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Magnitude and Origin of CO_2 Evasion From High-Latitude Lakes

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Key Points:

- Carbon dioxide evasion during spring ice breakup dominates annual evasion
- Carbon dioxide evasion is sourced by both external input and internal lake metabolism with large variability between lakes
- Seasonally resolved estimates are needed in order to understand the role of high-latitude lakes in landscape carbon budgets

Supporting Information:

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

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Abstract Lakes evade significant amounts of carbon dioxide (CO_2) to the atmosphere; yet the magnitude and origin of the evasion are still poorly constrained. We quantified annual CO_2 evasion and its origin (in-lake net ecosystem production vs. lateral inputs from terrestrial ecosystems) in 14 high-latitude lakes through high-frequency estimates of open water CO_2 flux and ecosystem metabolism and inorganic carbon mass-balance before and after ice breakup. Annual CO_2 evasion ranged from 1 to 25 g C m^{-2} yr^{-1} of which an average of 57% was evaded over a short period at ice-breakup. Annual internal CO_2 production ranged from −6 to 21 g C m^{-2} yr^{-1}, of which at least half was produced over winter. The contribution of internal versus external source contribution to annual CO_2 evasion varied between lakes, ranging from fully internal to fully external with most lakes having over 75% of the evasion sustained through a single source. Overall, the study stresses the large variability in magnitude and control of CO_2 evasion and suggests that environmental change impacts on CO_2 evasion from high-latitude lakes are not uniform.

Plain Language Summary Lakes release significant amounts of carbon dioxide (CO_2) to the atmosphere. This CO_2 evasion is mainly sustained by carbon from land, either via external inputs of CO_2 rich water or by internal breakdown of imported organic carbon to CO_2. The extent of CO_2 emission and the contribution of these two sources are poorly understood in regard to the numerous lakes at high latitudes. We studied 14 high-latitude lakes and found that all lakes emitted CO_2 on an annual basis and that 0%–100% (average 44%) of this CO_2 came from breakdown of organic carbon in the lakes. The spring ice-breakup period contributed, on average, 57% of the annual emitted CO_2 despite covering only 16% of the open water season duration. Our study defines the fundamental role of lakes on the landscapes as "reactors" or "chimneys" for carbon processing and emission to the atmosphere, and how these roles change over the course of the year.

1. Introduction

Most of the Earth's lakes evade carbon dioxide (CO_2) to the atmosphere (Cole et al., 2007; Drake et al., 2018). High-latitude lakes are of special importance as they are very abundant (Verpoorter et al., 2014) and evade large amounts of CO_2 (Raymond et al., 2013) with significance to regional carbon cycles (Lundin et al., 2013; Stackpoole et al., 2017). However, these systems are often in areas that are difficult to access, not least due to snow/ice cover during a large part of the year. They also often lack transportation and research infrastructure nearby, making intensive study of these lakes a challenge (Metcalfe et al., 2018). Consequently, important knowledge gaps remain in assessments of the contribution of high-latitude lakes to the contemporary and future C cycle. In particular, there is little data on the magnitude and control of annual CO_2 evasion from high-latitude lakes.

Fundamental to the understanding of CO_2 evasion from lakes is the quantification of various sources and sinks of CO_2. Evasion of CO_2 from lakes can originate from water rich in dissolved inorganic carbon (DIC) transferred laterally from the catchment, which is then evaded, making lakes function as "chimneys" in the landscape (Jones et al., 2001; Prairie, 2008). The CO_2 evasion can also be driven by microbial and photochemical mineralization of terrestrial organic carbon to CO_2 in lakes, making lakes function more like "reactors" in the landscape (Tranvik et al., 2009). The observation that net ecosystem production (NEP) is generally negative for lakes (i.e., ecosystem respiration (ER) exceeds gross primary production (GPP)) indicates that internal CO_2 production contributes to CO_2 supersaturation and evasion (Del Giorgio et al., 1999). On the other hand, external source contribution via soil export of DIC-rich water is also suggested to be of importance for lake CO_2 evasion (Martinsen et al., 2019; Wilkinson et al., 2016). The external contribution of DIC could explain CO_2 evasion from lakes even when NEP is positive (Bogard & del Giorgio, 2016; Stets et al., 2009). Yet, the contribution of internal versus external

sources to the CO_2 evasion from lakes is not well understood, implying a knowledge gap in the understanding of lake carbon cycling.

Variability in landscape conditions between lakes, such as catchment vegetation, hydrological connectivity, or nutrient status, may affect the source contribution (Lapierre & del Giorgio, 2012; Vachon, Solomon, & delGiorgio, 2017). Specifically, variability in flowpaths and chemistry of the inflows to lakes (e.g., stream and groundwater draining mires and/or carrying bedrock weathering products) lead to differences in external inputs among lakes (Dillon & Molot, 1997; Striegl & Michmerhuizen, 1998; Vachon, Prairie, et al., 2017). Likewise, variability in, for example, catchment net primary production and permafrost thawing cause different terrestrial export of dissolved organic carbon (DOC) and thus the potential for lakes to act as reactors (Klaus et al., 2021; McGowan et al., 2018).

The role of lakes in the carbon cycle is difficult to discern due to uncertainties in annual CO_2 flux estimates. Most studies assess magnitude and control of CO_2 air-water flux based on a single or just a few "snap shot" measurements (Klaus et al., 2019; Seekell et al., 2014). However, there is substantial temporal variability of air-water flux from high-latitude lakes (Denfeld et al., 2016; Ducharme-Riel et al., 2015; Klaus et al., 2019). In particular, CO_2-buildup under ice and in the hypolimnion during the open water season is evaded later during turnover at spring ice-melt and autumn cooldown with potentially high flux of CO_2 in these short periods, so called "hot moments." This flux, although significant, is often missed when upscaling from few open water measurements. Evasion at spring ice-melt potentially turns lakes that are net CO_2 sinks during the rest of the open water season into sources of CO_2 to the atmosphere on an annual basis (Karlsson et al., 2013). Additionally, there is also temporal variability in the sources of CO_2 to lakes. For instance, the amount of incoming DIC and DOC is strongly related to hydrological connectivity of the lake, which is affected by dry or wet periods throughout the year (Einola et al., 2011; Zwart et al., 2016). Similarly, in-lake production of CO_2 is known to be seasonally variable with more positive NEP in summer and more negative NEP in autumn and winter (Sadro et al., 2011; Staehr & Sand-Jensen, 2007). The potential strong temporal and spatial variability in air-water flux and control of CO_2 from lakes calls for annual assessments of CO_2 flux and sources among multiple lakes.

The aim of our study was to quantify annual CO_2 flux of high-latitude lakes and the source contribution from external DIC input versus internal CO_2 production. By combining both high-frequency estimates of CO_2 flux and NEP, we quantified source contribution to the annual CO_2 air-water flux from 14 lakes in subarctic Sweden. These systems have varying catchment conditions, such as drainage ratio (i.e., the ratio between catchment and lake area, a proxy for catchment inputs as it is related to the extent of (riverine) input from watersheds to lakes (Seekell et al., 2022)), and vegetation cover (e.g., percent forest cover), leading to distinct hydrological inputs, carbon processing times, and DOC concentrations. This variability allowed us to compare the effects of DOC concentration, drainage ratio and vegetation cover on magnitude, and sources of CO_2 evasion to evaluate the potential role of hydrology and terrestrial export in controlling annual CO_2 air-water flux. We hypothesize that the CO_2 fluxes increase with the lake DOC concentrations, reflecting input of terrestrial DOC that would promote negative NEP (Ask et al., 2012). However, as DOC is delivered to the lakes through catchment (e.g., stream) inputs, they can be concomitant with external inputs of DIC (Giesler et al., 2014). Therefore, DOC will not necessarily correlate with internal versus external source contribution for CO_2 evasion. Rather, the relative importance of the internal source of CO_2 evasion will mainly be controlled by nutrient and carbon availability in the lakes and may therefore be coupled to catchment forest cover (as a proxy for productivity in the catchment). Increased drainage ratio will most likely increase CO_2 fluxes with minor impact on the source contribution as both external DIC and DOC input presumably increase with an increased catchment influence per lake area.

2. Materials and Methods

2.1. Site Description

The 14 lakes in this study are located in the mountain region of Jämtland, Sweden. Nine lakes lie near Skalstugan (63°36′20″N, 12°15′55″E, area A in Figure 1) and five lakes near Edsåsdalen (N63°18′33″N, 12°55′13″E, area B in Figure 1). The elevation of the lakes ranges from 540 to 655 m above sea level for Skalstugan and 710–830 m above sea level for Edsåsdalen. Both areas are underlain with glacial till (SGU, 2020). There was a mixed catchment vegetation of mire, deciduous, and/or coniferous forest in Skalstugan, while Edsåsdalen had either a mixture of mire, birch-dominated deciduous forest and tundra or only tundra. The lakes are located in a subarctic climate

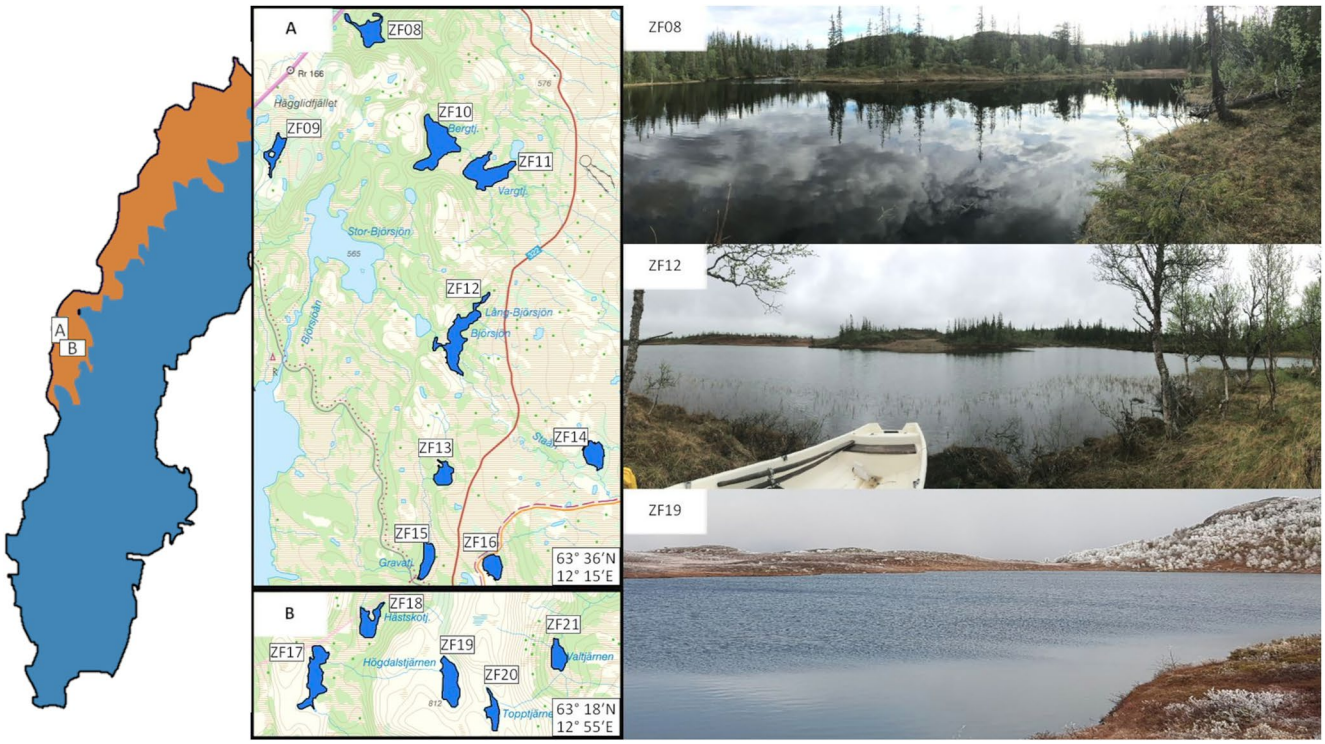

Figure 1. Maps and pictures of field sites. The mountain regions of Sweden are shown in orange (modified from map of the alpine biogeographical region from European Environment Agency, 2003). The top map is of the area near Skalstugan (a), the bottom map near Edsåsdalen (b). On the right hand are examples of lakes with predominantly coniferous forest (ZF08), mire, heath and deciduous forest (ZF12), and heath (ZF19).

(Köppen-Geiger Dfc; Beck et al., 2018) with some of the lakes in Edsåsdalen situated above the local tree line (between 700 and 800 m above sea level). Mean annual precipitation is around 1,000 mm per year for Skalstugan and 700–800 mm for Edsåsdalen of which 40%–45% falls as snow (SMHI, 2017). The surface area of the lakes ranged from 4 to 14 ha and the maximum depths from 3.5 to 33 m (Table 1).

2.2. Field Sampling and Chemical Analysis

We visited each lake three times over the open water season from June to October 2017. For each lake visit, we measured water temperature and dissolved oxygen (O_2) with an optical sensor (ProDO, YSI, Yellow Springs, OH, USA) for each meter of depth up to 10 m at the deepest point. Additionally, we measured photosynthetically active radiation (PAR) using a LI-193 Spherical Quantum Sensor (LI-COR Environmental Lincoln, NE, USA) for every 0.5 m up to 3 m, and every meter onward during each visit during the open water season. The vertical light attenuation coefficient (K_d) was calculated as the slope between the natural logarithm of PAR against depth (Kalff, 2002). The partial pressure of CO_2 in the water (pCO_2) was measured just below the water surface using a handheld CO_2 meter (GM70, Vaisala, Helsinki, Finland) attached with a nondispersive infrared probe (CARBOCAP GMP-222, Vaisala, Helsinki, Finland) enclosed in a semipermeable polytetrafluoroethylene membrane. We corrected these measurements for temperature and pressure according to Johnson et al. (2010). Water samples were taken at 1, 2, 4, 8, and 16 m as lake depth allowed and mixed to a composite water sample representing whole-lake conditions. These were later analyzed for DOC, dissolved nutrients, and absorbance. These composite water samples were filtered through 0.45 µm filters and samples used for the DOC analysis (of 45 ml) were acidified with 400 µl of 1.2M HCl. Samples used for absorbance and DOC measurements were kept refrigerated, while nutrient samples were kept frozen, until analysis. DIC samples were collected in the field, 1 m below the surface for epilimnion and 1 m above bottom for hypolymnion samples, and subsequently injected in 22 ml glass vials that were preflushed with N_2 and contained 100 µl of 1.2M HCl. The depth of the thermocline was determined from manually measured vertical temperature gradients for under-ice measurements and using the temperature loggers for the samples after ice-off, by the use of the "rLakeAnalyzer" package for R (Read

Table 1
Lake and Catchment Physicochemical Characteristics

Lake							Catchment				
ID	Area	Z_{max}	$\overline{Z}$	Alt	DOC	Temp	Area	Forest cover	Mire cover	Slope	DR
	ha	m	m	m a.s.l.	mg L^{-1}	°C	ha	%	%	°	Dimensionless
ZF08	7.1	15	4.3	540	4.0 (0.2)	10.0	42	53	0	14 (11)	6
ZF09	4.0	9	2.8	655	4.5 (0.5)	11.0	61	23	37	10 (8)	15
ZF10	13.6	33	9.3	580	2.0 (0.1)	9.1	45	48	9	12 (12)	3
ZF11	11.9	15	4.0	578	6.2 (1.1)	10.6	493	20	57	5 (4)	42
ZF12	13.4	11	3.1	580	5.1 (1.4)	10.8	910	15	59	5 (5)	68
ZF13	4.3	10	3.5	638	7.5 (1.1)	10.4	87	34	56	5 (5)	20
ZF14	4.6	9	2.9	591	4.9 (1.2)	10.3	606	14	56	5 (5)	132
ZF15	4.5	3.5	1.2	580	7.1 (1.6)	11.6	159	33	45	6 (5)	35
ZF16	4.7	5	1.8	580	7.5 (1.3)	11.5	112	26	62	5 (4)	24
ZF17	11.2	8	2.5	740	4.8 (0.1)	10.8	161	15	18	8 (7)	14
ZF18	6.0	9	2.3	758	4.5 (0.3)	10.9	57	50	18	11 (9)	9
ZF19	9.2	13	4.4	796	3.2 (0.2)	9.6	59	6	8	11 (10)	6
ZF20	4.6	8	2.6	830	2.7 (0.1)	9.7	18	0	0	9 (9)	3
ZF21	4.8	12	3.6	710	5.3 (0.4)	10.0	197	19	35	10 (7)	41

Note. Average (±SD). SD for DOC is from sampling events, SD for slope is based on each grid cell of the digital elevation model. Z_{max} = maximum depth, $\overline{Z}$ = mean depth, Alt = Altitude in meters above sea level, Temp = Whole-lake mean temperature (Klaus et al., 2021), DR = Drainage ratio (catchment area/lake area).

et al., 2011). A range of commonly used vertical density gradient thresholds (0.01–0.1 kg m^{-3} per meter) was investigated with no marked effect on the thermocline depth estimates (Gray et al., 2020). Lake bathymetry was mapped using an echo-sounder with internal GPS (HDS-5 Gen2, Lowrance, Tulsa, OK, USA). Bathymetric data were used to determine the volume of epilimnion and hypolimnion separated by the thermocline.

All water chemistry samples were analyzed at the Biogeochemical Analytical Facility at Umeå University, Sweden. Dissolved nutrients were analyzed using a segmented flow analyzer (QuAAtro, SEAL Analytical GmbH, Norderstedt, Germany). Absorbance at 420 nm was measured with a spectrophotometer (V-560, JASCO Corporation, Tokyo, Japan), and the absorption coefficient (α420) was subsequently normalized to pathlength of a meter (m^{-1}) according to Hu et al. (2002). DOC was measured using a TOC/Nitrogen analyzer (Formacs HT-I TOC/TN, Skalar Analytical B.V., Breda, The Netherlands). DIC samples were analyzed within 1–2 weeks after sampling with a gas chromatograph (Clarus-500, Perkin Elmer Inc., Waltham, MA, USA) equipped with elite plot Q columns and measured using a flame injection detector.

2.3. CO_2 Accumulation in Winter and Evasion in Spring

In April 2017, approximately 1.5 months prior to ice-off, water was collected at three locations per lake from the shoreline to deepest point. The samples were taken at 0.5 m under ice and 0.5 m above the bottom with an additional sample exactly in between these at the deepest point. From these samples, we measured DOC, DIC, absorbance, and dissolved nutrients as described in Section 2.2.

The accumulation of CO_2 during winter and subsequent evasion following ice-off in spring was estimated by mass-balance of DIC (Karlsson et al., 2013; Striegl & Michmerhuizen, 1998). For each mass balance, epilimnion and hypolimnion DIC concentrations were depth-integrated over the respective volumes to calculate complete DIC inventories for each lake. Spring CO_2 evasion was calculated as the difference between DIC inventory before (in April) and after ice-off (in June).

$$F_{CO_2\_ice} = M_{DICJune} - M_{DICApril},$$

where $F_{CO_2\_ice}$ is the CO_2 flux at ice breakup in g C m^{-2}, $M_{DICJune}$ and $M_{DICApril}$ are the total inventories of DIC in the lake in June and April in g C m^{-2}. In June, six lakes had only either an epilimnion or hypolimnion DIC sample, and the missing samples were inferred by linear relationship ($r^2 = 0.86$) between epi- and hyplimnion samples from the other lakes, excluding ZF15, which had extremely high hypolimnion DIC. We estimated a maximum "theoretical net CO_2 buildup" underneath the ice from the difference in the DIC inventory of the lakes in September and the DIC inventory in April 2017 (as a substitute for under-ice DIC in 2018, for which we had no data), subtracting the flux measured between the DIC sampling in September and termination of CO_2-logging. Net CO_2 accumulation underneath the ice was calculated as

$$M_{CO_2\_Ice} = M_{DICApril} - M_{DICSept} - F_{CO_2\_Sept},$$

where $M_{CO_2\_Ice}$ is the theoretical net CO_2 buildup underneath the ice in g C m^{-2}, $M_{DICApril}$ and $M_{DICSept}$ are the total inventories of DIC in the lakes for April and September in g C m^{-2}, and $F_{CO_2\_Sept}$ is the CO_2 flux between the September DIC sampling and ice formation in g C m^{-2}. The under ice DIC of 2017 is thought to be a reasonable representation of 2018 based on earlier papers showing similar DIC accumulation underneath the ice between years for a number of arctic lakes (Karlsson et al., 2013; MacIntyre et al., 2018). Three lakes had negative winter CO_2 buildup, which we have limited to 0 as net CO_2-consumption underneath the ice is likely negligible with snow cover limiting light penetration underneath the ice (Song et al., 2019; Tulonen et al., 1994).

2.4. Open Water Season CO_2 Flux and NEP

On the first visit to the lakes after ice-off, a chamber for CO_2 measurements (further detailed below) and a line with O_2 and temperature loggers were placed at the deepest point of each lake. The "loggerlines" carried two O_2 loggers (miniDOT, Precision Measurement Engineering, Inc., Vista, California, USA), one at 0.5 m below the water surface and one between 0.7 and 7.2 m (4.2 m on average) from the lake bottom. Furthermore, the loggerlines all had 7–12 temperature loggers (Hobo TidbiT v2, ONSET Corporation, Bourne, MA, USA) at 0.5 m intervals for the three top loggers and 1–5 m intervals for the rest, depending on total lake depths. A cup anemometer (S-WSA-M003, ONSET Corporation, Bourne, MA, USA) was set up around 2 m above the ground on the shoreline of four of the lakes, measuring wind speeds at a 5-min interval. Additionally, at one lake in Skalstugan (ZF11) and one in Edsåsdalen (ZF20), we deployed a weather station collecting air temperature, wind speed and direction, PAR, relative humidity, and atmospheric pressure data every 5 min (HOBO U30-NRC, ONSET Corporation, Bourne, MA, USA). In total, six stations gathering wind data were deployed. Lakes without a wind station were associated to the nearest wind station and wind speed data were corrected for the variability in drag coefficient caused by a near-shore catchment vegetation height according to Klaus et al. (2021) as detailed in Text S2 in Supporting Information S1. The loggers and weather stations were collecting data from 14 to 25 days after ice-breakup until ice-formation in autumn for a total of 124–136 days between June and October.

We measured the hourly CO_2 concentrations of the surface water by recording CO_2 concentrations of the equilibrated air in a floating chamber equipped with a CO_2 logger (K33 ELG, Senseair AB, Delsbo, Sweden). The chamber was designed to withstand waves and winds and was equipped with a drying chamber to prevent water from reaching the CO_2 sensor (Figure S1 in Supporting Information S1). The equilibration chamber was 8 by 8 by 11 cm^3 for a total volume of 704 cm^3. On the lakes, the outer walls of the chambers reached about 1 cm below the water surface; thus, the effective volume that equilibrated with the water surface was ~640 cm^3. Each hour, 150 cm^3 of air was pumped (200-GAS-5V, Xavitech AB, Härnösand, Sweden) from the chamber during 30 s. The sampled air circulated through Nafion tubing (PermaPure LCC, Lakewood, NJ, USA) through a container with silica to exchange moisture, but not gas, before reaching the CO_2 sensor and looping back into the chamber. There was a small time lag (between 1 and 4 hr) in equilibration from pCO_2 in the water to the chamber but this did not affect the daily means. CO_2 exchange between lake and atmosphere (positive going from lake to atmosphere, and negative from atmosphere to lake) during the logging period was calculated from these daily mean surface CO_2 concentrations using Fick's first law of diffusion with a wind-based model to determine piston velocity, k (Cole & Caraco, 1998; Wanninkhof, 2014) (Supplementary Text S5). The chosen "k"-model has been used in many studies on lake CO_2 exchange and has previously been shown to perform similarly to other common k-models over global lakes (Klaus & Vachon, 2020). We compared the chosen model against fluxes calculated from k-models by Crusius and Wanninkhof (2003) and Vachon and Prairie (2013). The model by Cole and Caraco (1998) yielded intermediate CO_2 fluxes and was therefore opted as least likely to either over- or underestimate the actual CO_2

fluxes in the lakes. The estimated annual source contribution was very robust, regardless of which "k"-model was used (being 2% lower and 1% higher using Vachon's and Crusius' models, respectively).

We estimated whole-lake NEP using the free-water diel oxygen technique (Staehr et al., 2010). This method assumes that the daily fluctuation in dissolved oxygen (DO) concentrations is a function of GPP, ER, and air-water O_2 flux (Text S4 in Supporting Information S1). Briefly, we defined NEP as GPP-ER, where GPP and ER are functions of incoming light and water temperature, respectively. We computed NEP for each day and DO logger and then integrated these daily depth-specific estimates over the whole sampling season and lake volume. Because of stratification effects, in-lake production of CO_2 does not necessarily lead to evasion immediately. This likely has negligible impact on our results as we evaluated internal CO_2 production and CO_2 fluxes over longer periods (i.e., the full open water season and/or the entire year), assuming that all net internal CO_2 production was exchanged with the atmosphere due to water column mixing by the end of these periods.

2.5. Calculation of Source Contribution to CO_2 Evasion

External contribution to CO_2 evasion was calculated from the difference between CO_2 evaded and CO_2 produced in the lakes, assuming that any evasion in surplus of internal production was supplied by external CO_2 sources, following use in Martinsen et al. (2019), Wilkinson et al. (2016).

$$CO_{2\_ext} = F_{CO_2} - CO_{2\_int}$$

where F_{CO_2} is the CO_2 evaded annually (open water flux + spring evasion), CO_{2_int} is the internal net CO_2 production (open water CO_2 production + under-ice accumulation), and CO_{2_ext} is the external contribution to the evaded CO_2. Internal net CO_2 production was taken to be equal to negative NEP, assuming a 1:1 molar ratio of O_2:CO_2. Photochemical production of CO_2 is incorporated in the net CO_2 production estimates (and thus internal source) as we could not distinguish between metabolic or photo-oxidative CO_2-production, but it is likely only a minor part given that estimates from similar lakes suggest it to be around 3% of the CO_2 produced during the open water season (Allesson et al., 2021). No calcite precipitation was taken into account, motivated by the low pH of the lakes (Table S1 in Supporting Information S1). We assume under-ice DIC accumulation to be primarily of internal origin as has been shown for a similar high-latitude lake (Karlsson et al., 2008). External inputs prior to or during ice-melt could have elevated DIC of our samplings in April and/or June by delivering CO_2 to lakes (Denfeld et al., 2018). However, we regard this to be minor in our systems since DIC export in streams in Swedish mountains has been found to peak close to the time of our under ice sampling and be back to relatively low levels at the time of ice off in the lakes (Giesler et al., 2014). Any DIC input in between these sampling occasions would have led to an overestimation of internal source contribution during winter. As exact source contribution of the winter buildup and subsequent flux is not known to us, we provide estimates for two hypothethical scenarios to give a range of uncertainty; one using the assumption that all under-ice CO_2 was internally produced (hereafter "full estimate"), and another assuming that 50% of under-ice CO_2 was internally produced (hereafter "conservative estimate"). Note that external contribution in winter is present even in the full estimate (Figure S7 in Supporting Information S1) as the evasion following ice breakup exceeded the theoretical under-ice production for several lakes. The tables and figures for the conservative estimate are in the supplemental material (Figure S3 and Table S3 in Supporting Information S1).

2.6. Further Computations and Statistical Analysis

Catchment delineations were made from a 2-m digital elevation model (Lantmäteriet, 2016) using Whitebox GAT (Lindsay, 2016), allowing to burn channels through road culverts, as outlined in Lidberg et al. (2017). Catchment forest and mire cover were calculated by overlaying vegetation maps (Lantmäteriet, 2012) to the catchment areas. Statistical analyses were performed using the program "*R*," version 4.0.3 (R Core Development Team, 2020). Given the non-normality of several variables in our data set, together with the potential effect of outliers, we opted using a rank-based estimate. Therefore, Spearman rank correlation tests were conducted to test the effect of lake DOC concentration, drainage ratio, degree of forest, and degree of mire in the catchments to both open water season and annual internal CO_2 production and flux, annual external contribution, and the ratio of annual internal CO_2 production:flux. We tested the effect of outliers (observations with Cook's distance >4/14 as there were 14 lakes), but these had very little influence on the rank-based correlations as specified in the correlation tables.

All correlation tests were run, and corrected for multiple tests according to the Holm-Bonferroni correction (Ludbrook, 1998) using the "*psych*" package, written by Revelle (2021). Data plots were made using the graphical package "*ggplot2*" (Wickham, 2016). In addition, we performed the Principal component analysis (PCA) using the "*stats*" package (R Core Development Team, 2020) and visualized the correlations between predictor variables in a biplot using the "*factoextra*" package (Kassambara & Mundt, 2020).

3. Results

3.1. General Characteristics of the Lakes

All studied lakes were oligotrophic with TN concentrations of 106–199 (mean 163) μg L^{-1} and TP of 3.7–5.3 (mean 4.4) μg L^{-1}. K_d ranged from 0.4 m^{-1} to 1.5 (mean 0.93) m^{-1}, which is a similar range to the 703 high-latitude Swedish lakes reported in Seekell et al. (2015). The DOC concentrations ranged from 2.0 to 7.5 (mean 5.0) mg L^{-1} (Table 1) and were strongly correlated with K_d and absorbance at 420 nm (Table S2 in Supporting Information S1), indicating that the DOC is mainly colored humic carbon of terrestrial origin (Forsström et al., 2015). Whole-lake DIC concentration was between 1.9 and 5.5 (mean 3.1) mg L^{-1} and 3.2–11.6 (mean 5.1) mg L^{-1} during open water season and late winter, respectively (Table S1 in Supporting Information S1).

3.2. Open Water Season CO_2 Flux and Metabolism

The CO_2 flux during the open water season as determined through the floating chamber pCO_2 loggers, ranged between −3 and 10 g C m^{-2} over the season across lakes (Table 2). An additional 0.2–16 g C m^{-2} was exchanged at ice-breakup. There were noticeable differences in CO_2 flux and net internal CO_2 production between lakes; in some lakes, the production and flux were similar during (a part of) the measuring period (illustrated by ZF08, Figure 2; Table 2). Other lakes had low or even negative internal net production, yet were evading CO_2 during all seasons (illustrated by ZF12, Figure 2; Table 2). Yet others had very high variability in production, but relatively constant flux (illustrated by ZF19, Figure 2).

Table 2
Annual and Seasonal CO_2 Flux and Internal Net CO_2 Production

Seasonal					Annual				
	Open water		Winter and spring			Full estimate		Conservative estimate	
Lake	Air-water flux	Internal net production	Ice breakup flux	Under-ice internal net production	Air-water flux	Internal net production	Internal production:flux	Internal net production	Internal production:flux
ZF08	6.0	5.6	1.4	0.0	7.4	5.6	0.8	5.6	0.8
ZF09	5.2	1.7	9.0	8.8	14.2	10.5	0.7	6.1	0.4
ZF10	−0.7	16.8	1.7	4.3	1.0	21.1	1.0	18.9	1.0
ZF11	6.1	1.0	12.4	1.9	18.5	2.9	0.2	2.0	0.1
ZF12	9.2	−0.6	6.0	2.4	15.2	1.8	0.1	0.6	0.0
ZF13	9.1	3.6	15.8	16.3	25.0	20.0	0.8	11.8	0.5
ZF14	7.1	−0.5	1.3	1.0	8.4	0.5	0.1	0.0	0.0
ZF15	10.3	3.7	0.2	1.2	10.5	4.9	0.5	4.3	0.4
ZF16	6.7	4.3	4.4	1.4	11.1	5.6	0.5	5.0	0.4
ZF17	1.1	−3.9	3.2	3.5	4.3	−0.4	0.0	−2.2	0.0
ZF18	1.0	2.7	1.0	4.3	1.9	7.0	1.0	4.9	1.0
ZF19	−1.2	−3.5	6.2	0.0	5.0	−3.5	0.0	−3.5	0.0
ZF20	−3.0	−5.8	5.5	0.0	2.5	−5.8	0.0	−5.8	0.0
ZF21	6.1	5.7	14.6	6.4	20.7	12.1	0.6	8.9	0.4

Note. All measures are in units of g C m^{-2} per time period. Two estimates for under-ice CO_2 production are used, yielding a full (100% under-ice CO_2 production was of internal origin) and conservative (50% of under-ice CO_2 production was of internal origin) estimate for annual metabolic CO_2 production. Ratios of internal CO_2 production:CO_2 flux have been limited between 0 and 1 as below or above this value internal CO_2 production does not contribute to the CO_2 evaded.

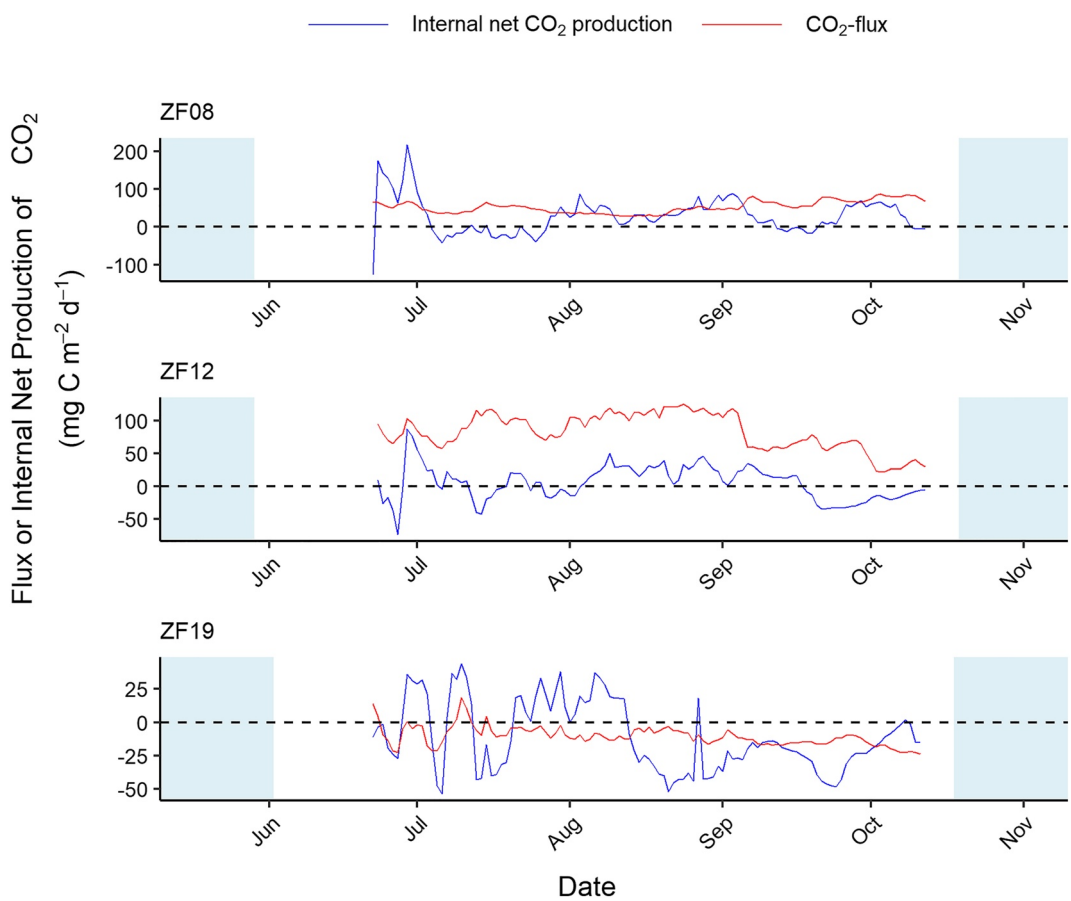

Figure 2. Daily mean open water lake-atmosphere CO_2 flux and 14-day running mean internal net CO_2 production (taking into account only estimates with acceptable daily uncertainty, Text S4 in Supporting Information S1) for selected lakes. Note that the scale of the vertical axis is different for each graph. Blue polygons denote ice-cover periods. The dashed lines denote 0 and data above this line equal CO_2 flux to the atmosphere or that CO_2 is being produced (negative NEP) in the lake, respectively. Data below this line equal CO_2 uptake from the atmosphere, or that the lake is net consumer of CO_2 (positive NEP). Note that even if internal net CO_2 production would be the only source for the CO_2 flux, they would not necessarily show a close day-by-day coupling. Stratification can trap CO_2 in the hypolimnion, which will be evaded following lake mixing.

Whole-lake internal net CO_2 production (negative NEP) estimated from the O_2 loggers was −6 to 17 g C m^{-2} (Figure 3; Table 2). Some lakes thus had internal CO_2 consumption (positive NEP) during the open water season, which may cause CO_2 influx from the atmosphere. However, when external inputs cause CO_2 supersaturation to the surface mixed layer (i.e., the homogenous layer of water i.e., subject to exchange with the atmosphere), outgassing can be sustained even in periods of negative internal CO_2 production (e.g., lake ZF08 and ZF12). Although most lakes were net producers that evaded CO_2, there were three lakes that evaded CO_2 despite having positive NEP and thus internal net CO_2 consumption, which thus required external contribution to sustain CO_2 evasion. We estimated internal net CO_2 production in winter to be 0–16 g C m^{-2} (0–8 for the conservative estimate).

3.3. Annual CO_2 Evasion and Metabolism

All lakes evaded CO_2 on an annual basis, ranging from 1 to 25 g C m^{-2} yr^{-1} (Table 2). Although the lakes evaded CO_2, not all of them were net producers of CO_2. Annual internal net CO_2 production was estimated between −6 and 21 or −6 and 19 g C m^{-2} yr^{-1} (assuming 100% or 50% of under-ice CO_2 was sourced by internal net production, respectively. Table 2, Figure S3 in Supporting Information S1). Annual CO_2 evasion exceeded internal net CO_2 production in 12 lakes (Figure 3) and the external CO_2 contribution needed to sustain the CO_2 evasion in these systems was between 0 and 16 g C m^{-2} yr^{-1} (full estimate) and 0–17 g C m^{-2} yr^{-1} (conservative estimate).

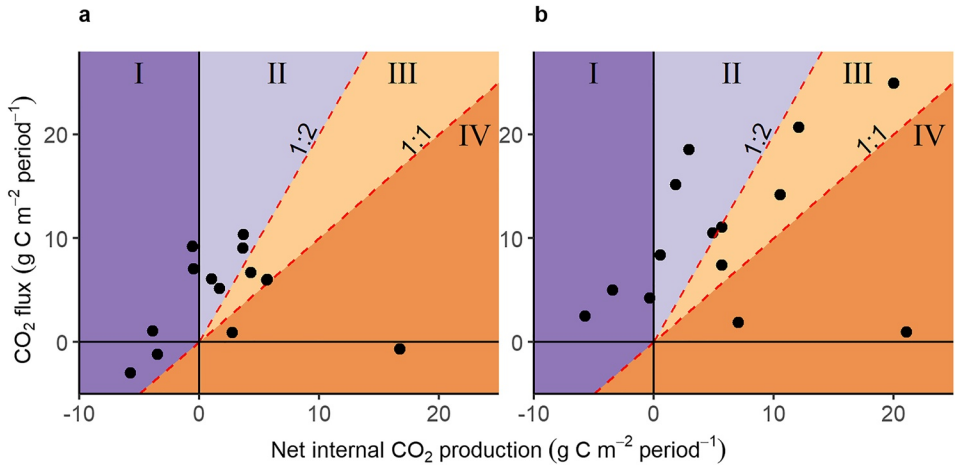

Figure 3. (a) Open water and (b) annual CO_2 flux plotted against internal net CO_2 production in the lakes. Sections separate ratios of internal:evaded CO_2 as follows: I. External CO_2 inputs exceed internal CO_2 losses (positive NEP) II. External CO_2 contribution dominant. III. Internal CO_2 production dominant. IV. Internal CO_2 production not fully evaded.

3.4. Source Contribution to Lake Evasion

The main source of evaded CO_2 varied across lakes and seasons (Figure 3). The source of the open water flux was mainly external for nine lakes, and internal for the other five lakes (Sections I and II, and III and IV in Figure 3, respectively). Five of the lakes with a dominant external source had negative internal CO_2 production (positive NEP, Section 1 in Figure 3). Three of these evaded CO_2 regardless of implying that external CO_2 inputs exceeded the total CO_2 evasion. Two lakes had higher internal CO_2 production than the total CO_2 evaded (Section IV in Figure 3), indicating not all of the CO_2 produced left the lake through evasion. On an annual scale, internal CO_2 production was between 0% and 2,080% (interquartile range 5–77%, median 49%) of CO_2 evaded and half of the lakes had >50% of evaded CO_2 produced by internal sources (Section III and IV in Figure 3). The dominant source changed over time for two lakes from mainly externally sourced during the open water season to mainly internally sourced annually. The conservative estimate gave similarly variable internal CO_2 production relative to evasion (0%–1,868%, interquartile 0–54%, median 42%), but two lakes shifted from mainly internal to mainly external source contribution (Figure S3 in Supporting Information S1).

The open water season flux was positively correlated with DOC, drainage ratio, and mire cover, while the annual flux was only positively correlated with DOC (to drainage ratio after removing an outlier; Table 3, Figures S4,

Table 3
Correlations of Flux, the Full Estimate of Net Internal Production of CO_2, and the CO_2 Contributed Externally to Lake or Catchment Properties

	DOC		DR		Forest cover		Mire cover	
	rho	*p*	*rho*	*p*	*rho*	*p*	*rho*	*p*
Open water flux	**0.85**	**0.00**	**0.81**	**0.01**	0.19	1.00	**0.79**	**0.02**
Open water internal net production	0.19	1.00	−0.06	1.00	**0.78**	**0.02**	0.07	1.00
Annual evasion	**0.80**	**0.01**	*0.71*	*0.07*	−0.02	1.00	0.66	0.15
Annual internal net production	0.22	1.00	−0.06	1.00	**0.76**	**0.03**	0.15	1.00
Annual external contribution	0.35	1.00	0.61	0.29	−0.67	0.13	0.38	1.00
Annual internal net production:evasion	0.06	1.00	−0.21	1.00	**0.91**	**0.00**	0.02	1.00

Note. Spearman rho coefficients. $n = 14$. Holm-Bonferroni adjusted for multiple tests. Bolded and italic values indicate $p < 0.05$ and $0.05 < p < 0.10$, respectively. When removing an outlier for annual CO_2 evasion to DR, rho went from 0.71 to 0.8, and p from 0.07 to 0.02. When removing two outliers of Forest cover against annual internal CO_2 production rho went from 0.76 to 0.82, p remained 0.03. When removing two outliers of Forest cover against the ratio of internal CO_2:flux, rho remained 0.91, and p remained <0.00.

S5a and S5b in Supporting Information S1). Internal net CO_2 production was positively correlated with forest cover in the catchment during the open water season and annually (Table 3, Figure S4c, Table S3, and Figure S5c in Supporting Information S1 for full and conservative estimates, respectively). The ratio between annual internal net CO_2 production and CO_2 evasion also increased significantly with increasing forest cover (two outliers did not affect interpretation; Table 3, Figure S4d, Table S3, and Figure S5d in Supporting Information S1). PCA revealed that predictor variables were not strongly correlated with each other, and no specific lake clustering was obvious from the resulting biplot (Figure S5 and Table S2 in Supporting Information S1).

4. Discussion

4.1. Lake CO_2 Evasion and Source Contribution

Our study is among the first to couple estimates of lake CO_2 flux with NEP at the annual scale. Most previous studies used snapshot data of pCO_2 and k, whereas our study provides high-resolution estimates and thereby shows the importance of temporal variability in flux and net CO_2 production to annual evasion. The ice-breakup CO_2 flux constituted, on average, 58% of the annual evasion in less than 16% of the total duration of the open water season, highlighting the importance of such hot moments to annual CO_2 flux. The average annual CO_2 flux of 10 g C m^{-2} yr^{-1} was similar to the average of 8 and 13 g C m^{-2} yr^{-1} from other arctic lakes (Jansson et al., 2008; Karlsson et al., 2013, respectively) but low compared to the average flux of 40 g C m^{-2} yr^{-1} from a study on boreal lakes (Vachon, Solomon, & delGiorgio, 2017). On the other hand, net CO_2 production of the studied lakes was lower in comparison to arctic (on average 13% of Ask et al., 2009 and Karlsson et al., 2008, based on DIC changes) and boreal (on average 45% of Vachon, Solomon, & delGiorgio, 2017, based on free water diel O_2 changes) lakes. The results of our study complement a small number of publications on source contribution of CO_2 evasion and are within the range of these publications. Specifically, estimates fall between previous results from boreal and arctic lakes (medians 26%, 68%, 94%, and 100% of CO_2 were sourced internally in Vachon, Solomon, and delGiorgio (2017), Karlsson et al. (2010), McDonald et al. (2013), and Jansson et al. (2008), respectively).

4.2. Seasonal Versus Annual Source Contribution

We found under-ice CO_2 accumulation was important at the annual-scale, exceeding open water CO_2 production in nine (seven for the conservative estimate) of the 14 lakes. Winter CO_2 production (100 or 50% of the winter CO_2 accumulation) was therefore an important component of the annual CO_2 production in both our full and conservative estimates (60% and 49% on average, respectively). Annually, this is close to the ice-cover duration of ~64% of the full year, indicating that under-ice CO_2-production rates are almost equal to those during the open water season. This means that the period of ice cover contributes considerably to yearly net CO_2 production, and in turn, to CO_2 evasion (at ice breakup). Internal CO_2 production in winter could be stimulated by DOC that originates from soil layers below frozen top soils and may be mobilized and enter lakes during winter melt events (Denfeld et al., 2018). Even if input of terrestrial organic carbon is low in winter it has been shown that respiration rates and negative NEP can be sustained by respiration of organic carbon present in sediments or the water column (Biddanda & Cotner, 2002; Karlsson et al., 2013). Furthermore, light limitation under ice in winter will constrain GPP and promote negative NEP (Song et al., 2019; Tulonen et al., 1994). The lakes had between 229 and 241 days of ice cover (Supplemental Text S6), and snow covers the ground for 175–200 days of the year (SMHI, 2017). For these relatively small, sheltered lakes, snow covering the ice is thus expected for most of the ice-cover periods. Specifically, the duration between onset of ice-cover and snow cover over the lakes after logger pickup was at most <2 weeks (Text S6 in Supporting Information S1). Any in situ produced organic carbon during this period would presumably be largely mineralized during the winter and thus have none to low net effect on the CO_2 accumulation under ice. The external source contribution may also play a role in winter, but may be less pronounced. The linear relationship between annual DIC load and flow reported for subarctic streams in Sweden (Giesler et al., 2014) implies that even with high DIC concentrations in incoming water, the total DIC input is relatively low due to low flow rates in winter. Aside from the limited shallow external inputs, there are also diminished deep external inputs due to dropping groundwater tables in winter (Okkonen & Kløve, 2010). While the internal source contribution can thus be sustained during winter, external inputs will be limited, and internal CO_2 production is likely largely driving winter CO_2 buildup.

Irrespective of the importance of winter for annual CO_2 production, it did not appear to significantly alter the dominant source supporting CO_2 evasion. The dominant source of CO_2 evasion can shift from the open water season to the annual scale, but did so for only two lakes in each scenario (in opposite directions, four lakes in total had a different dominant source between the two scenarios). The internal source supplied, on average, 44% (36% in the conservative estimate) of the annual CO_2 evasion although the variability among lakes was high with 10 lakes having over 75% supported through a single source (four internal, six external; or 9 lakes, three internal, six internal in the conservative estimate). Typically, either internal or external sources contribute a significant part of the annual CO_2 evasion for these lakes, and winter CO_2 production, although a significant part of annual CO_2, seldom shifts the dominant source from open water to annual periods.

4.3. Catchment Controls on Source Contribution

The internal net CO_2 production (excluding winter) was correlated with forest cover but not to DOC concentration of the lake water. One reason for lack of clear decrease in NEP with DOC is that the DOC in the lakes may have been largely processed already and therefore might not adequately reflect the quantity and quality of DOC entering the lake (Vachon, Prairie, et al., 2017; Wickland et al., 2007). Besides, the relatively low values and a small range of DOC and K_d in the studied lakes suggest not only difficulty to find clear patterns, but also that GPP was nutrient rather than light limited (Seekell et al., 2015). Given the strong correlation between nutrients (TN, TP) and DOC in the lakes (Table S2 in Supporting Information S1), both R and GPP likely increase at similar rates with DOC and result in no clear change in NEP. CO_2 evasion was however still found to correlate with DOC. Possibly DOC concentrations also reflect the degree of catchment input (correlation coefficient of 0.75, Table S2 in Supporting Information S1) and increases in DOC can therefore reflect increases in both internal as well as external CO_2 sources in the lakes. Thus, CO_2 evasion may increase with DOC (due to concomitant DIC) even when internal CO_2 production does not.

The observed relationship between internal CO_2 production and forest cover is in line with another study that included these and other lakes, where correlations between forest metrics and DOC as well as hypolimnetic O_2 consumption were found (Klaus et al., 2021). This supports the argument that the degree of forest cover in the catchment may effectively describe potential input of bioavailable chemical species (both nutrients and DOC), leading to CO_2 production in the lakes (Berggren et al., 2007; Kammer et al., 2009). In addition, we found that the ratio of internal CO_2 production relative to evasion was correlated with forest cover (Tables 3/S3 in Supporting Information S1). These results are also in line with a national survey of Danish lakes, where high O_2 drawdown and CO_2 evasion were found for especially small forested lakes (Martinsen et al., 2019). Although our study cannot fully reveal the underlying mechanisms controlling the magnitude and source contribution for lake CO_2 evasion, it does highlight that the carbon supply and sources of CO_2 evasion from lakes may change resulting from projected changes in forest cover (Harsch et al., 2009; Moen et al., 2004).

4.4. Concluding Remarks

In our comparative analysis of 14 high-latitude mountain lakes, we found that CO_2 evasion was largely (over 75%) supplied from a single source and thus, the lakes functioned mainly as either "chimneys" or "reactors" in the landscape carbon cycle. This implies there is not one single explanation for CO_2 emissions and that various changes on land (e.g., changes in forest cover) and in climate (e.g., hydrology) may affect various lakes differently. Furthermore, while the ice-covered season is relatively unstudied compared to the open water season, our data underline the importance of the winter season for lake carbon processing and CO_2 evasion. The contribution of winter (the ice breakup flux) to CO_2 evasion was significant and turned lakes to sources of CO_2 in the landscape. Overall, our study stresses the large variability in sources and magnitude of CO_2 evasion between lakes as these are strongly influenced by local catchment characteristics. Therefore, the effects of environmental changes to the magnitude and source contribution to CO_2 evasion from lakes are unlikely to be uniform.

Conflict of Interest

The authors declare no conflicts of interest relevant to this study.

Data Availability Statement

Data on CO_2 fluxes, internal CO_2 production, and lake characteristics used in this study are publicly available at https://zenodo.org/record/6405931. Formatting and layout of the graphs were aided by "*ggpubr*" (Kassambara, 2020).

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