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LETTER

Aquatic carbon fluxes in a hemiboreal catchment are predictable from landscape morphology, temperature, and runoff

Sivakiruthika Balathandayuthabani[1a] *Marcus B. Wallin*[2] *Leif Klemedtsson*[3] *Patrick Crill*[4] *David Bastviken*[1*]

[1]Department of Thematic Studies—Environmental Change, Linköping University, Linköping, Sweden; [2]Department of Aquatic Sciences and Assessment, Swedish University of Agricultural Sciences, Uppsala, Sweden; [3]Department of Earth Sciences, University of Gothenburg, Gothenburg, Sweden; [4]Department of Geological Sciences and Bolin Centre for Climate Research, Stockholm University, Stockholm, Sweden

Scientific Significance Statement

Inland waters such as lakes and streams receive large amounts of carbon (C) from the catchment soil (lateral C fluxes) and are important sources of greenhouse gases to the atmosphere. Lack of data on interrelationships between lateral fluxes and emissions of C at whole catchments is a major constraint in understanding the regulation of fluxes and their climate feedbacks. Here, we show that both lateral C fluxes and the whole catchment aquatic C emissions to the atmosphere were linearly correlated with water discharge for streams and temperature for lakes, and that the temporal patterns of these fluxes critically depended on local features and short-term events. Our results indicate that within time frames of stable land-cover, inland water C emissions and lateral C fluxes are strongly linked to landscape morphology and changes in temperature and runoff.

Abstract

Aquatic networks contribute greenhouse gases and lateral carbon (C) export from catchments. The magnitudes of these fluxes exceed the global land C sink but are uncertain. Resolving this uncertainty is important for understanding climate feedbacks. We quantified vertical methane (CH_4) and carbon dioxide (CO_2) emissions from lakes and streams, and lateral export of dissolved inorganic and organic carbon from a hemiboreal catchment for 3 yr. Lateral C fluxes dominated the total aquatic C flux. All aquatic C fluxes were disproportionately contributed from spatially restricted areas and/or short-term events. Hence, consideration of local and episodic variability is vital. Temperature and runoff were the main temporal drivers for lake and stream C emissions, respectively. Whole-catchment aquatic C emissions scaled linearly with these drivers within timeframes of stable land-cover. Hence, temperature and runoff increase across Northern Hemisphere humid areas from climate change may yield proportional increases in aquatic C fluxes.

*Correspondence: david.bastviken@liu.se

[a]Present address: School of Post Graduate Studies, Tamil Nadu Agricultural University, Coimbatore, India

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Additional Supporting Information may be found in the online version of this article.

Inland waters are important atmospheric sources of greenhouse gases (GHGs) CH_4 and CO_2 (Bastviken et al. 2011; Raymond et al. 2013; DelSontro et al. 2018). Global CH_4 and CO_2 emissions from inland waters could be upto 3.9 Pg C yr^{-1} if accounted as 100-yr CO_2 equivalents (Drake et al. 2018). Inland water CH_4, largely originating from anoxic organic matter degradation in sediments, reaches the atmosphere via many pathways, including diffusion-limited dissolved gas emission and ebullition, making them one of the largest and most uncertain global CH_4 budget components (Saunois et al. 2020; Rosentreter et al. 2021). Inland waters are typically supersaturated in CO_2 because of in-system organic matter mineralization and direct dissolved inorganic carbon (DIC) inputs from catchments (Maberly et al. 2013; Hotchkiss et al. 2015). Lakes and ponds are estimated to be greater CH_4 sources than rivers (Bastviken et al. 2011), and while Stanley et al. (2016) has reported significant stream CH_4 emissions, direct flux measurements are rare and the relative CH_4 contribution from low order streams are unclear at larger scales (Drake et al. 2018). Streams, in contrast, have been suggested to contribute disproportionately high CO_2 emissions despite occupying a smaller area (Lundin et al. 2013; Raymond et al. 2013; Wallin et al. 2013). The global mean lake and reservoir gas transfer velocity of 1.0 m d^{-1} (*k*; describing the gas transfer efficiency across water-atmosphere interfaces) is much lower than the mean *k* estimated for streams in the United States and globally (4.5 and 5.7 m d^{-1}, respectively) (Butman and Raymond 2011; Raymond et al. 2013). In addition, studies have noted higher CH_4 and CO_2 concentrations in streams than in lakes (Raymond et al. 2013; Stanley et al. 2016). Despite the differing magnitudes, both lakes and streams are important atmospheric C sources while knowledge about their relative C flux contribution and climate forcing across catchments is limited.

Inland water C emissions depend on lateral dissolved organic carbon (DOC) and DIC exports from soils to the aquatic networks, which is estimated to be upto 5.1 Pg C yr^{-1} globally (Cole et al. 2007; Aufdenkampe et al. 2011; Drake et al. 2018). For the C proportion reaching downstream lake, river, coastal or marine sediments, or oceanic water, this lateral soil C transfer can be considered as a displaced C sink (i.e., soil sink C becoming parts of the aquatic C sinks). However, a large share of the lateral C flux from soil to water results in C emissions along the aquatic network. Hence, terrestrial net ecosystem production (NEP) or net ecosystem exchange estimates relying on vertical C exchange of terrestrial habitats only, will overestimate NEP and underestimate whole-catchment GHG emissions. Accordingly, studies have recognized the importance of including the lateral C transport from land to water in the aquatic C budgets (Butman et al. 2016; Webb et al. 2019; Chi et al. 2020; Regnier et al. 2022). While some studies have reported total catchment lateral C fluxes (e.g., Rantakari et al. 2010; Wallin et al. 2013; Butman et al. 2016; Leach et al. 2016; Hutchins et al. 2020), the interdependence of lateral and vertical aquatic C fluxes at full-catchment scale is largely unknown (Tank et al. 2018), but understanding their relative significance and sensitivity to environmental change is critical. Lateral C fluxes have been linked to temperature, precipitation, and runoff (Tank et al. 2018), but the regulation of catchment-scale aquatic C emissions is unclear and several different driver variables have been suggested for lakes and streams, respectively (Dinsmore et al. 2013; Butman et al. 2016; Webb et al. 2019).

Most past assessments of drivers for whole-catchment lateral and aquatic C/GHG fluxes have been meta-analyses of data from multiple catchments. As often found in analyses where many non-measured environmental factors differing among sites can influence results, driver-flux relationships were weak. Consequently, knowledge on response of whole-catchment aquatic C emissions to future environmental change is limited (Dinsmore et al. 2013; Butman et al. 2016; Webb et al. 2019). Recent work demonstrated that detailed spatiotemporal studies over full years are needed to adequately characterize stream and lake GHG emissions (Natchimuthu et al. 2016, 2017*b*), and long-term full-catchment assessments are needed to evaluate past meta-analyses and to generate robust predictive capacity.

Here, we performed an integrated whole-catchment aquatic emission and lateral C flux assessment of the entire aquatic surface area including lakes and streams of the Skogaryd Research Catchment (SRC) situated in southwest Sweden. Based on detailed in situ measurements covering relevant spatiotemporal dynamics, we report vertical (CH_4 and CO_2) and lateral (DIC and DOC) C fluxes over a 3-yr period (2012–2014). The main variability drivers of vertical and lateral aquatic C fluxes were analyzed and the hypothesis that runoff and temperature are powerful variables for extrapolation in time and space was evaluated.

Methods

The study was conducted in SRC (58°22′N, 12°9′E; catchment area ~ 7 km^2; www.fieldsites.se) which includes two lakes of different successional stages and depths, Erssjön (maximum depth of 4.5–5.0 m), and Följesjön (a shallow lake in transition to a wetland). A stream network of ~ 9 km length, moves water through SRC before draining into Skottenesjön. Emissions from the delta area of the downstream lake (Skottenesjön) was also sampled, as they are likely derived from the organic matter exported from the catchment. The SRC is considered representative for hemiboreal and boreal regions of Fennoscandia in terms of land-cover, soil types and surface water area extent (Figs. S1, S2).

In the lakes, diffusion-limited (CH_4 and CO_2) and ebullitive (CH_4) emissions, were measured biweekly during 2012 (April–October) and 2013 (April–November) using floating chambers

and surface water concentrations from both manual grab sampling (Natchimuthu et al. 2016) and continuous CO_2 logger measurements (CO_2 Engine ELG; SenseAir AB) (Natchimuthu et al. 2017*a*). To include spatial variability, measurements were made in different depth zones of open water in lakes (*see* Supporting Information). In the lakes, 987 CH_4 and 326 CO_2 direct emission measurements were made in 2012 and 2013. Lake emissions were extrapolated to annual values using identified relationships with environmental variables such as water temperature, wind speed, water depth, and air temperature (Table S1).

Stream CH_4 and CO_2 water concentration measurements and propane-based k assessments in six representative reaches were made during 2013 (May–November) and 2014 (April–November) at locations and times selected to cover the variability in stream slope and discharge (Natchimuthu et al. 2017*b*) (Supporting Information). Stream CH_4 concentrations were measured biweekly while CO_2 concentrations were continuously logged. In 2013 and 2014, 292 CH_4 and 28,463 CO_2 stream concentration measurements were made. Using propane injection data during different discharge conditions, a k model using stream channel slope and water velocity was developed to extrapolate k to the whole stream network (Natchimuthu et al. 2017*b*). Daily k estimated from the stream k model was combined with spatially interpolated daily gas concentrations to estimate daily stream emissions (Supporting Information provides details on estimates of lake and stream surface water area, annual emissions, and uncertainties).

Daily downstream DOC and DIC export was calculated by multiplying measured DOC and DIC concentrations with daily average discharge measured at a stream station located near the SRC outlet. DOC and DIC were sampled approximately every 4 ($n = 200$) and 14 ($n = 47$) days, respectively, and were linearly interpolated between the sampling dates. Aquatic C flux data from SRC are available in Balathandayuthabani et al. (2022).

Results and discussion

Lake CH_4 and CO_2 emissions ranged from 0.02 to 4.6 and 13 to 67 mmol m^{-2} d^{-1}, respectively (Fig. 1; Table S2), indicating considerable within and between lake variability. The highest lake CH_4 emissions per m^2 came from shallow zones close to the shore and 66% of the emissions were derived from shallow water (< 0.5 m depth), constituting only 33% of the lake area (Table S3). Such depth-related spatial lake CH_4 emission variability has been demonstrated previously (e.g., Bastviken et al. 2010; DelSontro et al. 2011; Hofmann 2013). Temporally, lake CH_4 emissions were higher during the summer months (Natchimuthu et al. 2016), probably related to the increase in methanogenesis with temperature (Zeikus and Winfrey 1976; Yvon-Durocher et al. 2014). About 46% of total lake CH_4 emissions occurred during the summer months of July and August (Table S3). The open water CO_2 emissions from the lakes did not have a pronounced temporal variability (Table S3), while the spatial variability was often significant during thermally stratified periods (Natchimuthu et al. 2017*a*). CH_4 release during ice-melt was negligible (Natchimuthu et al. 2016) and ice-out CO_2 emissions were 2–11% of the integrated yearly CO_2 emissions from the three lakes (*see* Supporting Information).

Streams emitted 0.007–940 and 1.3–90,347 mmol m^{-2} d^{-1} of CH_4 and CO_2, respectively (Fig. 1; Table S2). Stream reaches with steep slopes were highest emitters due to the higher turbulence (Fig. S3). Ninety percent (90%) of the total stream area had slopes < 1% contributing only 59% and 45% of the total CH_4 and CO_2 emissions, respectively (Table S3). Streams with slopes between 4% and 21% occupied only 1% of the total stream area but emitted 14% and 24% of total CH_4 and CO_2 emissions, respectively. The large differences in k and gas concentrations in the streams explains the large spatial variabilities in fluxes, as suggested previously (Teodoru et al. 2009; Wallin et al. 2011; Hutchins et al. 2020). High discharge periods had higher stream emissions, due to the increase in k with increasing discharge (Natchimuthu et al. 2017*b*; McDowell and Johnson 2018). Periods with discharge > 2 times the mean daily discharge occurred during 15% of the study period but emitted 42% and 50% of the total CH_4 and CO_2 emissions, respectively (Fig. S3; Table S3).

Large variability in daily lateral C fluxes was noted in response to changing stream discharge. Periods with > 3 times the mean discharge exported 44% of the lateral C fluxes. Large interannual variability in the lateral C fluxes was noted, and the flux in 2013 was almost half the fluxes observed in 2012 and 2014, corresponding to differences in annual discharge (Fig. 2b; Table S2). This is consistent with studies observing positive relationships of lateral C exports with stream discharge (Clark et al. 2007; Wallin et al. 2015).

When comparing lateral with vertical fluxes on a daily timescale, the lateral fluxes constituted 10–98% of the total C losses, with the lower share during low stream water discharge (lateral C flux contributed < 50% of total flux during discharge < 25 L s^{-1}; Fig. S4). During July, August, and September of 2013 (2.2% of the annual stream discharge), the mean lateral fluxes were only 25–33% of the total C losses. In these periods the lake vertical C losses were the major component of the total catchment C loss (49–59%; Fig. S4). However, on a whole year basis, the lateral C fluxes constituted 80–86% of the total C export from the catchment over the three study years.

The results demonstrate that catchment-scale aquatic vertical and lateral C fluxes can be significantly biased if a few measurements in time and space are extrapolated to whole areas and years without including local and short-term variability (e.g., high-slope stream sections and high discharge period fluxes). Analyzing subsets of vertical fluxes indicated that, to be within ± 25% of the mean of all samples, data

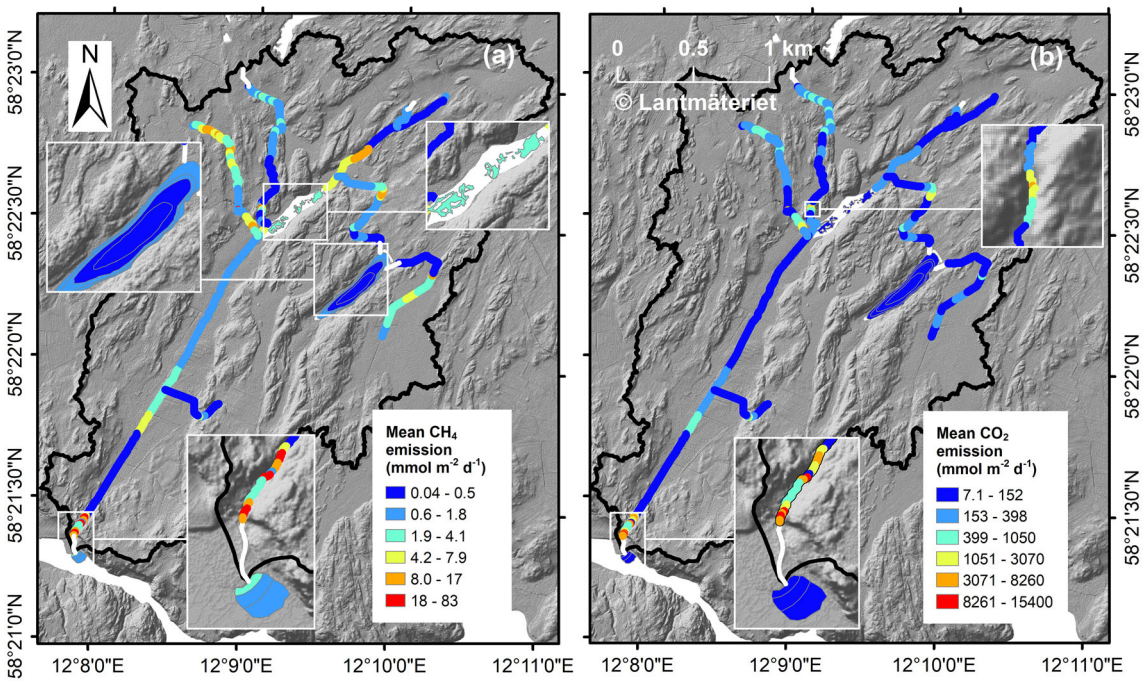
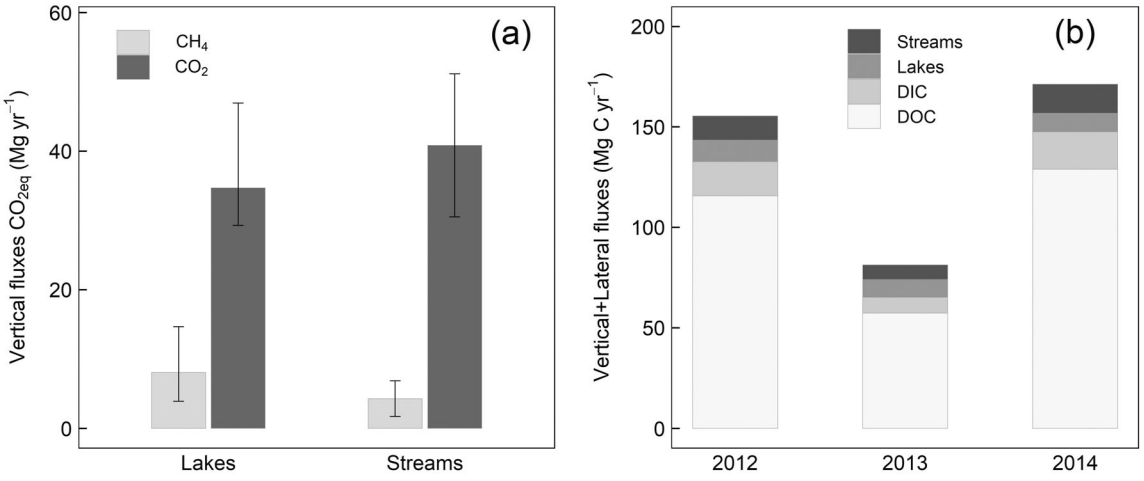


Fig. 1. Mean CH_4 (**a**) and CO_2 (**b**) emissions from the aquatic areas of Skogaryd Research Catchment (SRC) showing higher emissions from localized areas in streams and lakes. Note the variable rates of CH_4 emissions between the lakes and within the lakes. White areas in lakes and streams denote areas not studied. The background map of SRC was obtained from Lantmäteriet (National Land Survey of Sweden).

from 14 locations on 9 d (24 h) for lake CH_4, 8–5 locations and 8 d for lake CO_2, and 44 reaches and 10 d for stream C fluxes are required, with samples covering different spatiotemporal conditions (lake depths, stream slope, temperatures, discharge, etc.; Fig. S5). While some of the heterogeneity observed here has been reported previously we here present integrated analyses linking lakes, streams, CH_4 and CO_2, spatiotemporal scales, lateral and vertical fluxes from a whole catchment.

At the catchment scale, lakes and streams emitted 0.2 and 0.1 Mg yr^{-1} (Mg = 10^6 g) of CH_4 and 34.7 and 40.8 Mg yr^{-1} of CO_2, respectively (Table S4). When expressed as CO_2 equivalents (global warming potential enhancement of 34 times that of CO_2 by mass over a 100-yr period; Myhre et al. 2013), the impact of lake and stream CH_4 emission was 12.3 Mg (CO_{2eq}) yr^{-1} with 8.1 Mg (CO_{2eq}) yr^{-1} from lakes (Fig. S6). The CO_{2eq} vertical flux from the lakes and streams totalled 87.8 Mg (CO_{2eq}) yr^{-1} (Fig. 2a; Table S4). Lakes and streams contributed roughly equal to the total CO_{2eq} vertical aquatic flux, although the streams occupied only 11% of the catchment's aquatic area and emitted more C. The largest lake studied (Erssjön) received CO_2-rich water from an upstream mire, emitting considerable CO_2. Therefore, most of the CO_{2eq} was emitted as CO_2 (81% in lakes and 91% in streams) and the rest as CH_4. These results are similar to catchments with stream surface areas of 3–5% of the total aquatic area, where stream contributions were 39–41% (CH_4) and 14–96% (CO_2) of the total estimated catchment emission (Lundin et al. 2013; Campeau et al. 2014; Kokic et al. 2015), but differences in relative stream area and spatiotemporal measurements makes direct comparisons uncertain. The stream contribution to total aquatic C emissions is likely lower in catchments with large lakes, which are not represented in the SRC. Nevertheless, low order streams are major C emitters within most catchments both by flux per area unit and by total fluxes. This makes aquatic C emissions highly discharge dependent annually, while during hydrological base-flow, temperature dependent lake CH_4 fluxes were strong whole-catchment C flux modulators (Fig. 3).

The catchment exported 57.3–128.8 and 7.9–18.7 Mg C yr^{-1} as DOC and DIC, espectively, during the 3 yr (Fig. 2b). The lake and stream vertical C fluxes were 8.9–10.8 and 7.3–14.4 Mg C yr^{-1}, respectively (Fig. 2b; note the C units). Annually, the DOC export was the major C loss pathway in the catchment (70–75%), followed by the vertical C loss (14–20%) and the DIC export (10–11%). Although DOC exports have been reported to be larger than, smaller than, or similar to DIC (Buffam et al. 2011), a higher DOC than DIC export downstream is expected in boreal and hemiboreal regions where carbonate containing bedrock is rare (Wallin et al. 2013). The C proportion lost as lateral fluxes (80–86%) appears higher than estimates from the few other comparable studies (24–50%) (Lundin et al. 2013; Crawford et al. 2014; Hutchins et al. 2020), possibly due to differences in runoff,



(c)

Year	DOC	DIC	Lakes	Streams
	Unit: g C m^{-2} yr^{-1}			
2012	16.4 (13.9 –18.8)	2.4 (2.2 – 2.6)	1.5 (1.2 – 2.2)	1.7 (1.2 – 2.2)
2013	8.1 (6.9 – 9.3)	1.1 (1.0 – 1.2)	1.3 (1.0 – 1.8)	1.0 (0.7 – 1.3)
2014	18.3 (15.5 – 21.0)	2.7 (2.4 – 2.9)	1.3 (1.0 – 1.9)	2.0 (1.5 – 2.6)

Fig. 2. Vertical and lateral C fluxes from the catchment in the 3 yr. Panel (**a**) shows the CO_2 equivalent emissions (using a global warming potential of 34 for CH_4 over a 100-yr period) from lakes and streams of SRC. The error bars denote uncertainty ranges (*see* text for details). Panel (**b**) shows the inter-annual variability in the different components of the vertical and lateral C fluxes in the catchment. C fluxes normalized to the catchment area are given in the panel (**c**).

soil characteristics, and/or measurement frequency and duration.

When normalized to the catchment area (6.96 km^2), the lakes and streams emitted 1.3–1.5 and 1.0–2.0 g C m^{-2} yr^{-1} and the DOC and DIC exports were 8.1–18.3 and 1.1–2.7 g C m^{-2} yr^{-1}, respectively (Figs. 2c, S7). The catchment area normalized lake and stream vertical C fluxes (2.3–3.4 g C m^{-2} yr^{-1}) were comparable to the emissions from other catchments when considering aquatic area proportions of 1% in our catchment vs. 5% to > 10% in comparable studies (Lundin et al. 2013; Campeau et al. 2014; Crawford et al. 2014). The lateral DOC and DIC export were within the ranges reported at boreal latitudes (Rantakari et al. 2010; Wallin et al. 2013; Wallin et al. 2015; Leach et al. 2016).

The C proportion lost as vertical and lateral C fluxes was related to discharge and thereby also with the catchment's water residence time (Fig. 3a,b). Lake fluxes were less correlated with discharge than stream fluxes, although discharge was still the main predictor variable for whole-catchment C fluxes (Fig. 3c,d). Furthermore, with longer residence times, the proportion lost as vertical flux increased (Fig. 3b) agreeing with studies suggesting active DOC processing with longer residence times (Catalán et al. 2016; Casas-Ruiz et al. 2017; Cory and Kling 2018). Therefore, the fate of lateral vs. vertical C fluxes from catchments could vary depending on the runoff rates (Cory and Kaplan 2012), in combination with other factors influencing DOC processing (e.g., temperature; Lønborg et al. 2018), light exposure (Cory et al. 2015), C burial (e.g., land-use; Anderson et al. 2013), and microbial communities (Cory and Kling 2018).

Previous studies support the observed discharge dependency on some of the C fluxes. For example, higher streamflow during snow free periods led to higher CH_4 and CO_2 stream emissions in a Swedish boreal catchment (Gómez-Gener et al. 2021). Increased discharge resulted in increased CO_2 emissions in a turbulent headwater stream in British Columbia, Canada (McDowell and Johnson 2018). A 10-yr study in a catchment in western Oregon, USA, observed highest DOC and DIC exports during wet years (Argerich et al. 2016). This indicates that our results reflect a general pattern occurring in comparable environments.

Importantly, the observed linear relationships between relative changes in discharge and C fluxes applies to stable land cover periods. Land-cover and land-use changes can influence the absolute fluxes in ways not reflected in this study. However, within the represented land cover types, the results imply that projected changes in runoff patterns due to climate change (Collins et al. 2013) will influence future lateral C

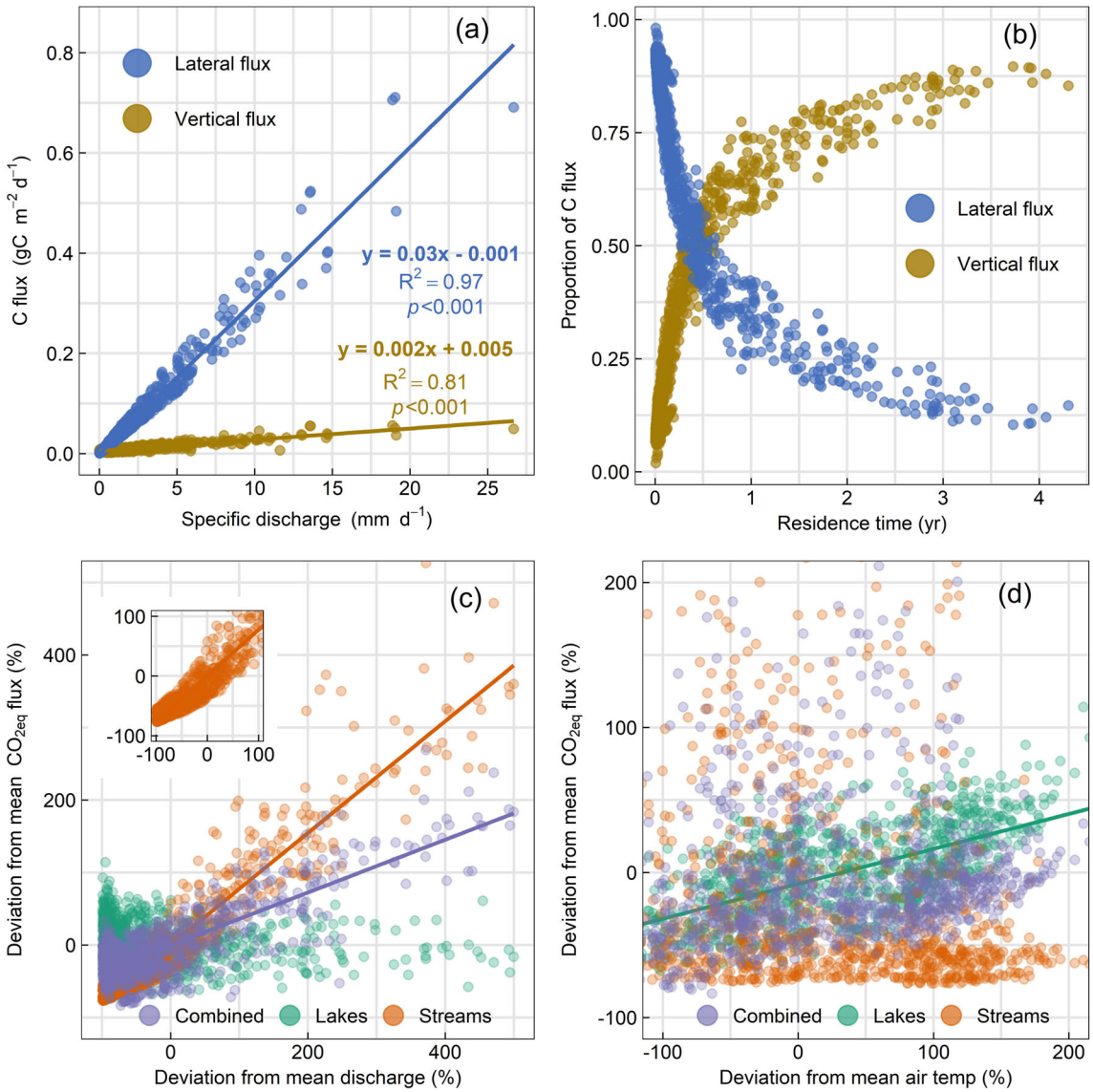


Fig. 3. Changes in catchment vertical and lateral C fluxes with discharge and temperature in SRC. Panels (**a**) and (**b**) show absolute and proportional C fluxes vs. specific discharge and residence times, respectively. In panel (**a**), each vertical flux point includes daily lake and stream emissions (CH_4 and CO_2) and each lateral flux point includes daily DIC and DOC export in g C m^{-2} d^{-1} normalized to catchment area for the years 2012–2014. Panel (**b**) has the same data in proportions of the total C flux and all data includes spatial variability (data is the sum of the emissions from the lake and stream surface). The daily residence times were calculated as the daily total water volume of the catchment (lake + stream) divided by the daily total discharge at the outlet of the catchment. Panels (**c**) and (**d**) show deviation in CO_{2eq} fluxes (relative to the mean flux) in response to deviation in discharge and air temperature, respectively, for stream, lake, and total combined fluxes. Regression lines in panels (**c**) and (**d**) are shown when $R^2 > 0.39$ and $p < 0.001$. Discharge had a dominating effect on streams ($y = 0.76x + 0.59$; $R^2 = 0.91$) and total combined fluxes ($y = 0.37x - 2.1E{-}10$, $R^2 = 0.76$), while lake fluxes were temperature dependent ($y = 0.24x - 7.53$; $R^2 = 0.39$) in panels (**c**) and (**d**).

transfer to aquatic networks and vertical aquatic C emissions at boreal/hemiboreal latitudes (Fig. 4). Accordingly, projected runoff changes can be useful to predict lateral and vertical aquatic C emissions under varying climate scenarios for the coming decades if stable land-cover can be assumed.

Some of the lateral C fluxes will contribute to vertical emissions along the aquatic continuum before reaching the sea, as observed here and also in studies proposing positive links between CO_2 emissions and DOC concentrations in aquatic systems (Tranvik et al. 2009; Lapierre et al. 2013; Nydahl et al. 2020). The remaining lateral C flux will relocate soil C to downstream sinks in sediments or water (e.g., HCO_3^- in the ocean). Hence, the clear positive relationship between aquatic C emissions and discharge indicates that future precipitation and runoff changes can influence the soil C proportion reaching the atmosphere as aquatic CO_2 or CH_4 emissions

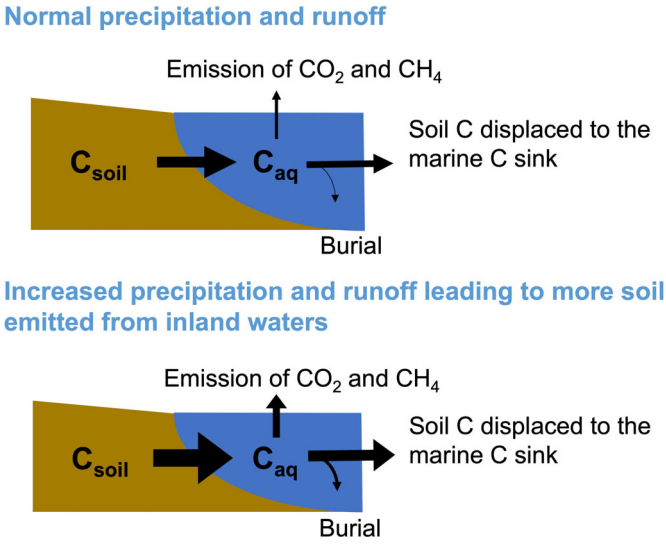


Fig. 4. The effect of increased precipitation and runoff on the aquatic vertical and lateral C fluxes. Burial is considered indirectly as it is the fate of aquatic C that is not emitted to the atmosphere nor stays as dissolved in the water, and is assumed to be approximately proportional to the lateral C transport.

(Fig. 4). In SRC, discharge was the best predictor for aquatic C fluxes at the landscape scale, and this is likely where streams are dominating inland water components. However, in lake-rich catchments, temperature could have a proportionally greater influence on total aquatic C and CO_{2eq} emissions, via CH_4.

Estimating large-scale impacts is challenging given the uncertainties in runoff projections. However, it can be illustrated using a detailed runoff prediction until 2061–2090 from a Swedish boreal catchment with headwater streams (Teutschbein et al. 2015). In this catchment, mean precipitation was projected to increase by 17%, leading to annual mean change in runoff of ca. 20% after accounting for changes in evapotranspiration and seasonality. If assuming (1) such a change in runoff, combined with (2) mean temperature changes of 1.5–4.5°C for this region (Collins et al. 2013), and (3) that soil C content is not a limiting factor for the lateral C transport to aquatic environments (supported by SRC's estimated annual NEP and top 100 cm soil C stocks of 582 g C m^{-2} yr^{-1} and 55,000 g C m^{-2}, respectively; Lindroth et al. 2020), the relationships for vertical emissions in Fig. 3c,d predicts a vertical aquatic C emission increase of 8–13%. This example highlights a strong hydrological and temperature feedback on landscape GHG emissions from streams and lakes, respectively. If the projected runoff increase is distributed irregularly in time (dry periods amidst intense rainfall events besides the predicted seasonal patterns; Teutschbein et al. 2015), feedbacks from e.g., changed organic C decomposition and CH_4 formation rates in soils and stream sediments (Gómez-Gener et al. 2020), and changed DOC export (Argerich et al. 2016) may further influence aquatic C emissions.

Our study indicates that lateral aquatic C transport sustain catchment C emissions in direct proportion to runoff and temperature. Despite the complexity and high spatiotemporal variability in the underlying processes, systematic and high-resolution data yielded clear integrated relative patterns at the catchment scale. This may facilitate landscape aquatic C flux assessments and additional work on replicating this study in other ecoclimates, and on predicting future spatiotemporal runoff and land cover, would be highly valuable for improved large-scale modeling.

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