral and open water habitats of boreal lakes

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10 **Abstract.** In recent years, the research interest of aquatic systems as natural carbon sinks has grown rapidly. Diffuse organic
carbon buried in lake sediments represents an important long-term carbon sink, with potential to mitigate climate change by
removing carbon from active biogeochemical cycling on timescales of millennia. This sink may be particularly significant in
boreal regions such as Finland, where lakes cover approximately 10 % of the land surface. However, major knowledge gaps
15 burial and remineralization of organic carbon, and the role of the vegetated littoral zone (“teal carbon habitat”) in carbon
storage remain poorly constrained.

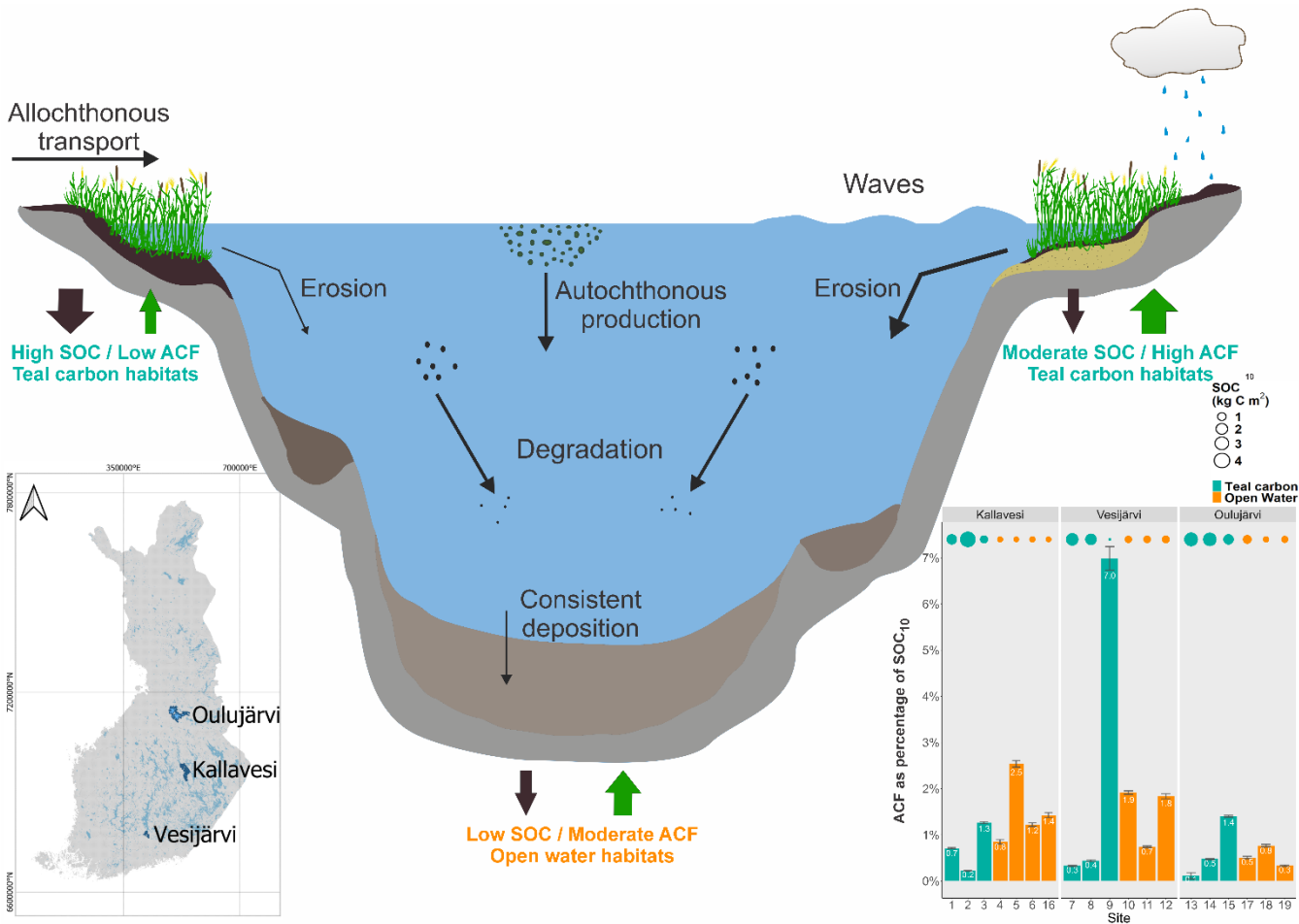
To address these gaps, we studied three boreal lakes along a latitudinal gradient across Finland, by sampling sediment,
porewater, and surface water from three sites in the teal carbon habitat and three to four in the open water (limnetic) habitat.
Our results reveal two contrasting carbon-cycling regimes: teal carbon habitats might accumulate substantial organic carbon
20 inventories in the top 10 cm (SOC₁₀) of the sediment, where turnover is negatively associated with inventory due to greater
retention of fine-grained sediments, resulting in lower diffusive turnover efficiency. In open water habitats, total diffusive
carbon flux is closely linked to organic matter quality, referring to its composition and reactivity, while SOC₁₀ remains
consistent among sites. Turnover efficiency across all sites is low (< 5.5%), implying only a small fraction of the near-surface
SOC pool is processed annually. These findings highlight the importance of protecting vegetated near-shore belts from physical
25 disturbance to safeguard SOC storage and managing catchment inputs to moderate open water carbon fluxes. Notably, not all
teal carbon habitats are equal; sandy sites possess small SOC stocks below the top 10 cm and exhibit higher turnover rates,
suggesting that interventions in these areas may carry lower risks.



30 **Short summary.** Lakes are important for the global carbon cycle, yet the variability in carbon burial and degradation, especially in vegetated shorelines, is not well understood. We found that vegetated shorelines can accumulate sediment carbon over long periods with low degradation or over short periods with high degradation, depending on hydrodynamic energy. In contrast, open water sediments accumulate less carbon but do so more reliably over time, with degradation influenced by the source of organic matter.



35 **Key figure.** Graphical illustration of the main findings, highlighting three carbon cycling regimes: (1) teal carbon habitats that accumulate sediment organic carbon (SOC) with low diffusive flux and erosion; (2) teal carbon habitats that accumulate SOC predominantly in the top 10 cm with higher diffusive fluxes and erosion; and (3) open water habitats with lower yet consistent SOC inventories, influenced by degradation during the settling of allochthonous and autochthonous organic matter (OM), along with moderate diffusive fluxes linked to the source and quality of OM.



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1 Introduction

Lakes are active components of the continental carbon (C) cycle, simultaneously processing, storing, and emitting carbon (Battin et al., 2009; Cole et al., 2007; Regnier et al., 2013; Tranvik et al., 2009, 2018). They receive substantial allochthonous inputs from their catchments as organic carbon (OC) and dissolved inorganic carbon (DIC), in addition to autochthonous production within the water column and littoral zone (Duarte and Prairie, 2005; Grasset et al., 2025; Gudas et al., 2017; Molot and Dillon, 1996). As a result, lakes can function both as carbon sinks, via sedimentation and burial, and as sources of greenhouse gases (CO₂ and CH₄) to the atmosphere (Bastviken et al., 2011; Cole et al., 2007; Grasset et al., 2025; Kortelainen et al., 2004; Mendonça et al., 2017; Raymond et al., 2013; Regnier et al., 2013; Tranvik et al., 2009). Global and regional syntheses suggest that lake carbon burial is significant and, per unit area, comparable to marine burial (Dean and Gorham, 1998; Grasset et al., 2025; Junna et al., 2025; Regnier et al., 2013), while emissions are reported as being similar in magnitude or even larger (Bastviken et al., 2011; Battin et al., 2009; Cole et al., 2007; Grasset et al., 2025; Mendonça et al., 2017; Raymond et al., 2013; Regnier et al., 2013; Tranvik et al., 2009). Despite advances in quantifying lacustrine C budgets, key knowledge gaps remain regarding the spatial heterogeneity of sources and sinks within lakes, particularly the contribution and controls of vegetated littoral zones.

The vegetated littoral zone, or so-called *teal carbon* habitat (Nahlik and Fennessy, 2016), is an exceptionally productive environment because of the high macrophyte productivity. In fact, stands of emergent macrophytes can generate organic matter per unit area at rates on the order of those observed in tropical rainforests (Wetzel, 2001), implying rapid carbon cycling that can drive substantial DIC and methane (CH₄) fluxes as well as elevated rates of below-ground carbon burial (Benoy and Kalff, 1999; Desrosiers et al., 2022; Juutinen et al., 2003; Lindroth Dauner et al., 2026; Partanen and Luoto, 2006; Peixoto et al., 2016). In addition, macrophytes attenuate waves and currents, trap fine particles, and reduce resuspension, thereby promoting net deposition and potential long-term storage of sediment organic carbon (SOC) in near-shore sediments (Stumpf, 1983; Barko and James, 1998; Benoy and Kalff, 1999; Temmerman et al., 2005; Horppila and Nurminen, 2005; Fagherazzi et al., 2012; Reef et al., 2018). Owing to their proximity to land, teal carbon habitats are expected to receive substantial terrestrial input and can export materials laterally to pelagic waters (Grant and Madsen, 1979; Hofmann et al., 2011; Luo et al., 2025; Miles et al., 2013). These dual roles, as sources and sinks over different timescales, make vegetated littoral zones pivotal to lake C cycling, yet their quantitative contribution to lake-scale C budgets remains poorly constrained. While many syntheses classify lakes as net C sources, emerging evidence suggests that incorporating teal carbon processes may shift net balances toward stronger burial in some systems (Grasset et al., 2025; Peixoto et al., 2016). However, large uncertainties persist because habitat-resolved data remain scarce and the physical and environmental controls governing burial versus rapid turnover in teal-carbon habitats are not fully understood.



Traditionally, long-term SOC burial has been attributed primarily to deep, open water (limnetic) zones, where low hydrodynamic energy, greater depths, and isolation from atmospheric oxygen favour preservation and reduce disturbance (Cole et al., 2007; Kortelainen et al., 2004; Mendonça et al., 2017; Tranvik et al., 2018). In contrast, littoral zones have been less studied, experience higher hydrodynamic energy, and strong biological structuring by macrophytes and benthic communities, complicating predictions of net accumulation versus turnover or lateral export. Consequently, a systematic, habitat-resolved comparison of SOC stocks and carbon turnover across teal carbon and open water habitats is needed to clarify when and where near-shore environments serve as significant carbon stores.

A mechanistic understanding of the physical and environmental controls is essential to resolve these contrasts. SOC may accumulate via deposition of OM derived from autochthonous production within the lake and from lateral transport of allochthonous OM from the catchment. After deposition, SOC can be transported laterally, transformed to DOC, mineralised to CH₄, and CO₂, or buried (Bastviken et al., 2011; Battin et al., 2009; Cole et al., 2007; Hofmann et al., 2011; Kortelainen et al., 2004; MacIntyre and Melack, 1995; Raymond et al., 2013; Regnier et al., 2013; Sobek et al., 2006; Tranvik et al., 2009). Transport is strongly influenced by hydrodynamic energy; wind, waves, currents and bioturbation can remobilise and erode sediments, which are then transported into deeper waters (Collins, 2025; Grant and Madsen, 1979; Hofmann et al., 2011; Luo et al., 2025; MacIntyre and Melack, 1995; Miles et al., 2013). Grain size is strongly linked to hydrodynamic setting; fine-grained material settles and is retained mainly in low-energy environments, and enhances sedimentary C accumulation via sorption and physical protection of OM (Van Veen and Kuikman, 1990; Keil et al., 1994; Keil and Cowie, 1999; Krull et al., 2001; Telles et al., 2003; Bianchi, 2006; Yu et al., 2017; Lindroth Dauner et al., 2026). The degradability of OM depends on its source and quality (i.e., its composition and reactivity): molar nitrogen-to-carbon ratios (N:C) are often used as bulk source and quality indicators, with higher N:C associated with more labile autochthonous OM and lower N:C with more refractory allochthonous OM (Gudasz et al., 2012; Guillemette et al., 2017; Meyers, 1994; Orozco et al., 2025; Sobek et al., 2009; von Wachenfeldt and Tranvik, 2008).

Microbial degradation proceeds via a cascade of redox processes. Complex organic polymers are first cleaved to monomers, which are fermented to low-molecular-weight (LMW) organic compounds or DOC. These are then oxidised to CO₂ through a sequence of electron-accepting reactions, broadly from the most to the least thermodynamically favourable (oxygen, nitrate, manganese oxides, ferric iron, sulphate), and only after these electron acceptors are exhausted does CH₄ production proceed, mainly via CO₂ reduction or acetate fermentation (Arndt et al., 2013; Conrad, 1999; Praetzel et al., 2020; Whiticar, 1999). High OM accumulation can cause electron acceptors to be consumed higher in the sediment column, leading to a shallower sulphate–methane transition zone (SMTZ) and enhanced CH₄ production (Myllykangas et al., 2020). Since oxygen is the most thermodynamically favourable electron acceptor, sediment oxygen availability has been linked to higher mineralisation rates (Ferland et al., 2014; Sobek et al., 2009). At the same time, OM residing in anoxic, methanogenic sediments for on the order of a decade can be considered effectively buried (Isidorova et al., 2019). Overall, the rate and depth distribution of degradation



has therefore been suggested to depend on OM quality, electron-acceptor availability, and temperature, as these reactions are temperature-dependent and typically increase in rate with increasing temperature (Fuchs et al., 2016; Gudas et al., 2010, 2012, 2015; Guillemette et al., 2017; Muri and Wakeham, 2006; Praetzel et al., 2020; Sobek et al., 2009; Tolu et al., 2017; von Wachenfeldt and Tranvik, 2008).

Due to the differences in proximity to the catchment and atmosphere, teal carbon and open water habitats are expected to differ markedly in OM source and quality, in the availability of thermodynamically favourable electron acceptors, in situ temperature, and other environmental conditions. Degradation also occurs in the water column, so depth can enhance pre-degradation of OM during sinking and lead to more strongly pre-processed material being deposited in open water sediments compared to teal carbon sediments (Junna et al., 2025; MacIntyre and Melack, 1995; Scheu et al., 2015). Owing to isolation by the water column, open water sediments can remain relatively cold throughout the year, whereas teal carbon sites experience warm conditions in summer and cold, potentially freezing, conditions in winter, affecting the rates of biogeochemical processes (Fuchs et al., 2016; Gudas et al., 2010, 2012, 2015). Because sediments ultimately receive oxygen from the atmosphere, differences in atmospheric proximity are expected to lead to differing supply of oxygen between habitats (Sobek et al., 2009). This may be further modified by temperature-driven density differences between surface and bottom water, as stratification can hinder oxygen supply to open water sediments (Ma et al., 2025). Catchment and atmospheric proximity also affect hydrodynamic energy between and among sites: teal carbon habitats are generally more exposed to winds, waves and currents, while open water basins are consistently low-energy environments (Grant and Madsen, 1979; Hofmann et al., 2011; Luo et al., 2025; Miles et al., 2013). Variation among teal carbon sites may also be large, ranging from highly sheltered to strongly exposed and thereby altering SOC distribution (Lindroth Dauner et al., 2026). Catchment proximity may also affect OM input. Teal carbon areas are situated directly along the shoreline, receiving allochthonous material directly from the terrestrial environment (e.g. via runoff), and are therefore expected to host a larger allochthonous OM fraction, whereas open waters sediments may receive a broader mixture of OM sources (Muri and Wakeham, 2006; Orozco et al., 2025; Sobek et al., 2006; von Wachenfeldt and Tranvik, 2008). Teal carbon habitats are further shaped by macrophytes themselves, which attenuate hydrodynamic energy and allow fine-grained particles to settle that would otherwise accumulate in deeper waters (Barko and James, 1998; Benoy and Kalff, 1999; Fagherazzi et al., 2012; Horppila and Nurminen, 2005; Reef et al., 2018; Stumpf, 1983; Temmerman et al., 2005) and influence redox potential in the rhizosphere (Van Der Nat and Middelburg, 1998b; Dean et al., 2018; Ding et al., 2002; Laanbroek, 2010). Macrophyte density and species composition can therefore modulate carbon cycling (Benoy and Kalff, 1999; Bernal and Mitsch, 2012).

Clarifying the role of vegetated littoral zones in lake carbon cycling addresses a critical gap for both science and management. Near-shore SOC inventories lie close to human activities and are vulnerable to disturbance (e.g., dredging, reed mowing, shoreline modification). At the same time, national and regional carbon accounting and water-quality management increasingly recognize the role of inland waters, yet process representation in lake models (e.g., burial, turnover, and flux partitioning) often



lacks explicit littoral components (EU, 2023; Grasset et al., 2025; Regnier et al., 2013). Habitat-resolved quantification of inventories, benthic fluxes, and their controlling mechanisms is needed to improve lake carbon budgets, guide shoreline management and restoration, and support climate-smart water governance.

145 In this study, we quantified and compared sediment carbon storage and turnover in helophytic macrophyte patches of vegetated littoral (teal carbon) habitats and open water habitats across three boreal lakes. Specifically, we (i) quantified near-surface SOC inventories (top-10 cm; SOC₁₀) and their spatial variability by habitat, (ii) estimated sediment upward diffusive fluxes of CH₄, TCO₂, and DOC and derived turnover efficiency as annual carbon flux expressed as a percentage of SOC₁₀ (ACF of SOC₁₀), and (iii) identified environmental controls on storage and turnover, and evaluated habitat-specific mechanisms.

150 2 Material and Methods

2.1 Study area

Three boreal lakes were studied along a latitudinal gradient across Finland to capture regional variability in environmental conditions (Table 1). These were Lake Vesijärvi, Lake Kallavesi, and Lake Oulujärvi (Fig. 1). Site selection was guided by the existence of extensive datasets from environmental monitoring (Syke, 2026a; Syke, 2026b), accessibility, water quality, 155 and aerial imagery indicating extensive macrophyte coverage.

Lake Vesijärvi, the smallest and southernmost of the three, is a dimictic, clearwater, mesotrophic seepage lake (chlorophyll-a: 5.1 (N basin), 7.6 (S basin) µg L⁻¹ (Syke, 2026b)) situated between the Salpausselkä I and II glacial sand ridges. The catchment is dominated by glaciofluvial sand deposits (GTK, 2025). Lake Vesijärvi has a history of eutrophication due to decades of sewage input from the city of Lahti, followed by extensive remediation efforts that began just in the mid-1970's. Today the 160 lake occasionally exhibits cyanobacterial blooms and hypolimnetic hypoxia during summertime stratification (Ruuhijärvi et al., 2020). Thermal stratification occurs in warmer months (mid-June to mid-August) and colder months (January to March), with complete water column turnover events in spring (early April to late May) and autumn (late August to late October) (Salminen et al., 2021; Syke, 2026b).

Lake Kallavesi, located in central Finland, is characterised as humic and oligotrophic. The surrounding landscape features 165 eskers, bedrock outcrops, and mixed soils, which reflect the glacially influenced terrain (Glückert, 1974; GTK, 2025). This dimictic lake undergoes mixing twice a year during the spring and autumn, experiencing thermal stratification in the warmer months (June to August) and the colder months (November to April; Noori et al., 2022).

Lake Oulujärvi, the largest and northernmost site, is humic and subject to significant water level regulation, with an allowed water level fluctuation of 2.7 m in the regulation basin. The lake is highly regulated due to extensive hydropower production 170 in the downstream catchment since 1951 when the first plant was constructed in the river Oulujoki (Enbuske, 2010). The catchment area of Lake Oulujärvi features sandy eskers but is primarily composed of mixed soils and thick peat layers (GTK,



2025). As a dimictic lake, it is covered by ice from November to May, and during the summer, surface water temperatures can reach up to ~20 °C (Korhonen, 2006; Syke, 2026b).

175 Table 1: Environmental descriptions of the studied lakes.

Parameter	Kallavesi	Vesijärvi	Oulujärvi
Area (km ²)	478	110	902
Max depth (m) ^a	75	42	35
Average depth (m)	10	6	8
Dynamic ratio ^b	2.19	1.75	3.75
Winter monthly average air temperatures (°C) ^c	-8.0	-5.8	-9.4
Summer monthly average air temperatures (°C) ^c	17.5	17.7	16.3
Ecological status ^d	Moderate to good	Moderate to good	Good
Main shoreline vegetation ^e	<i>Phragmites australis</i>	<i>Phragmites australis</i>	<i>Phragmites australis</i> and <i>Equisetum spp.</i>
Main land use type in the catchment area ^f	Boreal forest (73%)	Boreal forest (51%) and arable land (18%)	Boreal forest (78%)
Common primary producers ^g	<i>Cryptophyceae</i> , <i>Diatomophyceae</i> , <i>Chrysophyceae</i>	<i>Cyanophyceae</i> , <i>Prymnesiophyceae</i> , <i>Chrysophyceae</i>	<i>Chrysophyceae</i> , <i>Cryptophyceae</i> , <i>Diatomophyceae</i>
Main anthropogenic pressure ^h	Point source, diffuse (agriculture)	Diffuse (agriculture), storm water, summer house settlements	Point source, diffuse (agriculture, peat production)
Type ^g	Large humic	Large clearwater	Large humic
Total Phosphorus (µg L ⁻¹) ^h	20 (S basin); 27 (N basin)	15 (N basin); 33 (S basin)	13
Total Nitrogen (µg L ⁻¹) ^h	629 (S basin); 719 (N basin)	351 (N basin); 459 (S basin)	351
Chlorophyll-a (µg L ⁻¹) ^h	10.5 (S basin); 12.1 (N basin)	5.1 (N basin); 7.6 (S basin)	5.7
Colour (mg Pt L ⁻¹) ^h	65 (S basin); 102 (N basin)	14 (N basin); 25 (S basin)	86

^aKallavesi: Noori et al. (2022); Vesijärvi: Kairesalo and Vakkilainen (2004); Oulujärvi: Turunen et al. (2022).

^bFerland et al. (2012)

^cFMI (2025) last 30 years.

^dSyke (2019)

^eKallavesi: Partanen et al. (2006); Vesijärvi: Kankaala et al. (2004); Oulujärvi: Keränen (1992).

^fSyke (2026a).

^gSyke (2026b).

^hKallavesi and Vesijärvi: Syke (2026b); Oulujärvi: Laine et al. (2022).

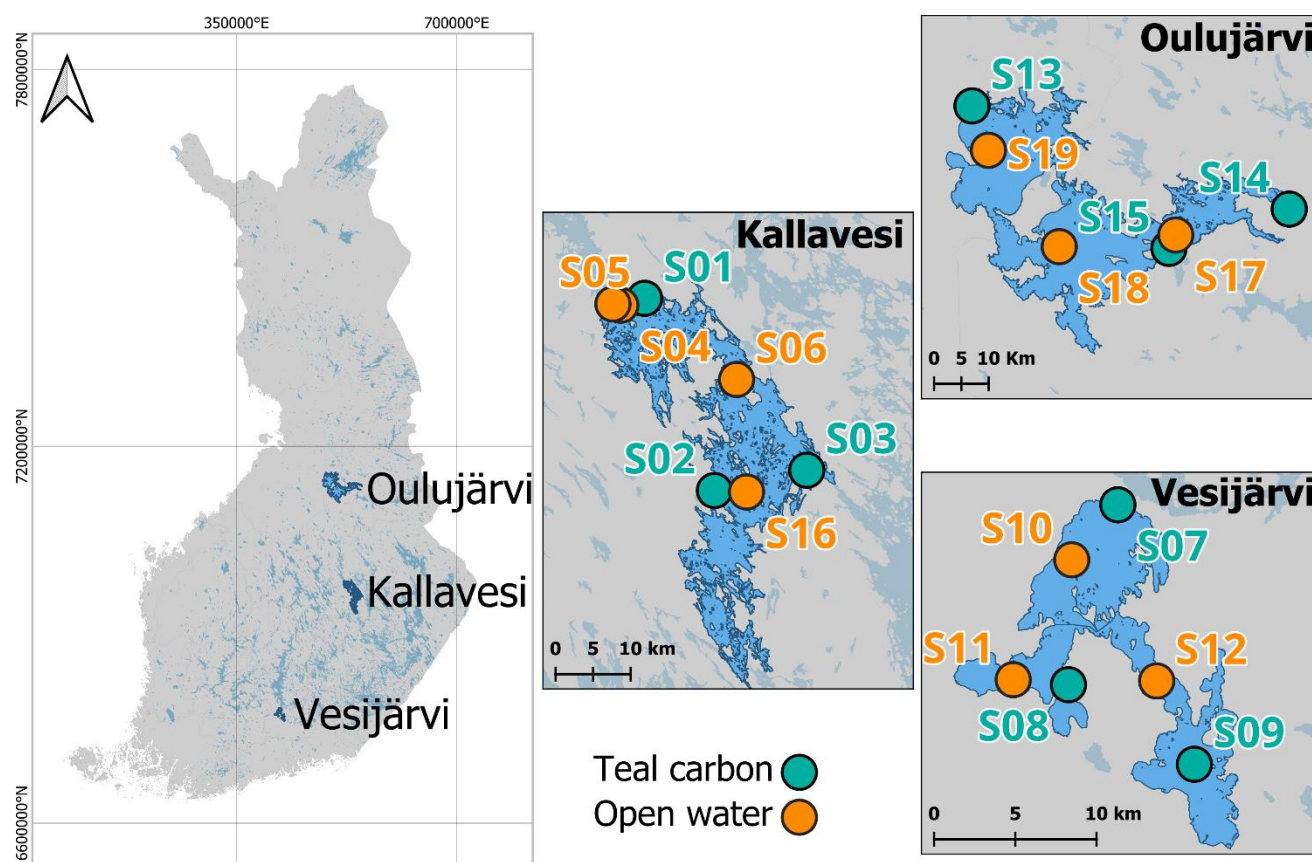


Figure 1: Sampling sites (S01-S19) across Finland. In each lake both teal carbon sites (orange dots) and open water sites (blue dots) were sampled. Finland shapefile was acquired through DVV (2023) and lake shapefile was acquired through the Finnish National Geoportal (2023).

2.2 Sediment sampling

Field sampling was carried out in August (Kallavesi and Vesijärvi) and September (Oulujärvi) of 2023. The teal carbon- and open water sites were sampled by two different teams with slightly different sampling protocols. For this reason, the sampling of the two habitats will be explained separately.

Open water sampling sites were selected to represent the distinct basins within each lake. A total of 10 open water sites were sampled, 3 sites in both Oulujärvi and Vesijärvi, and 4 sites in Kallavesi (Fig. 1). Sediment cores were retrieved using a hand-held Pylonex HTH gravity corer (50 cm long polycarbonate tube, internal diameter 8.6 cm), allowing recovery of undisturbed



190 sediments with a clear sediment water interface.. The top 10 cm of each core was sliced at 1 cm intervals, from 10 cm to 30
cm a 2 cm slicing interval was used, and beyond 30 cm a 4 cm slicing interval was used.

For teal carbon areas, a total of 9 sites were sampled, i.e. 3 sites in each lake (Fig. 1). Sampling sites were selected using
satellite data (Koponen et al., 2022) to identify macrophyte areas within each lake. Using QGIS, grids were created for each
195 vegetation patch, and sampling points were selected randomly using the software's "Random selection" tool (QGIS
Development Team, n.d.). Sediment samples were retrieved using either a box-corer (100 cm long, 8 x 8 cm cross-sectional
area) or a piston-corer (50 cm long, 4 cm internal diameter). The coring devices were pushed into the sediment by hand,
meaning that the length of each sample retrieved was limited by the penetrability of the sediment. The box-corer was favoured
as a sampling device due to the possibility of gaining larger cores, however, at sites where the penetrability of the sediment
200 was low, the piston-corer proved to be the better option. Sediment core lengths are illustrated in Table S1. The top 20 cm of
each core was sliced at 2 cm intervals, and beyond 20 cm a slicing interval of 10 cm was used. For more details on teal carbon
sediment sampling see Lindroth Dauner et al. (2026). The teal carbon samples used in this study are the sieved (< 2 mm)
samples from the transitional zones mentioned in Lindroth Dauner et al. (2026).

205 All sediment samples were placed into pre-labelled zip-lock bags and kept cool at approx. 6 °C during transport to Helsinki.
Sediment samples from open water areas were dried in an oven for 24 h at 105 °C and homogenized, while teal carbon samples
were freeze-dried and subsequently sieved (Lindroth Dauner et al., 2026). All samples were weighed both before and after
drying to determine dry mass and water content.

210 Additionally at each teal carbon site, macrophyte stems for all individual emergent species were counted inside a 1 m² area.

2.3 Porewater sampling

For the open water sites, porewater was extracted from sediment cores that were taken in parallel with the sediment sampling.
Coring tubes were pre-drilled with two columns of holes (*A* and *B*), vertically 0.5 cm apart, that were taped shut before coring.
After retrieving a sediment core, the tape was pierced at the locations of the pre-drilled holes and Rhizons™ (Rhizon CSS
215 sampler; 5 cm membrane length; 0.15 µm pore size) connected through a tree-way-tap to 10 ml PE-plastic syringes were
inserted. Porewater samples were extracted simultaneously from both columns. Through column *A*, a sample was extracted
into a pre-acidified syringe with 1 ml HNO₃ (0.1 M) for total dissolved inorganic carbon (TCO₂) and methane (CH₄) analyses.
Through column *B*, a sample was extracted into an empty syringe for determination of all other porewater parameters. The
pre-acidification of column *A* syringes was performed to guarantee that all dissolved inorganic carbon (DIC) is in the form of
220 CO₂. Porewater was extracted from the sediment by pulling the syringe piston, creating a vacuum, and drawing porewater into
the syringe (Jilbert et al., 2020). A depth series of 11 porewater samples were collected from each column with a 2 cm



resolution. One sample was further taken from the water column at 0.5 cm above the sediment-water interface to later calculate a concentration gradient.

225 For the teal carbon sites (Table S1), the porewater was collected using the same depth intervals as for the sediment sampling, i.e. every 2 cm for the top 20 cm and every 10 cm thereafter. In general, the same sampling protocol was used at the teal carbon sites as in the open water sites for sampling of porewater. Each depth interval was sampled in two columns (*A* and *B*), however, at teal carbon site the Rhizons™ were directly inserted into the sediment.

From both habitats, between approximately 2 ml and 4 ml of porewater was collected into each column *A* sample and the exact
230 volume was recorded for further calculations. For column *B* samples, up to 14.5 ml of porewater was collected. The bulk column *B* sample was transferred to a centrifuge tube from which a 1 ml subsample was taken, acidified (50 µl 65% HNO₃), diluted with 9 ml deionized water, and kept at approx. 6 °C in preparation for ICP-MS analysis. The remaining untreated bulk column *B* sample was frozen and stored for later analysis of ammonium (NH₄⁺) and dissolved organic carbon (DOC).

2.4 Water column sampling

235 Surface water samples were collected from the water column of each site using 50 ml syringes attached to 0.45 µm pore size polyether sulfone (PES) filters. At the open water sites, an additional water column sample was taken at 20 m water depth, where possible, using a 5 L LIMNOS™ water sampler. At the teal carbon sites the water depth varied between only 0.4 m and 1.2 m standing-depth, and therefore the water column was assumed to be completely mixed and only surface water was collected. At each sampling depth two water samples were collected in parallel. Syringe *A* was pre-acidified with 5 ml HNO₃
240 (0.1 M) for TCO₂ and CH₄ analyses and was filled with 25 ml samples. Syringe *B* was filled with a 21 ml sample from which a 1 ml subsample was transferred to a pre-acidified (50 µl 65% HNO₃) 10 ml PE centrifuge tube, diluted with 9 ml deionized water, and kept at 6 °C in preparation for ICP-MS analysis. The remaining untreated bulk syringe *B* sample was transferred to a separate polyethylene (PE) centrifuge tube, frozen, and stored for later DOC analysis. Two replicate samples were taken from each water column and depth. No LIMNOS samples were taken from Kallavesi site S05.

245 Temperature, specific conductance (SPC), and pH were measured at each site using a handheld multi-probe water meter (YSI Professional Plus). The measured parameters and depths are illustrated in Table S2. Measurements were not made at Kallavesi site S04, but since site S04 is so close in proximity to site S05, values are assumed to be identical at both sites. For the teal carbon sites only one measurement depth was used per site since the water columns were all < 1.1 m deep. For the open water
250 sites two measurements were made, one at 1 m water depth and one at 20 m, where possible. Additionally dissolved oxygen and oxygen saturation were retrieved from the HERTTA database (Syke, 2026b), for monitoring stations in close proximity to our sampling sites (Table S3). We calculated mean values for each station and all measurements conducted in August and September over the full monitoring period. No monitoring stations were found near Kallavesi sites S01, S02, and Vesijärvi S08.



255 2.5 Bulk sediment analyses

At the teal carbon sites the total organic carbon (TOC) and total nitrogen (TN) were measured from every other depth interval in each sediment core by dry combustion (LECO CN 828), i.e. every 4 cm in the top 20 cm of each core, starting at depth interval 2 – 4 cm, and every 20 cm beyond that. The limit of detection (LOD) for TOC analysis was 0.000017 % and for TN 0.000053 %. Furthermore, organic matter (OM) content was determined by loss on ignition (LECO TGA701; Method: SFS 3008 (1990)) at 550 °C from every sample. The OM analysis had a relative standard deviation (RSD) of 0.02 %. To estimate TOC in the remaining samples, a linear regression of the OM data was used (conversion factor 0.44; $R^2 = 0.98$; see (Lindroth Dauner et al., 2026)).

Sediment TOC inventories were estimated using Eq. (1) and (2) from Zhao et al. (2024):

$$SOC_{1cm_i} = TOC \cdot WBD \cdot (1 - W) \quad (1)$$

$$265 \quad SOC_{10cm} = \sum_{i=1}^{10} SOC_{1cm_i} \cdot 10 \quad (2)$$

Where W is the fractional water content of the bulk sediment weight; WBD is the wet bulk density in $g\ cm^{-3}$; TOC is in %; SOC_{1cm_i} is the total sedimentary organic carbon (SOC) mass in $1\ cm^3$ of bulk sediment in units $g\ cm^{-2}$; and SOC_{10cm} is the cumulative SOC inventory for the top 10 cm of bulk sediments in units of $kg\ m^{-2}$ where the factor 10 appears when converting from units of $g\ cm^{-2}$ to $kg\ m^{-2}$. To calculate WBD and W , we used wet and dry sample weights to calculate fractional water- and sediment content, and fractional sediment volume and volumetric porosity Φ as outlined in Lindroth Dauner et al. (2026) (Eq. S1 to S5). Particle density in units of $g\ cm^{-3}$ was estimated as follows:

$$Particle\ density = 1.4 \cdot \left(\frac{OM}{100}\right) + 2.65 \cdot \left(1 - \frac{OM}{100}\right) \quad (3)$$

Where 2.65 is the grain density of quartz in $g\ cm^{-3}$; and 1.4 is the assumed density for OM (Burdige, 2007; Pajunen, 2001). Finally, WBD was calculated using Eq. (4):

$$275 \quad WBD = \Phi + (1 - \Phi) \cdot particle\ density \quad (4)$$

For the open water sites, TOC and TN were measured from every other depth interval in each sediment core, identically to the teal carbon sites. TOC for the intervening samples was estimated by linear interpolation, and for 9 samples, by linear extrapolation. The 9 samples requiring extrapolation were the 0-1 cm sediment intervals of Kallavesi sites S05, S06, S16, Vesijärvi site S10, and Oulujärvi sites S17, S18, and S19, as well as sediment intervals 1-2 cm and 2-3 cm of site S05. Afterwards, the same calculations as for the teal carbon sites were performed to estimate SOC_{10cm} for all open water sites. For all teal carbon- and open water sites, only samples with $> 1\%$ of OM were included in inventory calculations (Kortelainen et al., 2004).



Molar N:C ratio (mol/mol) of organic matter was calculated from the TOC and TN data. Gray bars in the N:C figures are adapted from Goñi et al., (2003) and indicate reference ranges for phytoplankton and terrestrial C3 plants, respectively. These reference ranges assume that phytoplankton and terrestrial OM are the only sources of carbon and nitrogen and that source signatures are temporally constant. For this reason, they do not account for transformations during sedimentation.

Teal carbon sites were further analysed for sediment grain size using a Microtrac FlowSync particlesize analyser (precision ~3%). Measurements were performed on the inorganic sediment fraction left over after LOI analysis. Results are reported as the fraction of fine-grained sediment (particle diameter < 62.5 µm).

2.6 Porewater and water column CH₄ and TCO₂ analyses

Nitrogen gas with a purity of 5.0 was introduced into column A sample syringes, creating a minimum total headspace volume of 5 ml. The exact volumes for each sample were documented. The samples were brought to room temperature (20 °C) and then shaken to equilibrate CH₄ and CO₂ between the headspace and dissolved phases. A 5 ml portion of the headspace gas was drawn into a dry syringe via a 3-way valve and then transferred into a pre-evacuated 12 ml Exetainer® vial (Labco Ltd., UK). To store the vials at the normal pressure, an additional 7 ml of nitrogen gas was added directly into each vial. Before analysis, helium (He) was added to the vials to reach an internal pressure of 1.75 bar to facilitate autoinjection into a gas chromatograph (Agilent Technologies 7890B custom) equipped with a flame ionization detector (FID, for CH₄) and thermal conductivity detector (TCD, for CO₂), using He as the carrier gas. The instrument also measured N₂ and O₂ + Ar (TCD), allowing for a 100 % sum calculation to estimate CH₄ and CO₂ concentrations in the unpressurized headspace sample (expressed in ppmv, i.e., ppm by volume). To account for any temporal drifts in CH₄ and CO₂ concentrations due to changes in detector sensitivity during extended runs, standard gas samples were analysed at regular intervals, as described by Penttilä et al. (2013). The headspace CH₄ and CO₂ concentrations were converted to total dissolved phase concentrations in the acidified porewater sample (C_{tot}) using Henry's Law, as detailed for CH₄ in Myllykangas et al. (2017):

$$C_{tot} = \frac{X_{HS} \cdot P_{atm} \cdot V_{HS}}{R \cdot T \cdot V_{aq}} + F \cdot X_{HS} \cdot P_{atm} \quad (5)$$

Where C_{tot} is the total dissolved gas concentration in mol L⁻¹; X_{HS} is the mole fraction of gas in the headspace in ppmv; P_{atm} is the pressure in the headspace in atm (=1); V_{HS} and V_{aq} are the syringe headspace and water volume respectively in L; R is the gas constant (0.08206 L atm K⁻¹ mol⁻¹); T is the absolute temperature during equilibrium in kelvin; and F is a temperature- and salinity dependent equilibrium solubility constant of the gas in question in units mol L⁻¹ atm⁻¹, as outlined in (Wiesenburg and Guinasso, 1979) for CH₄ and in (Weiss and Price, 1980) for CO₂. Values for C_{tot} were further adjusted to account for dilution during acidification, to reflect the original porewater concentration.

Sediment porewater inventories were estimated using Eq. (6) and (7) (Zhao et al., 2024):



$$PWC_{2cm,i} = C_{PW} \cdot 2 \cdot \varphi \quad (6)$$

$$PWC_{10cm} = \sum_{i=1}^5 PWC_{2cm,i} \quad (7)$$

Where C_{PW} is the concentration of the dissolved molecule of interest; φ is the volume fraction of total porosity; $PWC_{2cm,i}$ is the porewater inventory in each 2 cm core interval expressed as a function of specific surface area in units $\mu\text{mol cm}^{-2}$; and PWC_{10cm} is the cumulative porewater inventory of the top 10 cm sediment expressed in units of $\mu\text{mol cm}^{-2}$.

2.7 Porewater and water column ICP-MS-, NH_4^+ and DOC analyses

Acidified column *B* samples were analysed for phosphorous (P), manganese (Mn), iron (Fe), and sulphur (S) by ICP-MS (Agilent 8900; Method: SFS-EN ISO 17294-2 (2016)). The method detection limits (MDL 10σ) were $0.06 \mu\text{g L}^{-1}$ for P, $0.1 \mu\text{g L}^{-1}$ for Mn, $0.08 \mu\text{g L}^{-1}$ for Fe, and $0.7 \mu\text{g L}^{-1}$ for S. If hydrogen sulphide is present, it is assumed to be lost during the acidification process. Therefore, the sulphur content in the measured porewater mainly represents sulphate (SO_4^{2-}), with potential minor contributions from dissolved organic sulphur and elemental sulphur (S^0). Manganese and iron are assumed to be in their divalent form, i.e. Mn^{2+} and Fe^{2+} . At in situ pH, P is expected to mainly represent HPO_4^{2-} and H_2PO_4 , with a small addition from dissolved organic P.

Untreated column *B* samples were thawed and analysed for NH_4^+ , and DOC. Ammonium concentration was determined by a manual spectrophotometric method following ISO 7150/1:1984, which is based on indophenol formation via sodium salicylate and hypochlorite in the presence of sodium nitroprusside. DOC was measured using an organic carbon analyser (Shimadzu TOC-VCPH). The limit of detection (LOD) was 0.5 mg/L and the method is described in more detail in Koistinen et al., (2020). Because all samples were prefiltered at $\leq 0.45 \mu\text{m}$, the DOC measurements are expected to reflect dissolved organic carbon only. Due to insufficient porewater volume, several samples could not be analysed for DOC. All water column samples were however analysed.

Because some DOC concentrations appeared unusually high for these systems, we selected 35 samples spanning a gradient from low to high DOC for reanalysis using a different organic carbon analyser (Shimadzu TOC-L). The measurement uncertainty was $\pm 30 \mu\text{mol C L}^{-1}$ for concentrations of $40\text{--}200 \mu\text{mol C L}^{-1}$ and $\pm 15 \%$ for concentrations $> 200 \mu\text{mol C L}^{-1}$. In addition, several porewater samples that had lacked volume for the initial DOC analysis had sufficient volume for this method and were analysed. Agreement between measurements was high (Fig. S1), with a fitted relationship $y = 0.9415x + 28.984$ ($x = \text{TOC-L}$; $y = \text{TOC-VCPH}$; $R^2 = 0.9934$; $n = 35$). Therefore, we used the mean of the replicate values. In total, 46 porewater samples lacked sufficient volume for any DOC measurement (Table S4).

Porewater inventories of P, Mn, Fe, SO_4^{2-} , NH_4^+ , and DOC were calculated using Eq. (6) and (7). Because the DOC dataset was fragmented, missing values were estimated prior to inventory calculations by linear interpolation for 12 samples and linear extrapolation for another 12 samples (Table S4).



The depth of the sulphate–methane transition zone (SMTZ) was estimated from porewater CH_4 and SO_4^{2-} concentration profiles, defined as the depth at which the molar concentrations of CH_4 and SO_4^{2-} are equal (Myllykangas et al., 2020).

350 2.8 Sediment upwards diffusive flux

Upwards diffusive fluxes of dissolved CH_4 , TCO_2 , and DOC, across the sediment-water-interface were estimated from porewater- and water column samples using Fick's first law:

$$F = \frac{\varphi \cdot D^0}{\theta^2} \frac{\partial C}{\partial z} \quad (8)$$

Where F is the calculated flux in $\text{mmol m}^{-2} \text{d}^{-1}$; φ is the volume fraction of total porosity; θ is the tortuosity estimated as $\theta^2 = 1 - \ln(\varphi^2)$; $\partial C/\partial z$ is the partial differential gradient estimated from the finite differential gradient $\Delta C/\Delta z$, which represents the concentration gradient of the substance in question, in the upper sediment column (Fig. S2 – S4). D^0 is the molecular diffusion coefficient in $\text{m}^2 \text{s}^{-1}$, and was estimated for CH_4 and TCO_2 using Eq. 4.57 in Boudreau (1997)

$$D^0 = 4.72 \cdot 10^{-9} \frac{T}{\mu \cdot V_b^{0.6} \cdot 10000} \quad (9)$$

Where μ is the dynamic viscosity of water in units poise ($\text{g cm}^{-1} \text{s}^{-1}$; Eq. 4.4 in Boudreau, 1997); T is the absolute temperature; V_b is the molar volume of the nonelectrolyte in $\text{cm}^3 \text{mol}^{-1}$ for which values for CH_4 and TCO_2 have been taken from Hayduk and Laudie (1974).

DOC consists of multiple different compounds of various sizes and variable quantities each with distinct values of V_b . Since we could not differentiate between each variety of DOC, we needed to use a different method for estimating D^0 . For this we used the Stokes-Einstein equation (Einstein et al., 1956):

$$D^0 = \frac{k \cdot T}{6 \cdot \pi \cdot \mu \cdot r_0} \quad (10)$$

Where k is the Boltzmann's constant ($1.380649 \times 10^{-23} \text{ J K}^{-1}$); T is the absolute temperature; μ is the dynamic viscosity of water in units poise ($\text{g cm}^{-1} \text{s}^{-1}$); and r_0 is the effective hydrodynamic radius of the particle in meters. The difficulty here lies in estimating r_0 , which varies between different DOC molecules, as well as among the same molecules depending on the specific properties of the solution, such as pH, ionic strength, and temperature (Cornel et al., 1986; Lead et al., 2000; Hosse and Wilkinson, 2001; Lead et al., 2003; Balch and Guéguen, 2015a). Another difficulty lies in the fact that the equation assumes DOC molecules would be roughly spherical, which is not always the case (Cornel et al., 1986; Chin and Gschwend, 1991; Burdige and Gardner, 1998). Acknowledging these caveats, we made estimations of r_0 and calculated the resulting DOC fluxes, for spherical organic molecules in the size range 400 Da – 10000 Da, including proteins (Eq. 2.2 in Erickson, 2009) carbohydrates, carboxyl-rich alicyclic molecules (CRAMs), aliphatic compounds (Zheng and Price, 2012), and humic acids



and fulvic acids (Cornel et al., 1986; Lead et al., 2000; Hosse and Wilkinson, 2001; Kawahigashi et al., 2011). The molecular weight (MW) distribution of DOM is typically between 400 Da and 10000 Da (Krom and Sholkovitz, 1977; Orem and Gaudette, 1984; Orem et al., 1986; Burdige and Gardner, 1998; Chin and Gschwend, 1991; Chin et al., 1994; O'loughlin and Chin, 2004; Asmala et al., 2013; Balch and Guéguen, 2015b; Pogodaeva and Khodzher, 2023) which is why this weight interval is often used in flux calculations (Burdige et al., 1992, 1999; Alperin et al., 1994; Burdige et al., 2004; Alkhatib et al., 2013; Peter et al., 2016). Calculations of D^0 were performed using r_0 values representing both the lowest molecular weight (LMW) and highest molecular weight (HMW) for each compound. Because HMW humic acid represents the largest molecule and LMW CRAMs the smallest, they yielded the lowest and highest D^0 values, respectively, across all sites. Therefore, the r_0 for these two molecules were used to calculate D^0 at each sampling site, and the resulting D^0 bounds were then used to calculate DOC fluxes, yielding an interval of plausible flux rates. The r_0 estimates used are listed in Table S5. The resulting D^0 values ranged from 3.1×10^{-7} to $5.4 \times 10^{-6} \text{ cm}^2 \text{ s}^{-1}$. Due to insufficient porewater volume in the uppermost samples at several sites, DOC measurement coverage was fragmented (Table S4). Consequently, some concentration gradients, and thus flux estimates, may have higher uncertainty, especially sites Kallavesi S01, S02, S03, S05 and Oulujärvi S13 (Fig. S4).

2.9 Statistical analyses

Total annual carbon flux expressed as a percentage of the top 10 cm SOC inventory (ACF of SOC_{10}) was calculated and used as an index of carbon turnover efficiency. We then computed Spearman's rank correlations among carbon metrics (ACF of SOC_{10} , PWC_{10} , total C flux, SOC_{10}) and environmental variables (open water: $n = 15$; teal-carbon: $n = 26$). To aid screening, we reported p -values at thresholds $p < 0.10$, $p < 0.05$, and $p < 0.01$; given the small sample sizes, these intentionally permissive levels should be viewed as hypothesis-generating. Spearman's correlation was chosen because it does not assume normality or linearity and is less sensitive to outliers than, for example, Pearson's correlation. We then selected a subset of mechanistically plausible associations and modelled them as simple linear regressions to quantify effect sizes, display variability, and evaluate robustness. Slope and fetch were taken from Lindroth Dauner et al. (2026), and mean DOC flux values (average across the estimated interval per site) were used for correlations and regressions. All statistical analyses were conducted in R version 4.3.0 (R Core Team, 2023).

3 Results

3.1 Sediment organic carbon

The sediment organic carbon inventory in the top 10 cm of the sediment column (SOC_{10}) ranges from 0.2 to 4.2 kg C m^{-2} (mean = 2.2 kg C m^{-2}) in the teal carbon habitats, and from 0.4 to 1.1 kg m^{-2} (mean = 0.7 kg C m^{-2}) in the open water habitats (Table 2). Teal carbon areas are highly heterogeneous in terms of SOC_{10} , both between lakes and sites, while the open water sites are significantly more homogeneous, indicated by both the range of SOC_{10} (Fig. 2) and by the mean TOC profiles (Fig.



S5). Among teal carbon areas Lake Oulujärvi shows the highest mean inventory followed by Lake Kallavesi and Lake Vesijärvi. In the open water, Lake Vesijärvi and Lake Oulujärvi have similar inventories, while Lake Kallavesi has the lowest.

410 The teal carbon sites show high variability in N:C ratios, where most sites lean towards an allochthonous signal, some towards an autochthonous signal, and others shift their source signal over time (Fig. S6). The open water sites generally have a mixed source signature, neither strongly allochthonous nor autochthonous, though most lean towards autochthony and the Vesijärvi sites are consistently autochthonous (Fig. S7). The open water sites have significantly lower within-site variability in N:C ratio, leading to relatively homogenous downcore signals compared to the teal carbon sites.



415 **Table 2: SOC₁₀, upwards diffusive fluxes of porewater carbon, and concentrations of dissolved carbon in the surface layer of the water column, at each site.**

Site	Area	Lake	^a SOC (kg C m ⁻²)	Upwards diffusive flux (mmol m ⁻² d ⁻¹)				Surface water concentration (µM)			
				CH ₄	TCO ₂	^{b,c} DOC	Total C	^d CH ₄	^d TCO ₂	^d DOC	Total C
S01	Teal carbon	Kallavesi	1.7	0.3	2.2	0.05 – 0.65	2.6 – 3.2	0.41	267	1019	1287
S02	Teal carbon	Kallavesi	4.2	0.1	1.8	0.08 – 1.02	2.0 – 3.0	2.32	387	1307	1696
S03	Teal carbon	Kallavesi	0.9	0.3	2.2	0.05 – 0.56	2.6 – 3.1	0.15	176	894	1070
		Total	6.7	0.8	6.3	0.18 – 2.22	7.2 – 9.3	2.88	830	3220	4053
		Mean	2.2	0.3	2.1	0.06 – 0.74	2.4 – 3.1	0.96	276	1073	1351
S04	Open water	Kallavesi	0.5	0.3	0.5	0.06 – 0.73	0.9 – 1.6	0.07	217	963	1180
S05	Open water	Kallavesi	0.4	0.8	1.6	0.08 – 0.94	2.5 – 3.3	-	-	-	-
S06	Open water	Kallavesi	0.5	0.6	0.8	0.05 – 0.66	1.4 – 2.0	0.09	155	890	1045
S16	Open water	Kallavesi	0.5	0.2	1.1	0.06 – 0.76	1.4 – 2.1	0.07	152	842	994
		Total	1.9	1.9	4.1	0.25 – 3.09	6.2 – 9.0	0.23	523	2694	3218
		Mean	0.5	0.5	1.0	0.06 – 0.77	1.5 – 2.3	0.85	174	898	1072
S07	Teal carbon	Vesijärvi	2.5	0.2	1.6	0.08 – 0.97	1.8 – 2.7	0.16	603	424	1026
S08	Teal carbon	Vesijärvi	2.1	0.1	1.8	0.10 – 1.19	2.0 – 3.1	0.55	617	439	1057
S09	Teal carbon	Vesijärvi	0.2	0.4	3.0	0.15 – 1.81	3.5 – 5.1	0.16	551	431	982
		Total	4.9	0.6	6.4	0.33 – 3.97	7.3 – 11.0	0.87	1770	1293	3065
		Mean	1.6	0.2	2.1	0.11 – 1.32	2.4 – 3.7	0.11	590	431	1021
S10	Open water	Vesijärvi	0.7	1.5	1.6	0.07 – 0.80	3.2 – 3.9	0.08	516	402	918
S11	Open water	Vesijärvi	0.8	0.5	0.8	0.04 – 0.49	1.3 – 1.7	0.19	595	394	989
S12	Open water	Vesijärvi	0.8	0.9	2.3	0.12 – 1.42	3.4 – 4.7	0.22	568	423	991
		Total	2.3	2.9	4.7	0.22 – 2.70	7.8 – 10.3	0.48	1679	1218	2898
		Mean	0.8	1.0	1.6	0.07 – 0.90	2.6 – 3.4	0.08	559	406	966
S13	Teal carbon	Oulujärvi	3.2	0.1	1.8	-6.62 – (-0.54)	-4.8 – 1.3	4.23	515	6079	6598
S14	Teal carbon	Oulujärvi	3.0	0.2	3.0	0.08 – 1.00	3.2 – 4.2	4.72	701	1962	2668
S15	Teal carbon	Oulujärvi	1.7	0.2	5.0	0.10 – 1.18	5.3 – 6.4	1.87	339	898	1239
		Total	7.9	0.4	9.8	-4.40 – (-0.36)	5.8 – 9.8	10.82	1555	8938	10505
		Mean	2.6	0.1	3.3	-1.47 – (-0.12)	1.9 – 3.3	0.08	518	2979	3501
S17	Open water	Oulujärvi	1.1	0.4	0.8	0.07 – 0.91	1.2 – 2.1	0.10	120	872	992
S18	Open water	Oulujärvi	0.5	0.3	0.6	0.03 – 0.41	0.9 – 1.3	0.04	153	732	885
S19	Open water	Oulujärvi	0.7	0.1	0.3	0.03 – 0.34	0.5 – 0.8	0.06	132	3376	3508
		Total	2.3	0.8	1.6	0.14 – 1.66	2.6 – 4.1	0.20	405	4979	5384
		Mean	0.8	0.3	0.5	0.05 – 0.55	0.9 – 1.4	0.11	135	1659	1794

^aSediment organic carbon inventory in the top 10 cm.

^bFull interval between HMW humic acid and CRAMs.

^cAverage of two replicates when possible.

^dAverage of two replicates.



3.2 Dissolved carbon and upwards diffusive flux

The total upwards diffusive flux of dissolved carbon ranges from -4.8 to $6.4 \text{ mmol m}^{-2} \text{ d}^{-1}$ (mean = $2.8 \text{ mmol m}^{-2} \text{ d}^{-1}$) in the teal carbon habitats and from 0.5 to $4.7 \text{ mmol m}^{-2} \text{ d}^{-1}$ (mean = $2.0 \text{ mmol m}^{-2} \text{ d}^{-1}$) in the open water habitats (Table 2). Overall carbon fluxes are of the same order of magnitude between habitats, however, partitioning between species differ. Methane flux is generally higher in the open water (Fig. 3a), though it varies across lakes and sites, being highest in Lake Vesijärvi, followed by Lake Kallavesi and Lake Oulujärvi. In the teal carbon habitats, CH_4 flux is similar among lakes.

Conversely, the upwards diffusive flux of TCO_2 is generally higher in teal carbon habitats than in the open water (Fig. 3b). In the teal carbon habitats, the highest fluxes occur in Lake Oulujärvi, followed by Lake Vesijärvi and Lake Kallavesi. In the open water, the highest TCO_2 fluxes are found in Lake Vesijärvi, followed by Lake Kallavesi and Lake Oulujärvi.

DOC fluxes vary by an order of magnitude depending on the molecular diffusion coefficient (D_0) used (Table 2). In general, upward diffusive DOC fluxes are of similar magnitude in both habitats, being slightly higher in teal carbon areas for lake Vesijärvi and lake Oulujärvi, and slightly higher in open water for lake Kallavesi (Fig. 3c). In the open water, DOC flux ranges from 0.03 to $1.4 \text{ mmol m}^{-2} \text{ d}^{-1}$ (mean = $0.4 \text{ mmol m}^{-2} \text{ d}^{-1}$). In the teal carbon habitats, all but one measurement are positive, ranging from 0.05 to $1.8 \text{ mmol m}^{-2} \text{ d}^{-1}$ (mean = $0.6 \text{ mmol m}^{-2} \text{ d}^{-1}$). The exception is Oulujärvi site S13, which exhibits a relatively large negative flux (-6.62 to $0.54 \text{ mmol m}^{-2} \text{ d}^{-1}$), mainly due to high DOC concentrations in the water column (Table 2).

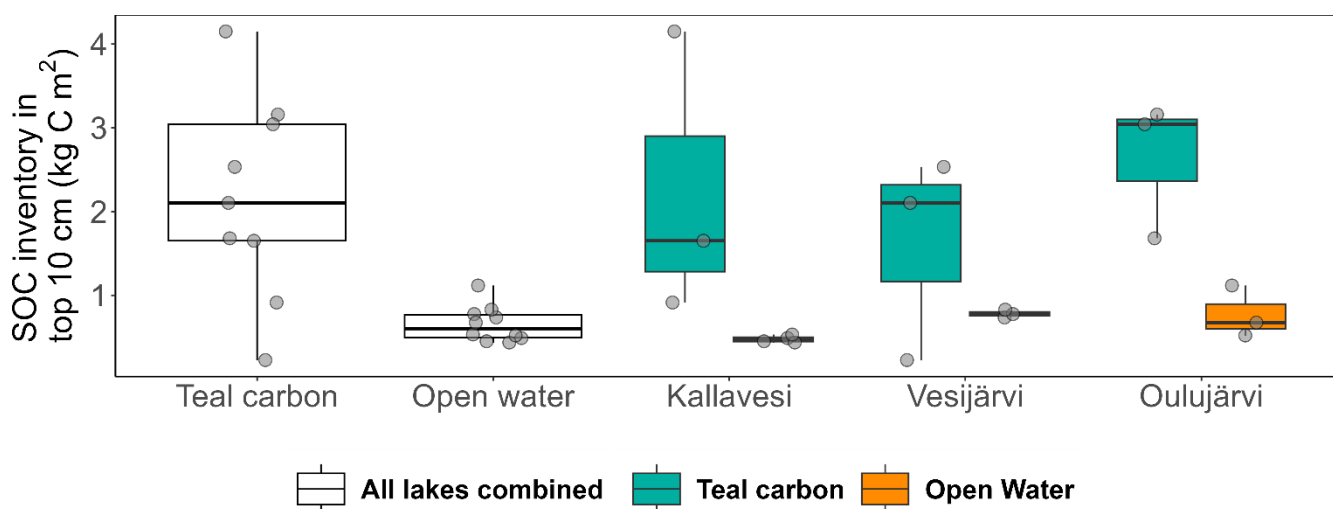
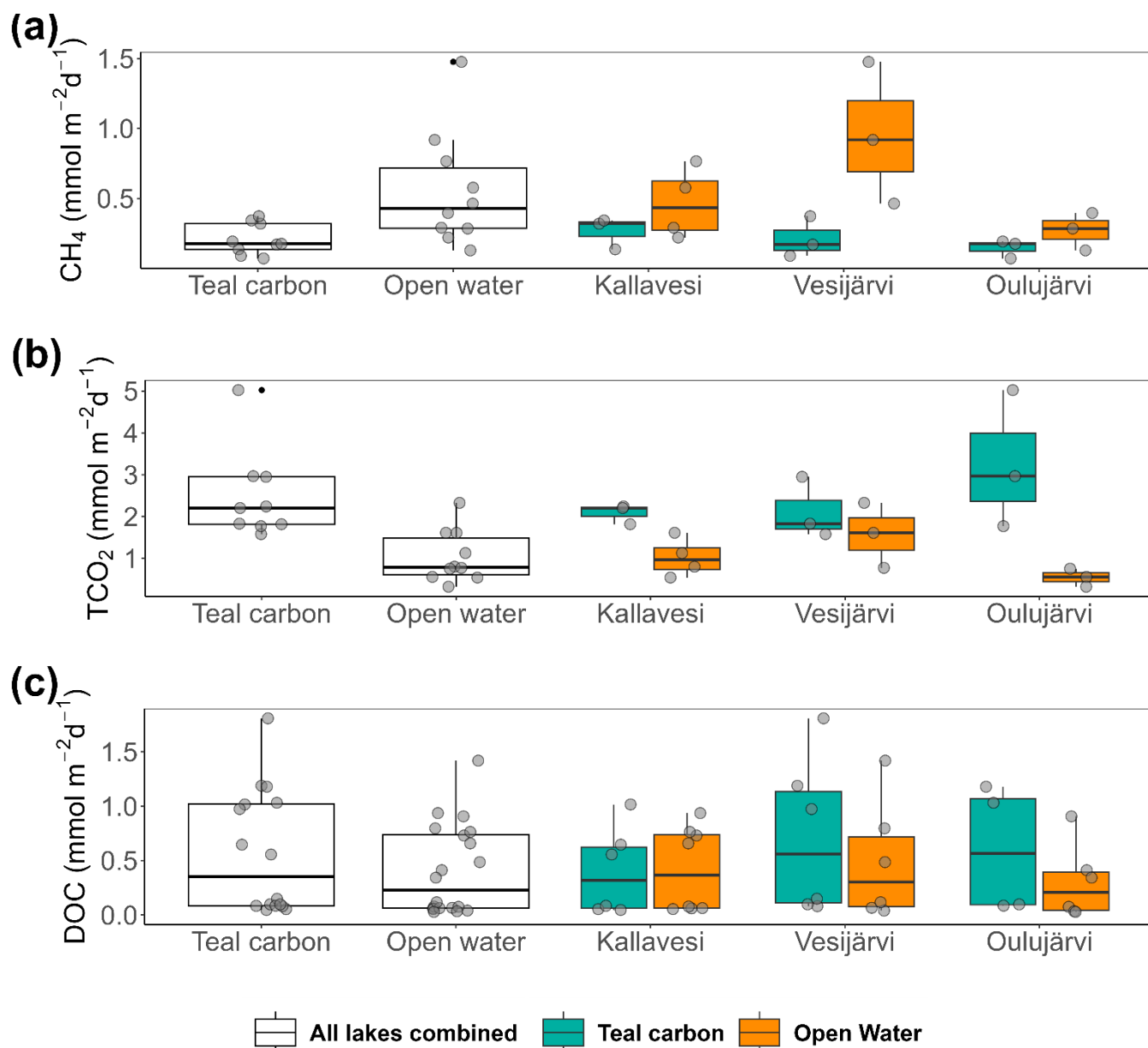


Figure 2: Sedimentary organic carbon inventory in the top 10 cm of the sediment column (SOC_{10}) arranged by lake and habitat.



440 **Figure 3:** Upwards diffusive flux of dissolved (a) CH_4 , (b) TCO_2 , and (c) DOC , arranged by lake and habitat. DOC fluxes were calculated for each site using both the smallest D^0 ($3.1 \times 10^{-7} \text{ cm}^2 \text{ s}^{-1}$) and largest D^0 ($5.4 \times 10^{-6} \text{ cm}^2 \text{ s}^{-1}$), forming an interval of possible DOC flux rates. At Oulujärvi teal carbon site S13, the DOC flux interval was negative (-6.62 to $-0.54 \text{ mmol m}^{-2} \text{ d}^{-1}$). These values were omitted from the figure to preserve scale.

445 Total porewater carbon inventories in the top 10 cm of the sediment column (PWC_{10}) range from 34 to 116 $\mu\text{mol cm}^{-2}$ (mean = 64 $\mu\text{mol cm}^{-2}$) in teal carbon habitats and from 19 to 81 $\mu\text{mol cm}^{-2}$ (mean = 43 $\mu\text{mol cm}^{-2}$) in open water habitats (Fig. S8). The partitioning among carbon species in PWC_{10} broadly mirrors the flux results, where methane inventories are generally



larger in open water habitats, and TCO_2 inventories are larger in teal carbon habitats (Fig. S8a–b). In contrast, for DOC, porewater inventory is clearly higher in teal carbon habitats across all lakes (Fig. S8c), unlike the fluxes.

450 The species fractions also differ between inventories and fluxes (Fig. 4). DOC constitutes a relatively large fraction of total PWC_{10} but contributes a much smaller fraction of the total upward diffusive flux, which is dominated by TCO_2 in teal carbon habitats and by a combination of TCO_2 and CH_4 in open water habitats (Fig. 4).

In the surface layer of the water column, CH_4 levels are generally higher in the teal carbon habitats (nr. of sites = 9; cumulative
455 CH_4 across all teal carbon sites = $14.6 \mu\text{mol L}^{-1}$; mean CH_4 concentration = $1.6 \mu\text{mol L}^{-1}$) than in the open water (Fig. S9a; nr. of sites = 9; cumulative CH_4 across all open water sites = $0.9 \mu\text{mol L}^{-1}$; mean CH_4 concentration = $0.1 \mu\text{mol L}^{-1}$). Surface water TCO_2 is also generally higher in the teal carbon habitats for Kallavesi and Oulujärvi, whereas in Vesijärvi they are of similar magnitude in both habitats (Fig. S9b). Surface water DOC concentrations are generally similar between teal carbon- and open water habitats within each lake, except in Lake Oulujärvi, where exceptionally high levels of DOC at site S13 elevate the teal
460 carbon median (Table 2 and Fig. S9c).

The annual carbon flux (ACF) as a percentage of SOC_{10} was below 7.3 % at all sites in both habitats (Fig. 5). The highest proportional fluxes were observed at Vesijärvi S09 (6.7 – 7.2 %) in teal carbon habitats and at Kallavesi S05 (2.6 – 2.7 %) in open water habitats. All remaining sites reported proportional fluxes at or below 2 %.

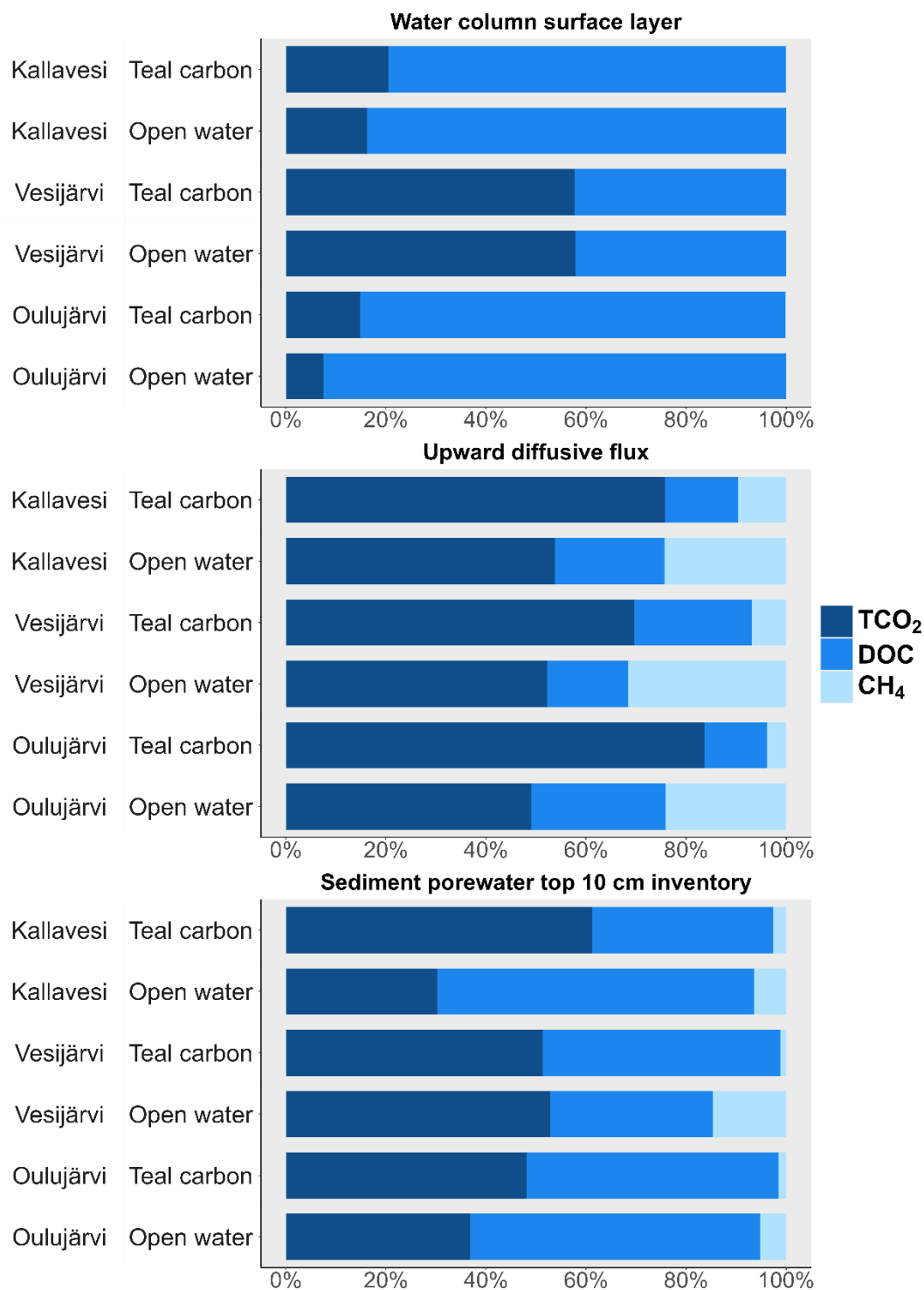
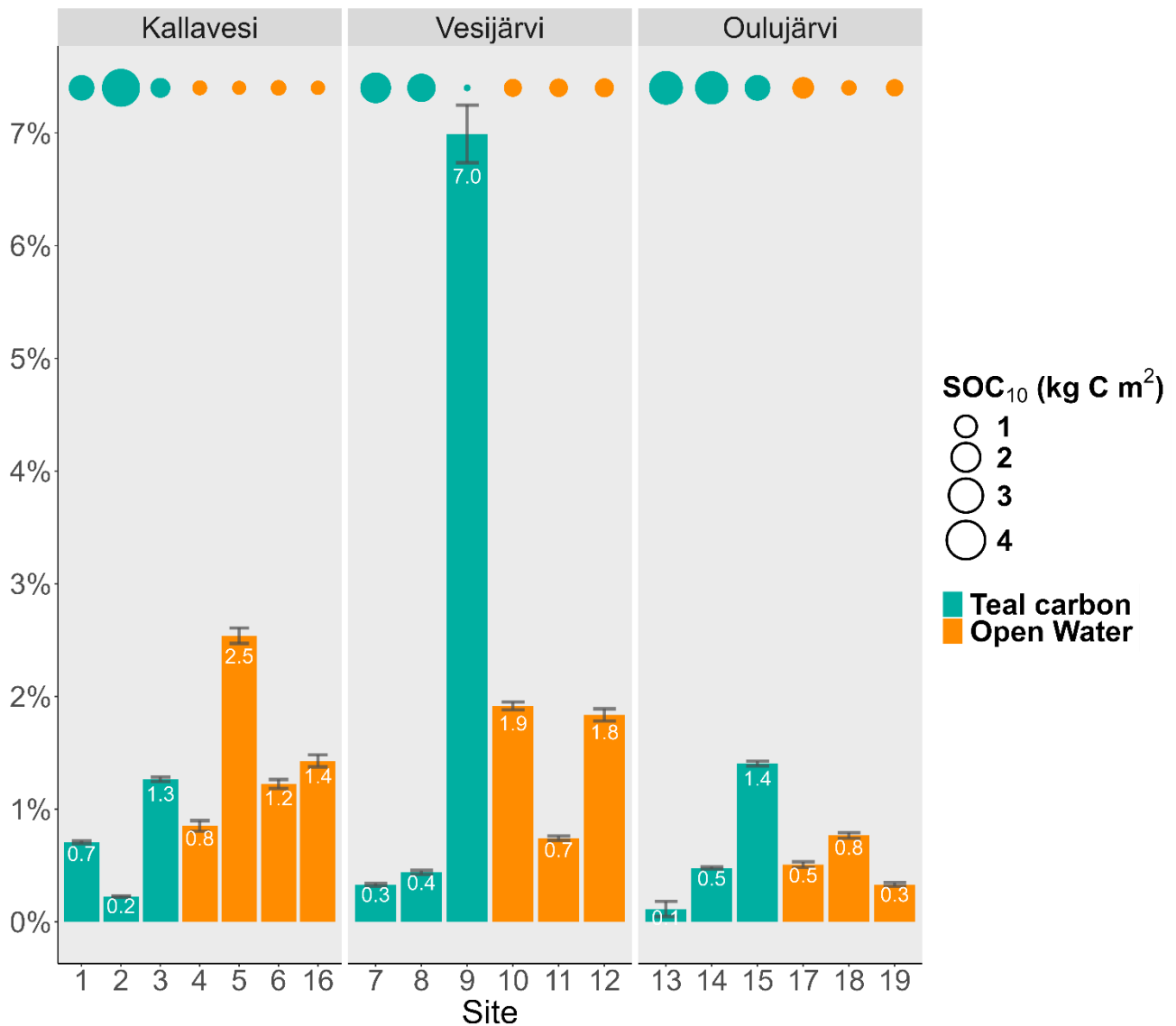


Figure 4: Fractions of dissolved CH₄, TCO₂ and DOC, presented as PWC₁₀, upwards diffusive flux, and water column surface water concentrations, arranged by lake and habitat. DOC flux fractions are based on the mean of the estimated interval.



470 **Figure 5: Total annual carbon flux expressed as a percentage of SOC₁₀ (ACF of SOC₁₀) for each study site. Bars show mean ACF of SOC₁₀; error bars reflect the range between the minimum and maximum DOC-based flux estimates. Circle size indicates the relative magnitude of SOC₁₀.**

3.3 Porewater redox zonation

475 The depth of the sulphate–methane transition zone (SMTZ) varied both between and within habitats. At three teal carbon sites (Vesijärvi S08, Oulujärvi S13, and S14) and one open water site (Kallavesi S16), no SMTZ was observed within the sampled



interval (Fig. 6). Where observable, SMTZ depth ranged from 4 to 45 cm in the teal carbon habitats and from 1.5 to 17 cm in open water habitats. Porewater NH_4^+ profiles indicate that concentrations increase rapidly and relatively consistently with sediment depth in open water habitats, whereas in teal carbon habitats vertical gradients are weak and often negative (Fig. S10).

3.4 Environmental drivers

Pairwise Spearman correlations among carbon metrics (ACF of SOC_{10} , total C flux; PWC₁₀, SOC_{10}) and environmental parameters are summarised in heatmaps (Fig. S11–S12). Guided by these results and a priori mechanisms, we visualised a subset of relationships as simple linear regressions to quantify effect sizes and assess robustness (Fig. 7–8 and S13).

In teal carbon habitats, ACF of SOC_{10} was negatively associated with SOC_{10} ($\rho = -0.88$; $p < 0.01$; Fig. S11). The regression (Fig. 7a) indicates that a 1 kg C m^{-2} increase in SOC_{10} is associated with a 1.29 % decrease in ACF. Conversely, ACF was positively associated with total C flux ($\rho = 0.9$; $p < 0.01$; Fig. S11), the regression (Fig. 7b) quantifies this effect (slope = 0.433). In open water habitats, the ACF– SOC_{10} association was weaker and not significant ($\rho = -0.39$, $p > 0.1$; Fig. S12), consistent with a small, uncertain slope (slope = -1.08 , $p = 0.354$; Fig. 7a), while the ACF–flux relationship remained positive and strong (slope = 0.531, $p = 0.003$; Fig. 7b). Notably, there was no significant association between total C flux and SOC_{10} in the open water habitat (Fig. 7c), while in the teal carbon habitat a significant negative association was observed between these metrics in the correlation heatmap ($\rho = -0.62$; $p < 0.1$; Fig. S11) but not in the simple regression (slope = -0.769 ; $p > 0.1$; Fig. 7c).

Teal carbon ACF of SOC_{10} correlated negatively with the fraction of fine-grained inorganic sediment ($\rho = -0.8$, $p < 0.05$; Fig. S11). The regression (Fig. 8a) indicates that increasing fines is associated with lower ACF (slope = -0.0797). Total C flux in teal carbon habitats correlates negatively with total macrophyte stem density ($\rho = -0.63$, $p < 0.1$; Fig. S11), with the regression showing a decrease of $0.00753 \text{ mmol m}^{-2} \text{ d}^{-1}$ of flux per additional stem m^{-2} (Fig. 8b)

In open water habitats, total C flux correlated positively with sediment N:C ($\rho = 0.48$; Fig. S12). The regression (Fig. 8c) quantifies this association (slope = 20.5, $p = 0.07$). This relationship was not observed in teal carbon habitats (slope = -6.74 , $p = 0.716$; Fig. 8c).

In teal carbon habitats, SOC_{10} was positively associated with fraction of fine-grained inorganic sediment ($\rho = 0.82$; $p < 0.05$; Fig. S11), total macrophyte stem density ($\rho = 0.62$; $p < 0.1$; Fig. S11), and with mean volume fraction of total porosity in the top 10 cm ($\rho = 0.68$; $p < 0.1$; Fig. S11). The regression (Fig. S13a) indicates a 10.6 kg C m^{-2} increase in SOC_{10} per 1 % increase in porosity. In open water habitats, SOC_{10} showed a negative Spearman association with porosity ($\rho = -0.82$; $p < 0.01$; Fig.

S12) and water depth ($\rho = -0.73$; $p < 0.05$). The regressions (Fig. S13a–S13b) quantify these effects (porosity: slope = -6.21; depth: slope = -0.0117).

For statistical analyses, sites where the SMTZ could not be directly identified were assigned an SMTZ depth 5 cm below the deepest sampled horizon, because CH_4 and SO_4^{2-} profiles at these sites approached but did not reach a clear crossover.

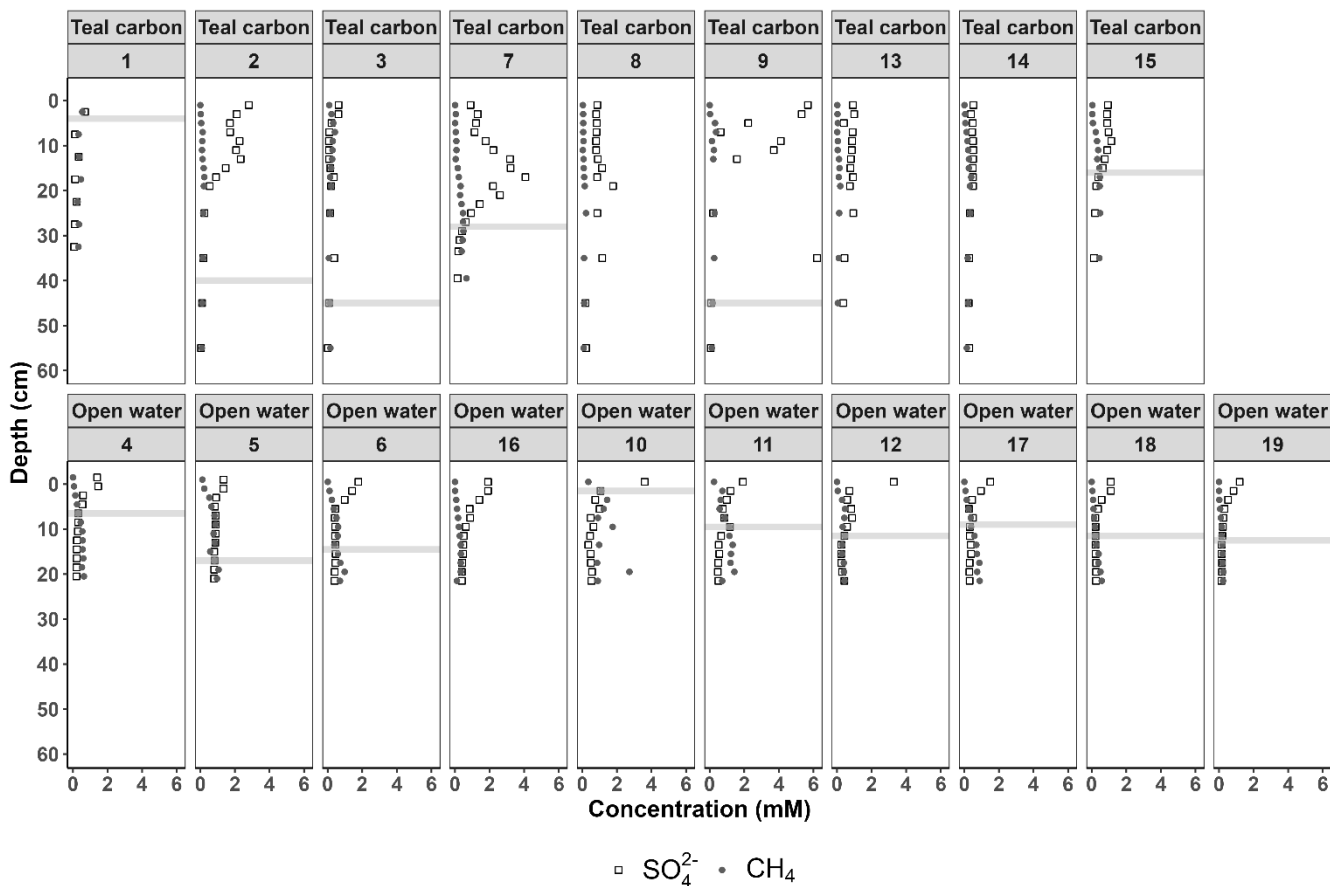


Figure 6: Sediment porewater concentrations of sulphate (white squares) and methane (black circles) for each site. The grey horizontal line represents the depth of the sulphate methane transition zone (defined here as the point where the methane and sulphate concentration profiles cross).

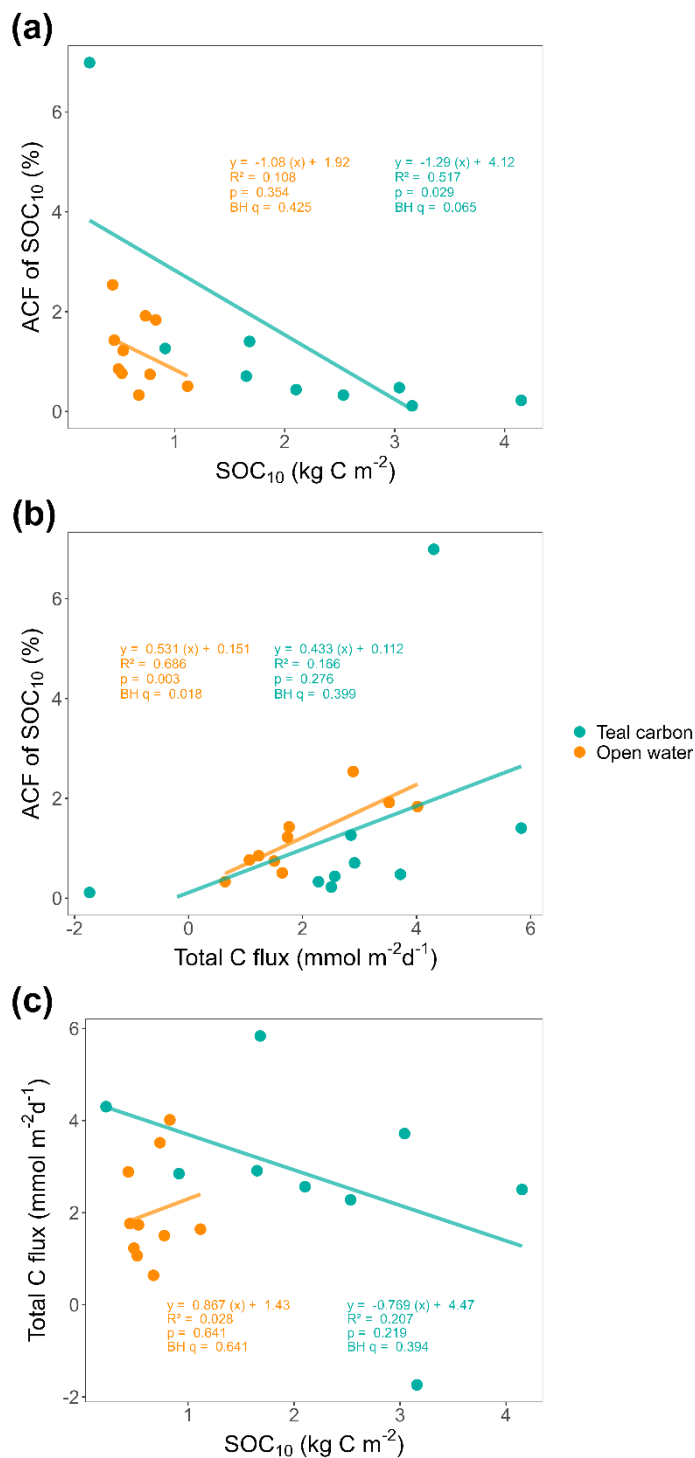


Figure 7: Relationships among carbon metrics in teal carbon and open water habitats. Simple linear regressions of (a) ACF of SOC₁₀ vs SOC₁₀, (b) ACF of SOC₁₀ vs total C flux, and (c) total C flux vs SOC₁₀. Panel annotations report the fitted equation, R^2 , p -value, and BH-adjusted q -value.



525 4 Discussion

4.1 SOC inventories across habitats

Our results suggest that the top 10 cm SOC inventory is significantly larger in the teal carbon habitats than in open water across all three lakes (Fig. 2), a pattern that aligns with previous studies in lakes and wetlands (Benoy and Kalff, 1999; Nahlik and Fennessy, 2016; Grasset et al., 2025).

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A likely reason is that the two habitats might differ in the relative contributions of carbon sources. Both habitats receive allochthonous inputs from the terrestrial environment and autochthonous production (Hanson et al., 2004; Sobek et al., 2006; Cole et al., 2007; Tranvik et al., 2009; Sobek et al., 2009; Lin et al., 2022), but teal carbon habitats also receive substantial inputs from emergent macrophytes that inhabit them (Sobek et al., 2006; Grasset et al., 2025), which can achieve areal OM production rates comparable to or exceeding tropical rainforests and an order of magnitude higher than pelagic phytoplankton (Wetzel, 2001, p.527–575). Proximity to land further enhances terrestrial inputs, and consistent with this, N:C patterns suggest more variable and frequently more allochthonous-leaning source signatures in teal carbon sediments than in open water sediments (Fig. S6 and S7). Because allochthonous OM is typically more refractory than autochthonous OM, teal carbon habitats may be exposed to a larger refractory fraction, enhancing accumulation (Sobek et al., 2009; Guillemette et al., 2016; Grasset et al., 2018). However, since N:C reference ranges do not account for transformations during sedimentation, these results should be considered hypothesis generating and warrant more robust proxies.

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Hydrodynamics and particle settling further differentiate habitats. In shallow teal carbon habitats, short settling distances and flow attenuation by macrophytes (e.g., wave/current reduction, particle interception, reduced resuspension) favour deposition and retention (Stumpf, 1983; Barko and James, 1998; Benoy and Kalff, 1999; Temmerman et al., 2005; Horppila and Nurminen, 2005; Fagherazzi et al., 2012; Reef et al., 2018), at least on short timescales. However, a previous study with sediment Cs profiles showed pronounced mixing and resuspension, suggesting that long-term retention in these habitats may be limited (Lindroth Dauner et al., 2026). In contrast, deeper open water habitats require longer settling times, increasing opportunities for particle reworking and degradation prior to deposition (MacIntyre and Melack, 1995; Scheu et al., 2015).

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Teal carbon SOC₁₀ also show greater variability between sites ($SD = 1.1 \text{ kg C m}^{-2}$) than open water SOC₁₀ ($SD = 0.2 \text{ kg C m}^{-2}$). This heterogeneity likely reflects variations in hydrodynamic energy (fetch, wind/wave exposure) and fine-fraction trapping (Lindroth Dauner et al., 2026; Luo et al., 2025). Open-water sediments, by contrast, experience more uniform conditions and greater remineralisation before deposition, producing more homogeneous inventories. Notably, open water habitats are relatively consistent accumulation zones. Mean TOC profiles show elevated carbon contents at essentially all measured depths

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(Fig. S5), although topmost SOC₁₀ is typically lower than in teal carbon sediments. In teal carbon habitats, accumulation beyond the top 10 cm appears more site-specific (Fig. S5), likely governed by local energy and trapping capacity (Lindroth Dauner et al., 2026; Luo et al., 2025; Reef et al., 2018).

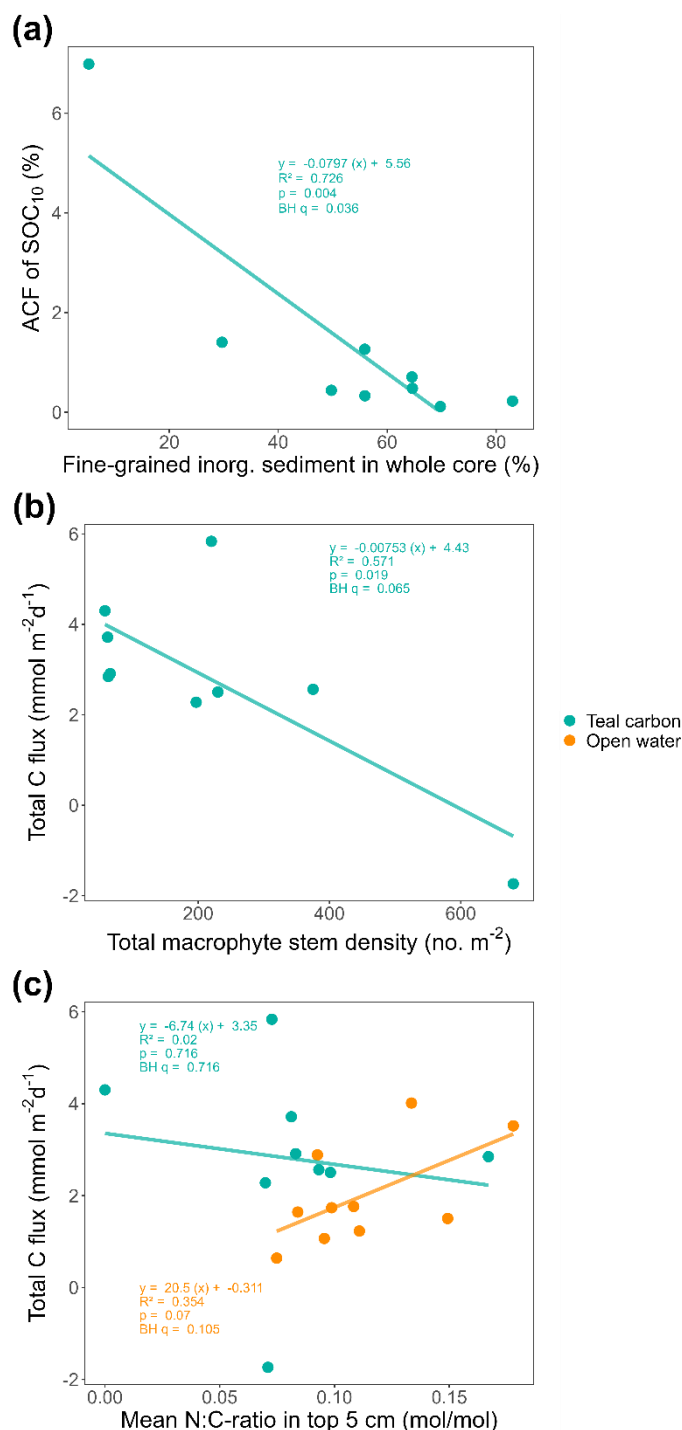


Figure 8: Relationships between carbon flux metrics and environmental parameters. Simple linear regressions of (a) ACF of SOC₁₀ vs. fraction of fine-grained inorganic sediment (whole core) in teal carbon habitats (%), (b) total C flux vs. total macrophyte stem density (no. m⁻²) in teal carbon habitats, and (c) total C flux vs. mean molar N:C ratio in the top 5 cm of sediment (mol/mol) in teal carbon and open water habitats. Panel annotations report the fitted equation, R^2 , p -value, and BH-adjusted q -value.



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4.2 Contrasting carbon turnover pathways

The speciation of benthic carbon turnover differs between habitats, where the upward diffusive flux of CH₄ is generally higher in the open water habitats, whereas teal carbon habitats exhibit higher TCO₂ fluxes. These differences likely reflect contrasting sedimentary redox zonation. In lacustrine sediments, redox structure is shaped by proximity to the atmosphere and electron acceptor supply (Ferland et al., 2014; Huttunen et al., 2006; Praetzel et al., 2020; Sobek et al., 2009). Because open water habitats are deeper and often seasonally stratified (Table S2), they tend to exhibit more compacted redox zonation than shallow, macrophyte-influenced teal carbon habitats. Consistent with this, the SMTZ occurs higher in open water sediment columns (Fig. 6), and porewater NH₄⁺ concentrations increase much more rapidly and consistently with depth in open water habitats (Fig. S10). In addition, environmental monitoring data indicate more oxygenated bottom waters in teal carbon than open water habitats (Table S3). Together these patterns suggest a larger contribution of anaerobic CH₄ production in open water habitats, whereas aerobic TCO₂ production is relatively more important in teal carbon habitats (Beutel, 2006; Myllykangas et al., 2020). Furthermore, since the partitioning among porewater carbon species in PWC₁₀ broadly mirrors the flux results, this suggests that the diffusive flux is directly proportional to the concentration in the top 10 cm of sediment. In this layer, the substance is moving upward without being actively consumed, or, if consumption is occurring, it is proportional across sites. Additionally, this indicates that at the time of sampling, most of the porewater carbon flux occurred as upward diffusion of dissolved carbon, or that the other potential pathways (such as plant-mediated transport and ebullition) are roughly proportional among sites.

Across all sites, TCO₂ turnover exceeds that of CH₄ and DOC (Fig. 4), yielding generally higher total C flux in teal carbon habitats (Table 2). DOC fluxes are relatively small, consistent with slower diffusivity of larger organic molecules (see Eq. (10)). Our estimated DOC D⁰ (3.1×10^{-7} to 5.4×10^{-6} cm² s⁻¹) and fluxes (Table 2) align with studies in estuaries (Aleksandra and Katarzyna, 2018), marine settings (Burdige et al., 1992; Lahajnar et al., 2005), and diffusive cell experiments on freshwater DOM (Balch and Guéguen, 2015b). Surface waters are DOC-dominated at most sites (Fig. 4), particularly in humic lakes Kallavesi and Oulujärvi (DOC = 79.4 – 92.5 % of surface water carbon), which reduces vertical DOC gradients and further suppresses diffusive DOC flux. In lake Vesijärvi, DOC fractions are lower, and TCO₂ accounts for roughly 60% of surface-water carbon (Fig. 4), suggesting a larger role for in-lake production/respiration. Overall, high surface-water DOC likely reflects catchment inputs and in-lake processing rather than sediment diffusion.

Despite higher diffusive CH₄ fluxes from open water sediments (Fig. 3a), surface waters in these habitats contain less CH₄ (Fig. S9a), consistent with extensive aerobic oxidation during transit through a deeper, oxic water column (Dean et al., 2018; Hermans et al., 2024). Stratification can further suppress vertical diffusion, where dissolved carbon accumulates in bottom waters and porewaters until mixing events or pressure changes (leading to CH₄ ebullition) trigger release (Casper et al., 2000). Thermoclines between 1 and 20 m depth at most open water sites (Kallavesi S05, S06, S16, Vesijärvi S10, and S11) indicate stratification (Boehrer and Schultze, 2008; James et al., 2017), whereas Vesijärvi S12, Oulujärvi S17, S18, and S19 lack a



clear thermocline (Table S2). At Oulujärvi S18, a thermocline may exist below the sampled interval (maximum depth 31 m).
600 Sites without strong stratification (Vesijärvi S12, Oulujärvi S17, and S19) exhibit some of the highest surface-water CH₄ and
DOC concentrations among open-water sites in their lakes (Table 2), yet DOC is unlikely to derive primarily from sediment
diffusion due to slow diffusivity, and CH₄ is not substantially elevated relative to other open water sites. These patterns,
together with the observation that surface water TCO₂ is not elevated at these sites, suggest that stratification does not
significantly affect site-specific dissolved carbon concentrations in the surface waters of our study sites.

605 Because our flux estimates capture only diffusion, they likely underestimate total CH₄ efflux in shallow vegetated zones where
ebullition and plant mediated transport (PMT) can be substantial. Ebullition is depth-dependent, with shallow sediments
emitting more due to lower hydrostatic pressure and greater sensitivity to pressure changes (Mattson and Likens, 1990; Casper
et al., 2000; Bastviken et al., 2004; Tokida et al., 2007; Shakhova et al., 2014). Consequently, in teal carbon habitats, ebullition
610 and PMT may represent a significant methane-release pathway not captured by our diffusive-flux estimates (Desrosiers et al.,
2022).

4.3 Decoupling of SOC inventories and diffusive turnover

As expected from its definition ($ACF = 100 \times \text{Total C flux} / \text{SOC}_{10}$), ACF increased with total C flux and decreased with
SOC₁₀ in both habitats (Fig. 7a–7b). However, total C flux did not scale linearly with SOC₁₀. Instead, the relationship was
615 weakly negative in teal carbon and non-existent in open water habitats (Fig. 7c). Thus, in teal carbon habitats, sites with smaller
SOC₁₀ can exhibit proportionally higher turnover efficiency, whereas in open water habitats, ACF variability is driven
primarily by flux differences rather than by SOC₁₀, which varies relatively little among sites (Fig. 7a).

In teal carbon habitats, ACF was negatively associated with the fraction of fine-grained sediment (Fig. 8a). Mechanistically,
620 shifting from coarse to fine sediments can reduce microbial mineralization via physically protection and mineral association,
while simultaneously enhancing accumulation via sorption (Van Veen and Kuikman, 1990; Keil et al., 1994; Keil and Cowie,
1999; Krull et al., 2001; Telles et al., 2003; Bianchi, 2006; Yu et al., 2017). These mechanisms also help explain contrasts
among teal carbon sites: those that trap fines tend to exhibit larger SOC stocks but lower diffusive turnover, whereas coarser
sites have smaller stocks and higher turnover. In essence, in teal carbon habitats, carbon turnover becomes less effective as
625 SOC₁₀ increases, because the same condition that increase SOC₁₀ (grain size) tend to suppress turnover.

Macrophytes also influence turnover. Root exudation supplies labile substrates, and oxygen release modifies rhizosphere redox
conditions, potentially inhibiting methanogenesis locally (Van Der Nat and Middelburg, 1998b; Dean et al., 2018; Ding et al.,
2002; Laanbroek, 2010). Conversely, plant aerenchyma can transport CH₄ directly to the atmosphere, bypassing oxidation
630 (Van Der Nat and Middelburg, 1998a; Dorodnikov et al., 2011; Riutta et al., 2020; Villa et al., 2020; Yang et al., 2022; Ge et
al., 2023, 2024; Chanton et al., 1989; Whiting and Chanton, 1993; Joabsson et al., 1999). The observed negative association



between ACF and stem density (Fig. S11) suggests that increasing stem density may enhance non-diffusive CH₄ export (plant-mediated transport) relative to diffusive pathways while simultaneously promoting SOC accumulation via fine-trapping and detritus production. Species differences could also matter (Fig. S11). *P. australis* is highly efficient in CH₄ transport due to pressurized convective flow and is often linked to high emissions (Brix et al., 1992; Armstrong et al., 1992, 1996; Brix et al., 1996; Bergström et al., 2007), *Equisetum spp.* can also have high CH₄ emissions linked to detritus turnover (Kankaala and Bergström, 2004; Kankaala et al., 2005), whereas *Carex spp.* show variable effects, including enhanced rhizospheric oxidation (Ding et al., 2003, 2004, 2005). Given the small number of *Carex* sites (n = 3), species-specific inferences should be considered tentative.

In open water habitats, ACF was not significantly correlated with any environmental parameter and appeared primarily driven by total C flux (Fig. S12). While total C flux correlated with surface-water temperature and SPC, these reflected between-lake contrasts, and the small number of lakes limited inference. Of the site-level parameters, N:C showed the strongest association with flux, consistent with higher flux where OM quality is more labile/autochthonous (Fig. S12 and 7c). It is surprising that this relationship is not observed in teal carbon habitats. The lack of a similar pattern likely reflects stronger physical and plant-mediated controls (grain size, macrophytes) and mixing/source effects that decouple simple N:C proxies from turnover.

As noted previously, SOC₁₀ correlates positively with the fraction of fine grained inorganic sediment in teal carbon habitats, consistent with previous studies (Lindroth Dauner et al., 2026), and because organic matter has generally low density, freshly accumulated OM-rich sediments have high porosity (Avnimelech et al., 2001), as is evident in our data (Fig. S13a). Conversely, in open water, SOC₁₀ decreased with porosity. This is surprising, but as all open water sites have a high porosity (> 90 %), the negative relationship likely reflects extremely low-density OM in the tops of some cores, forming a thick fluff layer such that, as porosity approaches 100 %, the water fraction outweighs the amount of OM present. Open water SOC₁₀ also decreased with water depth (Fig. 13b), consistent with longer settling times promoting degradation before deposition (Junna et al., 2025; Sobek et al., 2009).

4.4 Limitations and implications

Our flux estimates capture diffusion but not ebullition or plant-mediated gas transport, which can be substantial in shallow vegetated zones. As a result, CH₄ efflux is likely underestimated in teal carbon habitats. Additionally, DOC gradients were sometimes constrained by fragmented measurements. We addressed gaps through interpolation and extrapolation and validated concentrations with replicate analyser runs, however, residual uncertainty remains.

Seasonal variations should also be considered, as teal carbon habitats are expected to present significant fluctuations in temperature, runoff and resuspension events. Moreover, the macrophyte life cycle will influence the processes of accumulation, transport and turnover throughout the seasons. A larger dataset would also make statistical inference more reliable.



665 Despite these limitations, our results suggest two contrasting regimes: (i) teal carbon habitats that accumulate substantial near-shore SOC stocks while exhibiting low diffusive turnover efficiency, and (ii) open water habitats where diffusive fluxes are more responsive to organic matter source/quality than to SOC pool size.

Teal carbon habitats can hold large, relatively stable near-shore SOC inventories. However, disturbances such as dredging, winter storms, or intensive harvesting cause risks in remobilizing and reoxidising these inventories, thereby potential reducing
670 long-term carbon storage.

Importantly, not all teal carbon habitats are equal; sandy, low-fines sites possess small SOC stocks past the top 10 cm and exhibit higher turnover rates, suggesting that interventions in these areas may involve lower risks.

Management should therefore prioritize the protection of fine-trapping, vegetated shorelines to safeguard SOC stores, and reduction of catchment nutrient inputs to moderate open water fluxes fuelling autochthonous production.

675 **5 Conclusions**

This study elucidates the contrasting carbon-cycling regimes of boreal lakes, highlighting the considerable role of teal carbon habitats as significant carbon stores with substantial sediment organic carbon inventories (SOC₁₀) and low turnover efficiency. Our findings indicate that while teal carbon habitats accumulate considerable amounts of organic carbon, disturbances such as dredging are risks to their carbon storage capacity. Notably, our results demonstrate that total diffusive carbon flux in open
680 water habitats is more closely tied to the quality of organic matter than to SOC₁₀ levels, as evidenced by the association with N:C ratio. This insight underscores the necessity for targeted management strategies that regulate catchment level nutrient inputs to mitigate autochthonous carbon production and subsequent carbon fluxes in open water environments. Future research should aim to explore the dynamics of carbon cycling in varying environmental conditions, quantify all available carbon flux pathways, and assess the long-term impacts of anthropogenic activities on carbon storage in these crucial habitats.

685 Overall, our work underscores the importance of understanding freshwater ecosystems' contributions to global carbon cycling and the need for effective conservation strategies to safeguard these vital resources.

Data availability

All new data generated during this study is available as supplementary material to this article, via <https://doi.org/10.5281/zenodo.21061456> (Kankainen et al., 2026). All previously published data used in this study are openly
690 available via Pangea (<https://doi.org/10.1594/PANGAEA.986726>, Dauner et al., 2025a, and <https://doi.org/10.1594/PANGAEA.986727>, Dauner et al., 2025b).



Supplement

The supplemental material is supplied in a separate file

Author contributions

695 Tom Jilbert and Karoliina Koho conceptualised the study. Data collection was carried out through fieldwork campaigns by Tom Jilbert, Karoliina Koho, Tuomas Junna, Ana Lindroth Dauner, and Max Kankainen. Asko Simojoki, Tuomas Junna, Ana Lindroth Dauner, and Max Kankainen carried out the laboratory analyses. Max Kankainen performed the formal data analysis and wrote the original manuscript draft. All authors contributed to manuscript writing, data interpretations, and approved the submitted version.

700 Competing interests

The authors declare that they have no conflict of interest.

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