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Carbon dioxide fluxes increase from day to night across European streams

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Globally, inland waters emit over 2 Pg of carbon per year as carbon dioxide, of which the majority originates from streams and rivers. Despite the global significance of fluvial carbon dioxide emissions, little is known about their diel dynamics. Here we present a large-scale assessment of day- and night-time carbon dioxide fluxes at the water-air interface across 34 European streams. We directly measured fluxes four times between October 2016 and July 2017 using drifting chambers. Median fluxes are 1.4 and 2.1 mmol m^{-2} h^{-1} at midday and midnight, respectively, with night fluxes exceeding those during the day by 39%. We attribute diel carbon dioxide flux variability mainly to changes in the water partial pressure of carbon dioxide. However, no consistent drivers could be identified across sites. Our findings highlight widespread day-night changes in fluvial carbon dioxide fluxes and suggest that the time of day greatly influences measured carbon dioxide fluxes across European streams.

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Inland waters are important sources of atmospheric carbon dioxide (CO_2) partially offsetting the terrestrial carbon sink[1,2]. Streams and rivers therein represent major CO_2 emitters[3]. Fluvial CO_2 fluxes are primarily controlled by the gas exchange velocity at the water-air interface (k) and the gradient between the water and atmospheric partial pressures of CO_2 (pCO_2)[4]. Both parameters are highly variable in space and time[5,6], causing uncertainty in the magnitude of regional and global fluvial CO_2 emissions[2].

The high spatiotemporal variability of k and water pCO_2 can be attributed to a complex interplay of underlying controls. While k in streams is mostly driven by water turbulence created by variations in flow and stream morphology[7], the water pCO_2 is influenced by the degree of hydrological connectivity between the stream and the adjacent riparian soils[8] as well as by in-stream processes (e.g., stream metabolism). The supply of CO_2 from external sources, such as soil water or groundwater, into streams, varies with reach and season[5,9]. Furthermore, seasonal and diel changes in stream pCO_2 are attributed to stream metabolism driven by temperature and solar radiation[10–13]. Ecosystem respiration, a source of CO_2 in the stream, takes place throughout the whole day, and gross primary production, a sink of CO_2, occurs only during daylight. Temperature and solar radiation also directly influence water pCO_2, the former by changing the solubility of the gas and the latter due to photomineralization[14]. However, questions remain regarding the magnitude and relative drivers of seasonal and diel fluctuations of CO_2 fluxes in streams.

Presently, most fluvial CO_2 emission values are derived from k estimates based on water velocity and stream channel slope and on water pCO_2 values indirectly calculated from alkalinity, pH, and temperature[3]. This approach fails to capture the high spatiotemporal variability observed for k and pCO_2 and therefore can provide imprecise estimates of CO_2 fluxes[15,16]. Direct field observations provide the means to improve estimates and understanding of the drivers behind spatiotemporal variability, and thus the dynamics of CO_2 outgassing from running waters. However, besides mostly local studies that indirectly infer CO_2 fluxes from pCO_2 and k[11,12,17,18], no direct measurements exist that compare day-time and night-time CO_2 fluxes from streams on a larger spatial scale.

The aim of this study was to assess the magnitude and drivers of stream CO_2 flux variations between day and night across European streams. We hypothesized that CO_2 fluxes would differ between day and night due to diel variations in terrestrial inorganic carbon inputs, in situ metabolism, and temperature. As higher temperatures and solar radiation may drive differences in pCO_2, we expected a higher difference between day-time and night-time fluxes with warmer temperatures and at lower latitudes. Hence, we measured day-time and night-time fluxes of CO_2 at four different periods throughout one year from 34 streams (Strahler stream orders from 1 to 6) in 11 countries across Europe following a standardized procedure. CO_2 fluxes were measured starting at midday (11 a.m. Greenwich Mean Time (GMT)) and midnight (11 p.m. GMT) with drifting flux chambers equipped with CO_2 sensors as described in Bastviken et al.[19]. In the majority of the European streams, we found increased CO_2 fluxes at the water–air interface in the night compared to the day with a median increase of 0.5 mmol m^{-2} h^{-1}. Most of the observed CO_2 flux variability was explained by changes in pCO_2 from day to night with more pronounced changes at lower latitudes.

Results and discussion

Magnitude of CO_2 flux variation from day to night. Midday CO_2 fluxes at the water–air interface ranged from −2.7 (uptake) to 19.9 mmol m^{-2} h^{-1} (emission) (1.4 [0.5, 3.1]; median [interquartile range (IQR)]; $n = 107$) and midnight fluxes ranged from −0.3 to 25.6 mmol m^{-2} h^{-1} (2.1 [0.9, 3.7]; $n = 107$) (Fig. 1a; Supplementary Table S3). Our measured fluxes are comparable to other studies conducted in temperate and boreal streams that used chambers[20,21] or empirical models[12,22,23], although they were in the lower range of the numbers modeled in a study in the USA[23] (Supplementary Fig. S2). The lower numbers might be due to the lack of tributary inflows, large woody debris, and strong hydraulic jumps in the selected stream sections (Supplementary Sampling manual).

To assess stream CO_2 flux variations between day and night, we computed the difference of night-time minus day-time fluxes for each stream and sampling period, where positive numbers indicate an increase from day to night and vice versa (Fig. 1b). Differences in CO_2 fluxes amounted to 0.5 mmol m^{-2} h^{-1} [0.1, 1.4] ($n = 107$) across all sites and sampling periods, which is equivalent to a relative increase of 39% [4%, 100%] ($n = 101$; n reduced due to exclusion of relative comparisons to zero flux at day-time) (Fig. 2). Altogether, these results point towards a high relevance of night-time CO_2 fluxes as reported earlier for single pre-alpine streams[12], stream networks[13,17] or rivers[18], and in a recent compilation of diel CO_2 data from 66 streams worldwide[24]. A rough annual extrapolation of fluxes from our study sites (Supplementary Methods) shows that the inclusion of night-time fluxes increases annual estimates of site-specific stream CO_2 emissions by 16% [6%; 25%] (Supplementary Table S4). Hence, our measurements and the simplified extrapolation of our data emphasize the need to collect and integrate night-time CO_2 flux data into sampling protocols as well as regional upscaling efforts.

Looking into the individual comparisons, we found 83 increases in median CO_2 fluxes from day to night with seven comparisons where the stream even switched from a sink to a source of CO_2 to the atmosphere (Supplementary Table S3). However, we also found four comparisons where median CO_2 fluxes at day and night were the same and 20 decreases in the night (Supplementary Table S3). These results and also other studies[13,25,26] suggest that the direction and strength of diel pCO_2 pattern can be largely variable across space and time.

Diel CO_2 flux differences vary as a function of latitude and water temperature. The diel differences in CO_2 fluxes were significantly negatively related to latitude (Table 1A), with substantial diel variation more likely at lower latitudes. Likewise, the interaction with latitude and the water temperature was significant (Table 1A), which might be explained by higher temperatures at lower latitudes during the sampling periods and higher solar radiation boosting in-stream primary production[27]. This dataset is derived from only 34 streams distributed across different climate zones in Europe. However, to our knowledge, it is currently the largest study of its kind, using flux chambers to measure CO_2 fluxes, and compare those fluxes at day-time and night-time on such a spatial scale.

We found no significant differences in the magnitude of diel differences in CO_2 fluxes related to water temperature (Table 1A) using a linear mixed-effect model (LME). However, comparing the CO_2 fluxes at midday to midnight at the different sampling periods, we detected significant diel changes in CO_2 fluxes in October, January, and April (Fig. 1a). Contrary to our expectation that higher differences can be expected at higher temperatures, we did not detect significant changes from day to night in July (Fig. 1a), during which period the lowest changes in absolute numbers were recorded (0.3 mmol m^{-2} h^{-1}; Fig. 1b). The highest differences of CO_2 fluxes from day to night were measured during April (1.1 mmol m^{-2} h^{-1}), followed by January (0.5 mmol m^{-2} h^{-1})

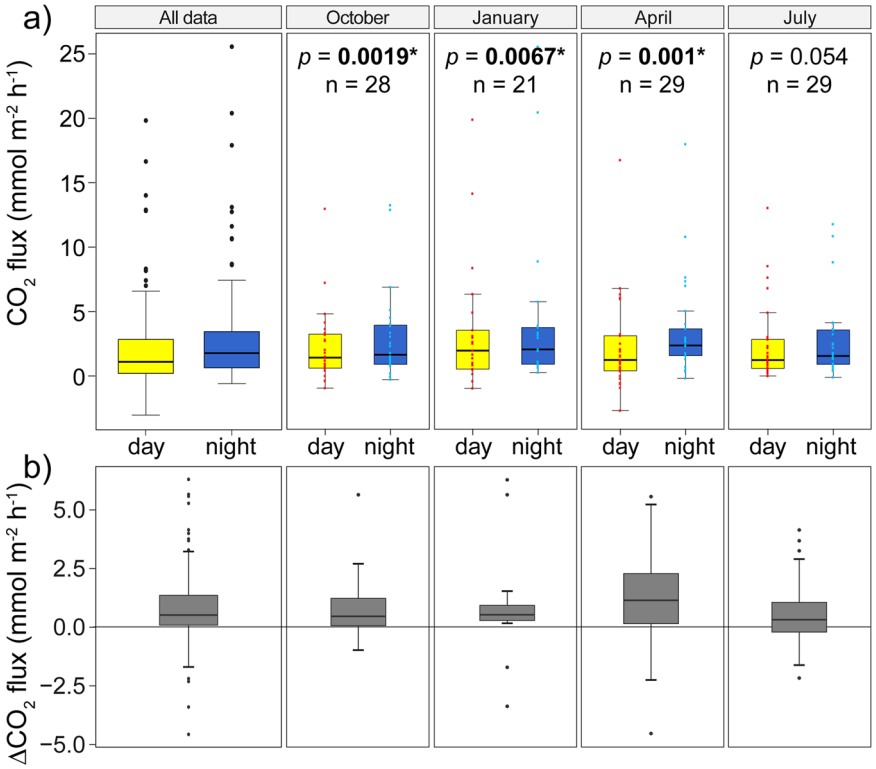

Fig. 1 Day-to-night changes of CO_2 fluxes at the water–air interface of the sampled European streams. Stream CO_2 fluxes (in mmol CO_2 m^{-2} h^{-1}) at day-time (yellow) and night-time (blue) (**a**) and the calculated changes from night minus day (ΔCO_2 flux) (**b**) for all data and separately for each sampling period. In the sampling periods comparisons in (**a**), CO_2 fluxes for individual stream sites are indicated by red (day) and light blue (night) dots. The boxplots visualize the median of all stream sites (line), the first and third quartiles (hinges), the 1.5*inter-quartile ranges (whiskers), and the outliers outside the range of 1.5*inter-quartile ranges (black dots). On top of (**a**) are *p* values retrieved from paired comparisons of median CO_2 fluxes tested by Wilcoxon signed-rank tests and the sample size (*n*). Significant *p* values with $p < 0.05$ are in bold with an asterisk. The differences in the CO_2 fluxes (**b**) in mmol CO_2 m^{-2} h^{-1} from day to night are for October: 0.5 [0.1, 1.2]; January: 0.5 [0.3, 0.9]; April: 1.1 [0.1, 2.3]; July: 0.3 [−0.2, 1.1] (median [IQR]).

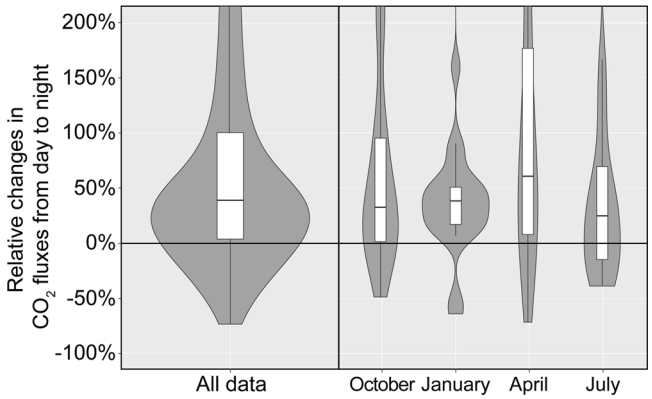

Fig. 2 Relative changes in CO_2 fluxes from day to night for all data together and for each sampling period. A positive value indicates an increase in CO_2 fluxes during the night and vice versa (expressed as a %-change of the daytime values). Outliers (>1.5*IQR) were excluded for illustration purposes as the large relative variation in these fluxes was due to minor absolute variation in fluxes close to zero. The median relative changes were positive throughout all sampling periods, ranging from 32% [0.6%, 95%] in October, 38% [16%, 50%] in January, 60% [7%, 177%] in April, to 24% [−16%, 69%] in July (median [IQR]; $n = 26$, 21, 28, and 26, respectively).

and October (0.5 mmol m^{-2} h^{-1}). Lower day-night changes in July could be explained by increased riparian shading reducing photosynthesis[28,29]. For example, reduced in-stream photosynthesis in summer compared to spring has been shown for a subalpine stream network[29] or a temperate forested headwater stream[28]. However, comparing the canopy cover of the streams and the differences in CO_2 fluxes from day to night (Supplementary Fig. S3h) revealed no clear pattern. A probable alternate explanation is that CO_2 production via photomineralization during the day counteracted a decrease via CO_2 fixation by photosynthesis[30] and diminished diel pCO_2 and ultimately CO_2 flux changes. This highlights the complex interplay between different light-dependent processes in streams influencing pCO_2 on a diel scale.

The importance of year-round measurements is highlighted by the January data set containing the second-highest diel CO_2 flux changes. European ice-free streams may be perceived "dormant" during these periods and representative CO_2 flux estimates are thus often missing[3]. Our January data showed a magnitude of flux compared to the rest of the year across the European streams as well as high diel variability in CO_2 fluxes (Fig. 1). This may be attributed in part to the latitudinal coverage of our study as we included streams from the boreal to the Mediterranean. For example, the water temperatures of the Spanish streams were still relatively high in winter with around 2.8–9.5 °C during the day whereas Swedish streams showed these temperatures in October and April. A study in the coterminous US looking into stream pCO_2 variability also reports varying strengths of diel pCO_2 variability, dependent on the investigated stream and time[25]. Hence, diel pCO_2 and CO_2 flux variability can be large in streams of the northern hemisphere, stressing the need to unravel the site-specific drivers of and mechanisms behind these diel changes.

Table 1 Results of the linear mixed-effect models (LME).

Response variable	Fixed effect	χ^2 (1)	*p*	Sign
(A) *Testing spatial and temporal hypotheses*				
CO_2 flux difference from day to night	Latitude	7.4207	**0.006**	–
	Water temperature (day)	0.0168	0.897	
	Water temperature (day)*latitude	4.9594	**0.026**	+
(B) *Testing physical and biogeochemical drivers of CO_2 flux changes*				
CO_2 flux difference from day to night	Δ Water pCO_2	4.9497	**0.026**	+
	Δ Gas transfer velocity *k*	0.5613	0.454	
(C) *Testing biogeochemical drivers of pCO_2 changes*				
pCO_2 difference from day to night	Δ Water O_2 concentration	7.9879	**0.005**	–
	ΔpH	0.0345	0.853	
	Δ Conductivity	0.0293	0.864	
	$\Delta T_w - T_a$ [a] (proxy for heat flux)	1.6720	0.196	
	ΔWater temperature	0.8731	0.350	
(D) *Testing catchment and hydromorphological drivers of pCO_2 changes*				
pCO_2 difference from day to night	Day length	1.7244	0.189	
	Stream wetted width	0.3748	0.540	
	Discharge	3.4458	0.063	
	% forest	0.0950	0.758	
	Catchment area	2.3656	0.124	

[a]Heat flux calculated as water temperature (T_w) minus air temperature (T_a).
(A) Marginal $R^2 = 0.12$, conditional $R^2 = 0.18$, sample size = 107.
(B) Marginal $R^2 = 0.08$, conditional $R^2 = 0.10$, sample size = 77.
(C) Marginal $R^2 = 0.13$, conditional $R^2 = 0.33$, sample size = 78.
(D) Marginal $R^2 = 0.11$, conditional $R^2 = 0.13$, sample size = 68.
The effects of latitude and water temperature during the day (A) and the effect of day-to-night differences of pCO_2 and the gas transfer velocity (Δ = night minus day values) (B) on the day-to-night difference of CO_2 fluxes were tested. Furthermore, the effect of day-to-night differences of physical and biogeochemical parameters (C) and the effect of catchment and hydromorphological related parameters (D) on the day-to-night differences of pCO_2 were evaluated. Stream ID was included as a random effect on the intercept. Significances of fixed effects were assessed with likelihood ratio tests with degrees of freedom = 1. The slope direction (sign) of the effect is indicated with – or + when significant. Significant *p* values < 0.05 are in bold.

Diel CO_2 flux variability driven by changes in water pCO_2. To understand the mechanisms behind the observed changes in CO_2 fluxes from day to night, we first selected the two primary controls of CO_2 fluxes at the water–air interface, i.e., the gas exchange velocity and water pCO_2 and explored the influence of these parameters on absolute CO_2 flux changes using an LME. The diel CO_2 flux variability in European streams could be mostly attributed to changes in water pCO_2 (Table 1B), whereas changes in the gas exchange velocity *k* appeared less important. In fact, we did not measure significant variations in *k* from day to night in our streams (Fig. 3; Supplementary Fig. S4h). Although diel variabilities of gas exchange velocities have been reported for CO_2 and other gases[31,32], the majority of the investigated streams in this study did not show those changes. The pCO_2 as a major driver of diel CO_2 flux variability was also identified by a global compilation of high-frequency CO_2 measurements[24]. Consequently, if no major changes in physical drivers of gas exchanges occur that strongly affect the turbulence, such as heavy rain events, it is sufficient to focus on pCO_2 for assessing diel flux changes at the water–air interface.

In a second step, we tested the influence of biogeochemical parameters that vary on a diel scale on water pCO_2 day-to-night differences (Table 1C). This LME identified a link between the day-to-night changes in water pCO_2 and water dissolved O_2, with pCO_2 generally increasing and O_2 decreasing from day to night (Supplementary Fig. S4b, c). This potentially reflects a diel cycle

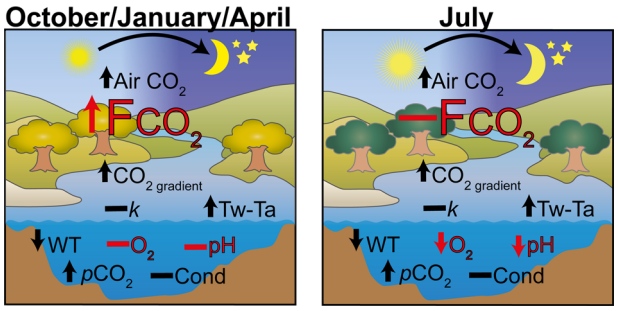

Fig. 3 Diel changes in CO_2 fluxes (FCO_2) and other physical and chemical parameters for October/January/April and July, respectively. The physical and chemical parameters comprise atmospheric CO_2 (Air CO_2), the differences of CO_2 concentrations in the water minus the air ($CO_{2\ gradient}$), the water–air gas transfer velocity (*k*), the differences of temperatures in the water minus the air ($T_w - T_a$), the water temperature (WT), the oxygen concentration in the water (O_2), pH in the water, the partial pressure of CO_2 in the water (pCO_2), and conductivity (Cond). The arrows indicate significant increases (↑) or significant decreases (↓) from day to night and the line indicates no significant change (——) tested by a Wilcoxon signed-rank test (see Supplementary Fig. S4 for more information). The differences between the sampling periods October/January/April and July, respectively, detected in this European study are highlighted in red.

of CO_2 controlled by aquatic primary production and respiration (in-stream metabolism). Hence, even though in situ metabolism may play a minor role in determining the baseline pCO_2 and flux in smaller streams (mostly controlled by terrestrial inputs[23]), our results suggest that metabolism can be an important driver of the diel fluctuations in CO_2 fluxes. Indeed, increased water pCO_2 during the night has been attributed to a decrease in CO_2 fixation by primary producers[13,18,24], although a recent study suggests that the adjacent groundwater can also show measurable but less pronounced diel pCO_2 variations[33]. Previous research suggests that in situ mineralization of CO_2 should play a larger role in CO_2 dynamics in larger streams because they are less influenced by external CO_2 sources[23]. Nevertheless, we did not find any trend in CO_2 flux day-to-night differences with stream width or discharge as a proxy for size (Supplementary Fig. S3c, f) or with stream order (Supplementary Fig. S5) although other studies suggest change over a size gradient[23,34]. Furthermore, the LME testing hydromorphological and catchment variables on pCO_2 day-to-night differences (Table 1D) did not reveal significant relationships with either of these drivers. This could either be due to the fact that we missed the best proxy that determines day-to-night differences in pCO_2 in European streams or that there are no common drivers among the investigated streams. Large diel variability of CO_2 patterns within one Swedish stream[26] or among US headwater streams[25] have been described, which complicates the identification of general drivers. Hence, further research is needed to decipher the diel variability of the sources and dynamics of pCO_2 in streams and to understand the environmental, hydromorphological, and catchment drivers before their importance on a regional or global scale can be assessed.

In-stream metabolism with photosynthetic CO_2 fixation diminishing pCO_2 during the day may explain the increase in CO_2 fluxes from day to night, but cannot explain why in some instances we measured a lower CO_2 flux at night. Potential explanations for a lower night flux might include: (i) higher atmospheric CO_2 concentrations due to the absence of terrestrial CO_2 fixation during night and therefore a lower water–atmosphere pCO_2 gradient, (ii) photomineralization of

organic matter to CO_2 counteracting the CO_2 fixation by primary producers during day-time, and (iii) lower turbulence due to a decrease in stream discharge in the night. We found significant increases in atmospheric CO_2 close to the investigated streams at night. However, this was usually accompanied by concomitant increases in water pCO_2 and therefore did not translate into smaller CO_2 gradients between the water–air interface (Fig. 3; Supplementary Fig. S4b, e, i). Production of CO_2 due to photomineralization of dissolved organic carbon (DOC) could play a role in diel CO_2 dynamics in streams with high amounts of colored terrestrial organic matter[35]. In the highly colored streams, diel CO_2 patterns can additionally be influenced by DOC shading diminishing benthic primary production[36]. In October, we measured DOC concentrations in a subset of the investigated streams for another study[37] where an agricultural stream in Sweden and peatland-dominated streams in Great Britain had high DOC concentrations (>10 mg L^{-1}) whereas the median DOC was much lower with 2.6 mg L^{-1} [37]. Due to the limited data, we could not test the effect of DOC on pCO_2 changes and we can neither confirm nor exclude that photomineralization might play a role for diel pCO_2 and consequently CO_2 flux variability in the studied streams. We did find, nonetheless, that the majority of the streams where CO_2 fluxes were lower during the night also had a lower gas transfer velocity (k_{600}), likely due to a slight decrease in stream discharge and therefore turbulence. Thus, while there was a general tendency of increased pCO_2 from day to night (only 4 out of 20 decreases in CO_2 fluxes from day to night showed a concomitant decrease in water pCO_2), individual streams at single time points seemed to experience diel fluctuations in discharge as described elsewhere[38]. This can simultaneously reduce the gas exchange velocity of the stream and therefore cause lower night-time CO_2 fluxes. In this study, we only measured stream discharge during the day, and therefore the importance of this mechanism remains to be confirmed.

Maximum CO_2 flux differences might be even higher—limitations of the study design. For organizational reasons, the sampling scheme of this collaborative study was standardized to fixed times of measurements for the day and the night. All teams across Europe started their measurements at 11:00 (midday) and 23:00 GMT (midnight) during each sampling period, which has consequences for the magnitude of the observed diel variability of the CO_2 fluxes. The largest diel differences in stream pCO_2 have generally been detected at the end of the day compared to the end of the night[12,18,39]. In an agricultural Swedish stream, diel maximum and minimum CO_2 concentrations were reached at 04:00 and 16:00 (GMT), respectively, during spring and early summer periods (late April to early July) where diel dynamics were most pronounced[26]. In these scenarios, sampling midday and midnight, as conducted in this study, would be close to those maxima and minima as they can be reached already earlier during the day (see Supplementary Fig. S6 in May). However, the maxima and minima of diel CO_2 dynamics in streams can vary largely (see Supplementary Fig. S6 in October, April, July). In another example of German streams[39], the times of minima and maxima differ between streams and times, and the fixed time points chosen in this study would miss the maximum differences that can be observed (see Supplementary Fig. S7 in August). Hence, our estimates could be conservative as we compared fixed time points at midday and midnight. In general, CO_2 flux measurements in streams are highly sensitive towards the time of the day because diel minimum and maximum of pCO_2 can vary largely from month to month but also from day to day. As we found that the diel variability of pCO_2 was the major driver of diel CO_2 fluxes, we recommend future studies that plan to measure CO_2 fluxes directly with the chamber method, to additionally monitor the diel variability of pCO_2 with loggers at a high temporal resolution. This approach will provide the opportunity to estimate if the measurements are done during peak times or not.

While our results provide a first insight into the drivers of day-night differences in CO_2 fluxes, the high uncertainty in the models as well as the sometimes opposing patterns—increases and decreases from day to night in different streams and sampling periods—point towards different drivers varying on a temporal and spatial scale. We recommend that future study designs incorporate high-frequency CO_2 data together with biogeochemical variables from the stream (e.g., O_2) and the atmosphere (e.g., CO_2 or temperature)[40]. Additionally, we recommend including radioactive or stable carbon isotope signatures to track potential sources of CO_2 and their changes in streams[41,42] to better assess terrestrial–aquatic linkages. Linking temporal patterns of fluvial CO_2 fluxes with their drivers across large spatial scales is a path towards a more accurate understanding of their role in regional and global carbon cycles. Our results demonstrate that, in many streams across Europe, night-time CO_2 fluxes exceed day-time, resulting in a potential underestimation of global CO_2 emissions from inland waters if not considered. It is thus critical to account for the diel variability of fluvial CO_2 fluxes for accurate daily and annual estimates of CO_2 emissions from inland waters.

Methods

Sampling scheme. The project included 16 teams distributed across 11 European countries. Every team sampled one to three streams (Supplementary Table S1) every 3 months (October 2016/January 2017/April 2017/July 2017) within a time frame of 2 weeks throughout a whole year. These sampling periods roughly cover the seasons autumn/winter/spring/summer although, due to the large latitudinal coverage of the sampling sites, the seasons and their characteristics vary largely. In total, 34 stream sites (Supplementary Fig. S1) were visited each sampling period during the specified 2 weeks' time frame except for 11 streams in January that were frozen during the sampling weeks (Supplementary Table S3).

CO_2 fluxes were measured once every sampling period with drifting flux chambers equipped with CO_2 sensors. This method has proven to be a reliable and least biased direct measurement of CO_2 fluxes at the water–air interface in streams[19,43]. CO_2 concentrations in the chamber headspace were logged every 30 s over a period of 5–10 min during each run, and CO_2 fluxes were calculated based on the rate of change over time in pCO_2 in the chamber headspace. At each stream, we measured CO_2 fluxes with the flux chamber (five times), pCO_2 in the atmosphere and water with the CO_2 sensors in the flux chamber (details described in Supplementary Methods), pH, temperature, conductivity, and oxygen in the water with a multiprobe (Supplementary Table S2). These measurements were started at 11:00 and 23:00 (GMT) and lasted approximately two hours and are referred to as midday and midnight throughout this article. Stream width, depth, canopy cover, and discharge were determined during the day (see Supplementary Sampling manual for details). In addition, the following information was collected for each stream once during the study: stream order, climate zone, catchment area until the endpoint of the investigated stream site and the percentage of coverage of different land use classes in this catchment area, and predominant geology (Supplementary Table S1).

Calculations of CO_2 fluxes and gas transfer velocity. Flux rates were obtained from the linear slopes of the pCO_2 in the chamber headspace over time and flux was accepted if the coefficient of determination (R^2) of the slope was at least 0.65[44]. An exception was made in cases where the slope was close to zero and the pCO_2 in the atmosphere and water (measured at the same time) were at equilibrium. These fluxes were set to zero. Final flux rates F (mmol CO_2 m^{-2} h^{-1}) were calculated according to Eq. (1)[45]:

$$F = S * 10^{-3} \frac{PV}{RTA} * 60 * 60, \quad (1)$$

where S is the slope (ppm s^{-1}), P is the pCO_2 in the atmosphere (atm), V is the volume (mL) of the drifting chamber, R is the gas constant (82.0562 mL atm K^{-1} mol^{-1}), T is the chamber air temperature (K), A is the bottom area of the chamber (m^2), and the last term is the conversion from seconds to hours. In this study, we followed the sign convention whereby positive values indicate a CO_2 flux from the stream to the atmosphere (source) and negative values indicate a flux from the atmosphere to the stream (sink). The magnitudes of variations between day-time and night-time measurements are additionally stated as percent increases, which

were computed by dividing the difference between the values at night minus day by the value at day and expressing the result as a percent change from day to night.

We used F (Eq.(1)) to calculate the gas transfer velocity (k in cm h^{-1}) by inverting the equation for Fick's law of gas diffusion, according to Eq. (2):

$$k = \frac{F}{kH(CO_{2_{water}} - CO_{2_{air}})} * 100, \quad (2)$$

where kH is Henry's constant (in mol L^{-1} atm^{-1}) adjusted for temperature[46].

For comparison of transfer velocities between sites and sampling periods and with the literature, k (Eq. (2)) was standardized to k_{600} (Eq. (3)):

$$k_{600} = k\left(\frac{600}{Sc}\right)^{-0.5} \quad (3)$$

where k is the transfer velocity at in situ temperature (T), Sc is the Schmidt number for in situ temperature T, the Schmidt number for 20 °C in freshwater is 600, and representing a hydrodynamic rough water surface typical in streams the exponent of −0.5 was chosen[47].

Statistical analyses. All statistical analyses were performed with median values of three to five floating chamber runs per day and night, respectively, using the statistical programming language R[48] (version 3.5.1). Samplings that generated less than three values for either day or night due to an R^2 of the slope <0.65[44] were excluded from further analysis reducing the number from 136 to 107 day–night comparisons. For our statistical tests, the alpha level was set to $\alpha = 0.05$. Significant differences between day-time and night-time measurements for each sampling period across all streams were tested with Wilcoxon signed-rank tests[49] where median day-time and night-time values for each stream site were paired (Fig. 1a). The same tests were conducted for the other biogeochemical variables measured at midday and midnight (see Fig. 3; Supplementary Fig. S4).

With a first linear mixed-effect model (LME) we tested the latitudinal and water temperature effect on CO_2 flux differences from day to night. A second LME was built to evaluate the two major drivers of CO_2 flux differences from day to night: pCO_2 and gas exchange velocity (k). A third LME was subsequently used to determine the biochemical factors potentially influencing the differences of the night-time minus day-time pCO_2, which was identified as the only significant driver in the second LME. Finally, a fourth LME was built to evaluate the effect of catchment and hydromorphological parameters on the day-to-night differences of pCO_2. For these tests, we used the "lmer" function of the R-package "lme4"[50] with maximum-likelihood estimation. Fixed effects for the LME with biogeochemical parameters for pCO_2 differences from day to night included absolute differences from day to night of oxygen concentration in the water, pH, conductivity, temperature gradient of atmosphere and water, and water temperature. Fixed effects for the LME with catchment and hydromorphological parameters included day length (i.e., sun hours from sunrise to sunset), stream wetted width, discharge, % forest of the catchment, and catchment area. These variables are mostly remotely available for streams. For the LMEs we included stream ID as a random effect allowing different intercepts for each stream to account for pseudoreplication (one data point per sampling period per stream) and z-scaled all fixed effects with the "scale" function before running the models. Statistical significances of fixed effects were assessed with likelihood ratio tests using the function "drop1"[51]. The respective LMEs were followed by a model validation, checking the residuals for normal distribution and homogeneity of variances[52]. A separation of the dataset to check if drivers between increases from day to night and decreases from day to night differ did not reveal acceptable models in terms of model validation (i.e., residuals were not normally distributed). Although our dataset provided a large spatial coverage on day–night differences in CO_2 fluxes in European streams, it did not have the statistical power to test for significant drivers separately for increases and decreases.

Data availability

The data that support the findings of this study are openly available in figshare at https://doi.org/10.6084/m9.figshare.12717188.

Code availability

This manuscript includes no code.

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Author contributions

K.A. and P.B. conceived the study design, coordinated the project and contributed equally to this work; all authors collected and analyzed the field data and K.A. and P.B. gathered and performed the quality check of all data; K.A., P.B., and J.P.C.-R. co-wrote the paper with the help of M.K., G.H.N., and N.C. All authors (K.A., J.P.C.-R., T.F., A.P., S.C.-F., D.S., A.C.N., Al.D., A.P.P., B.C.D., N.S., C.G.R., G.H.N., X.T., V.E., L.B.-F., T.B., J.A., An.D., G.B., S.F., N.C., E.d.E., F.P., J.-R.M., J.M., D.F., C.N., M.C., M.N., L.L., C.R. G.-Q., F.R., N.P., J.L.J.L., J.P., M.K., A.F., S.H.O., C.M.-L., A.B., J.A.F., P.J.G., L.A.K., M.R., P.B.) commented on the manuscript.

Competing interests

The authors declare no competing interests.

Additional information

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