






Mapping variability in CO₂ saturation in Amazonian rivers at a large spatial scale indicates undersaturated areas

Mapeamento da variabilidade na saturação de CO₂ em rios amazônicos em larga escala indica áreas subsaturadas

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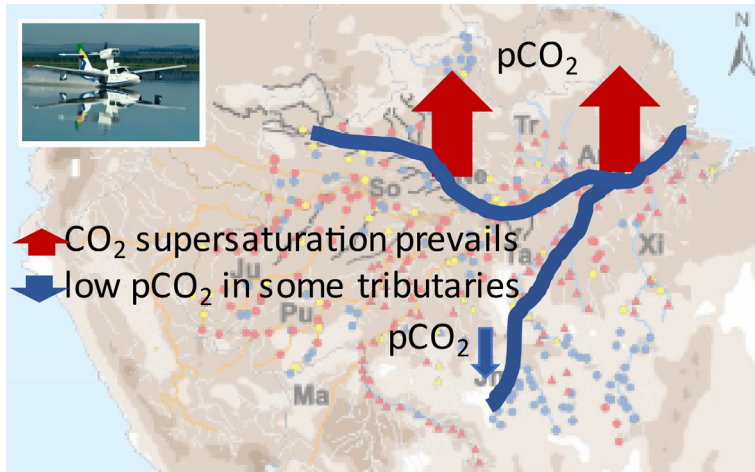
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Abstract: Aim: Amazonian rivers outgas high amounts of carbon dioxide (CO₂). However, the outgassing estimate remains uncertain due to the limited spatial distribution of data on water-atmosphere CO₂ fluxes. So far, the vast extent of the basin and the difficult access to some regions have hampered complete mapping. We hypothesize that 1) CO₂ supersaturation prevails in most Amazonian rivers and 2) undersaturation occurs only at a few locations, particularly during the low-water period. **Methods:** To obtain insight on the spatial distribution of partial pressure of CO₂ (pCO₂), an essential determinant of CO₂ fluxes, we analysed water sampled by a specially equipped hydroplane at an unprecedented sizeable spatial scale in the Amazon basin at 419 locations. **Results:** Confirming our hypothesis, most rivers were supersaturated with CO₂ concerning the atmosphere. In contrast to our expectations, however, we also found below equilibrium CO₂ concentrations in several tributaries, particularly during low-water periods, when light availability in the water column is highest likely coinciding with the highest aquatic primary production rates. Correlation analyses further indicated that pCO₂ values are positively related to the organic carbon density in the soils, net primary production, and the proportion of flood-able land in the sub-basins. **Conclusions:** We conclude that supersaturation with CO₂ occurs in most rivers, but several tributaries are undersaturated. Our findings highlight the different roles that Amazonian rivers can play in the regional carbon cycle. We argue that up-scaling should explicitly incorporate areas with riverine CO₂ uptake, particularly at the sub-basin scale.

Keywords: pCO₂; spatial variability; autotrophy; hydroplane sampling.



Graphical abstract



Resumo: Objetivo: Rios amazônicos liberam quantidades expressivas de dióxido de carbono (CO₂). Entretanto, essas estimativas permanecem incertas devido à limitada distribuição espacial de dados sobre fluxos água-atmosfera. A vasta extensão da bacia hidrográfica e a dificuldade de acesso a algumas regiões têm impedido um mapeamento completo até o momento. As hipóteses deste estudo são que: 1) a supersaturação de CO₂ prevalece na maioria dos rios amazônicos; e 2) a subsaturação ocorre somente em poucos locais, particularmente durante períodos de águas baixas. **Métodos:** Para melhor compreender a distribuição da pressão parcial de CO₂ (pCO₂), um determinante essencial de fluxos de CO₂, nós analisamos amostras de água coletadas por um hidroavião especialmente equipado em uma escala espacial sem precedente em 419 locais na bacia Amazônica. **Resultados:** Confirmando nossa primeira hipótese, a maioria dos rios esteve supersaturada em relação ao CO₂ da atmosfera. No entanto, ao contrário de nossas expectativas, nós também encontramos concentrações de CO₂ abaixo do equilíbrio em vários tributários, particularmente durante períodos de águas baixas, quando a disponibilidade de luz na coluna de água é maior provavelmente coincidindo com maiores taxas de produção primária. Análises de correlação indicaram que valores de pCO₂ estão positivamente relacionados com a densidade de carbono nos solos, com a produção primária líquida e com a proporção de área alagável nas sub-bacias. **Conclusões:** Nós concluímos que a supersaturação em CO₂ ocorre na maioria dos rios, mas vários tributários são subsaturados. Nossos achados trazem luz aos diferentes papéis que os rios amazônicos podem desempenhar no ciclo do carbono regional. Também argumentamos que extrapolações espaciais deveriam explicitamente incorporar áreas com absorção de CO₂ fluvial, particularmente na escala de sub-bacias.

Palavras-chave: pCO₂; variabilidade espacial; autotrofia; amostragem por hidroavião.

1. Introduction

1.1. Role of rivers in Amazonian carbon fluxes

Amazonian forests are well known for their carbon uptake and storage (Poulter et al., 2010; Rödig et al., 2018; Sullivan et al., 2020). Concurrently, a considerable amount of CO₂ is outgassed from the Amazonian rivers (Melack, 2016). Current estimates of C outgassed from Amazonian waters - including rivers, floodplains, lakes, and hydropower reservoirs - range between 0.8 and 1.8 Pg C yr⁻¹ (Rasera et al., 2013; Melack, 2016; Sawakuchi et al., 2017).

However, the outgassing estimate remains uncertain due to the limited spatial distribution of data on water-atmosphere carbon dioxide (CO₂)

fluxes (Raymond et al., 2013; Melack, 2016; Sawakuchi et al., 2017). So far, the vast extent of the basin and the difficult access to some regions have hampered complete mapping. Nevertheless, high spatial variability in CO₂ concentrations and fluxes can be expected because of the substantial heterogeneity within the basin, including differences in geological formations, soil characteristics, and climate. These differences drive the variability in primary production in the basin (Huete et al., 2006) and the C fluxes to and from the rivers. Organic matter produced in the *terra firme* (i.e., permanently dry areas) (Richey et al., 1988; Mayorga et al., 2005; Ward et al., 2013) and in the extensive wetlands in the basin (Junk, 1997; Melack et al.,

2009; Melack & Engle, 2009) will, in part, end up in the rivers. In-stream mineralization processes subsequently enhance the CO₂ concentration in the water. In addition, in smaller headwaters, the subsurface flow of CO₂ - rich water, fuelled by soil and root respiration, is an essential source of CO₂ (Johnson et al., 2008). Together with gas exchange velocity between the water and the atmosphere, these processes govern CO₂ emissions.

1.2. Processes driving CO₂ uptake and emission from Amazonian rivers

The flux of CO₂ depends strongly on the concentration gradient between the surface water and the air and the gas exchange velocity (MacIntyre et al., 1995). CO₂ outgassing occurs when the partial CO₂ pressure (pCO₂) in the water is higher than in the atmosphere. Riverine CO₂ uptake occurs when the pCO₂ in the water is lower than in the atmosphere due to, for instance, intensive aquatic primary production by phytoplankton, periphyton, or submerged macrophytes. Low CO₂ concentrations may limit primary production and select species capable of dealing with low CO₂ availability. Clearly, CO₂ is not the only driver of primary production; the availability of light and ions – which is highly spatially and temporally variable in Amazonian rivers also plays a role. Globally, the CO₂-producing processes and the groundwater inflow of CO₂ generally overrule the consumption of CO₂ in rivers, resulting in a considerable net emission of CO₂ from the world's rivers (Duarte & Prairie, 2005; Cole et al., 2007; Battin et al., 2008; Tranvik et al., 2009).

Amazonian rivers generally have higher pCO₂ values than the atmosphere, particularly in the most extensively studied central Amazon region (Richey et al., 2002) and the lower Amazon River (Sawakuchi et al., 2017). The concentration of CO₂ in the river water tends to fluctuate with the water level, with the highest CO₂ concentrations occurring at peak water levels and peak discharge when the terrestrial-aquatic coupling is strongest (Devol et al., 1995; Richey et al., 2002; Almeida et al., 2017; Sawakuchi et al., 2017).

Nevertheless, values below atmospheric pCO₂ in Amazonian rivers have also been reported. In the Araguaia-Tocantins River basin, for instance, which is part of the Amazonian biome and is situated east of the Amazon basin, recurrent pCO₂ pressures below atmospheric values occurred at two locations in clear-water rivers during low-waters over a 5-year

measuring period (Rasera et al., 2013). Additionally, CO₂ concentrations near atmospheric equilibrium have been observed at three locations in the main stem of the Tapajos River (425 µatm) and in the upper Purus River (414 µatm), both located in the Amazon River basin (Alin et al., 2011). High photosynthetic rates in clear-water rivers during low-water periods – when light availability in the water column is highest – importantly contribute to the aquatic metabolism (Ellis et al., 2012), likely explaining the low pCO₂ values. However, also in black-water rivers, especially in the mouth bays located at sites where tributaries enter the main channel, within river aquatic primary production rates are similar to aquatic respiration rates (Wissmar et al., 1981). In some mouth bays, CO₂ consumption rates were equal to or higher than the CO₂ production rates, coinciding with CO₂ emission to the atmosphere. This indicates that CO₂ produced elsewhere played a role here (Wissmar et al., 1981).

1.3. Spatial variability in CO₂ concentrations and fluxes in Amazonian rivers

Although considerable effort has been made to quantify pCO₂ and water-atmosphere CO₂ fluxes in the basin (Richey et al., 1988, 2002, 2009; Mayorga et al., 2005; Rasera et al., 2013; Abril et al., 2014; Scofield et al., 2016; Sawakuchi et al., 2017; Amaral et al., 2019, 2020), the spatial distribution of pCO₂ during high and low-water periods is not well known in hard to reach rivers far from the river mouth and the main channel. To obtain insight on the spatial distribution of pCO₂ we acquired data on dissolved inorganic carbon (DIC) and pH retrieved by a specially equipped hydroplane at an unprecedented large spatial scale in the Amazon basin at 419 locations (Moss & Moss, 2005, Abe et al., 2006). Samples were taken between June 2003 and December 2004, covering different stages of hydrography. We hypothesize that 1) CO₂ supersaturation prevails in most rivers and 2) under saturation occurs only at a few locations, particularly during the low-water period.

2. Material and Methods

2.1. Study region and sampling

All locations (n= 419, CO₂; n=361, O₂) were sampled within the Brazilian territory of the Amazon basin in 2003 and 2004 as part of the Brasil das Águas project (www.brasildasaguas.com.br). Sample locations were selected and georeferenced by Empresa Brasileira de Pesquisas

Agropecuárias (EMBRAPA) Monitoramento por Satélite, Campinas, SP, Brazil, aiming to encompass different types of watercourses surrounded by different types of land use.

All samples were taken between 11:12 and 20:39 h, with the vast majority (i.e. 78%) between 13:00 and 18:00 h. River orders ranged from 3 to 10 (Mayorga et al., 2012). Samples were taken through a tube 20 cm below the water surface connected to an auto-sampler on board a hydroplane (Lake Renegade, model LA-250, USA). For more sampling details, see Abe et al. (2006). The system was flushed with river water four times before samples were taken. Oxygen (O_2 ; % saturation and concentration), temperature, pH, and conductivity were measured directly on board the hydroplane with YSI multiparameter water quality model 6600 (Yellow Springs, USA). The sonde contained a YSI 6562 oxygen rapid pulse sensor (range -0.999 to 999; precision: 0.1 mV; accuracy: +/- 20 mV), a YSI 6561 pH sensor (range: 0 to 14; precision: 0.01; accuracy: +/- 0.2) and a YSI 6560 conductivity sensor (0 to 100 $\mu\text{S}/\text{cm}$; precision: 0,1 $\mu\text{S}/\text{cm}$; accuracy: +/- 0.5%). The sensors were calibrated daily before the cruise flights. The pH sensor was calibrated with YSI-certified standards with a pH of 4, 7, and 10 units. The conductivity sensor was calibrated with a 100 $\mu\text{S}/\text{cm}$ YSI-certified solution. Samples for the remaining analyses were frozen immediately after sampling using liquid nitrogen. Upon arrival in the laboratory, they were kept at -20°C and analyzed within 20 days after sampling.

2.2. Sample analysis and GIS data sources

Dissolved inorganic carbon (DIC) and dissolved organic carbon (DOC) were measured using a Shimadzu TOC analyzer, model 5000, after carefully filtering through a GF/F Whatman filter. Filters were rinsed with Milli-Q ultrapure water before use, and filter blanks were monitored according to Eaton et al. (1998). To screen for potential relationships between pCO_2 and environmental conditions, including potential carbon sources, we gathered data on the organic carbon density in the soil (kg C m^{-2} to 1 m depth) from The Nelson Institute Centre for Sustainability and the Global Environment (IGBP-DIS, 1998), and on the terrestrial net primary production (NPP) data from Numerical Terradynamic Simulation Group (NTSG) from the University of Montana (product MOD17A3) ($n=407$ due to missing data for some sampling locations). Boundaries of hydrographic

sub-basins and their wetland area and vegetation cover were retrieved from Melack & Hess (2010).

2.3. Calculations and data analysis

pCO_2 (partial CO_2 pressure) in water was calculated based on DIC and pH as in Cole et al. (1994), adjusting the equilibrium constants for water temperature according to Butler (1991) and ionic strength according to Davies & Shedlovsky (1964). Ionic strength (in moles/L) was estimated based on the electric conductivity (in $\mu\text{S}/\text{cm}$) using a conversion factor of 16 (Ponnamperuma et al., 1966). When DIC was below the detection limit (2.5 μM), a DIC concentration equal to the detection limit was used for visual displays ($n=47$) - which overestimates the pCO_2 value - statistics were conducted with and without these values.

We tested the effect of freezing on DIC and pCO_2 by using test samples in which we measured DIC and pH before and after freezing and calculated pCO_2 as described above. We found that DIC and pCO_2 before and after freezing were strongly correlated ($R^2=0.94$; $p<0.001$; $n=20$ for both correlations). Importantly, pCO_2 values below atmospheric levels increased due to sample treatment but stayed below equilibrium concentrations ($R^2=0.90$; $p<0.001$ $n=9$). pCO_2 values above atmospheric levels decreased but remained above equilibrium concentrations ($R^2=0.92$; $p<0.001$; $n=11$). In other words, in line with what is expected based on physics, freezing led to a CO_2 loss in samples above atmospheric levels and a CO_2 increase in samples below atmospheric equilibrium. This indicates that we likely underestimated the number of locations with pCO_2 values below and above equilibrium concentrations and overestimated the number of locations in equilibrium with the atmosphere.

Samples were taken during high- or low-waters as follows: the larger rivers were classified as taken during low (LW) and high-water (HW) based on the sampling date and the hydrographs of the river where we took samples. Because for the smaller rivers, no hydrographs are available, we used the hydrograph of nearby rivers. Hydrographs were obtained from Junk et al. (2011, 2014) and the Brazilian National Water Agency, ANA (2019). Next, we extracted the minimum and maximum water levels and calculated the average. Sampling dates with above-average water levels were classified as HW and below the average as LW.

To screen for potential relationships between pCO_2 and environmental conditions, we worked on

two scales. First, we used individual pCO₂ sampling points and local environmental variables: water temperature, DOC concentration, NPP, and the soil organic carbon density (pCO₂ and DOC were log-transformed to approach normality). We used Pearson correlation (one-tailed) to test for significant correlations. Subsequently, we used linear regression to quantify the relationship between pCO₂ and the environmental variables that correlated most strongly. In addition, we categorized the individual data points by stream order. We used a one-way ANOVA and a *post-hoc* Tukey test to evaluate potential differences between the stream orders. Second, we used aggregated data on a sub-basin scale. For each sub-basin in which at least four water samples were taken (seven sub-basins for the high-water period and 13 for the low-water period), we determined the median pCO₂. Next, we again used Pearson correlation to

disclose possible relationships between pCO₂ on the one hand and basin characteristics on the other: mean soil organic carbon density, mean NPP, the percentage of the subbasin area that is floodable (as a proxy for the relative importance of wetlands in a sub-basin), the percent of the floodable area made of herbaceous and woody vegetation (to further zoom in on potential essential characteristics of the wetlands). All analyses were performed in IBM SPSS Statistics 21.

3. Results

Our data show high spatial variability in partial CO₂ pressure (pCO₂). pCO₂ ranged from below equilibrium concentration to almost 60*10³ μatm during our sampling campaigns. At most locations, the water had CO₂ concentrations above the equilibrium concentrations (Figure 1). Notably, however, various tributaries to the Amazon main

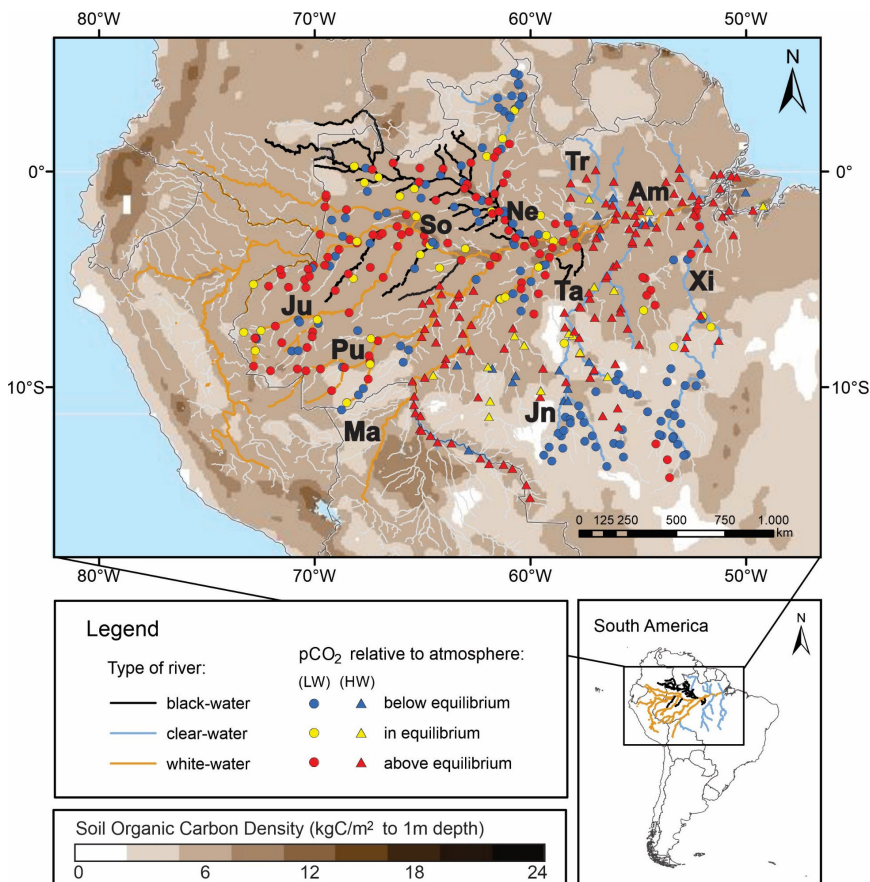


Figure 1. The spatial distribution of partial CO₂ pressure (pCO₂) in Amazonian rivers. An aquatic pCO₂ within 20% of the atmospheric pCO₂ (~380 μatm at the time of sampling) was considered to be “in equilibrium” with the atmosphere *sensu* Cole et al. (1994). Above and below equilibrium values are depicted in red and blue, respectively. Triangles depict locations sampled during the high-water stage, and dots depict locations sampled during the low-water stage. The background shows soil organic carbon content (which positively correlates with pCO₂ - see main text). Abbreviations of main river names as follows: Am - Amazon, Jn - Juruena, Ju - Juruá, Ma - Madeira, Ne - Negro, Pu - Purus, So - Solimões, Ta - Tapajós, Tr - Trombetas, Xi - Xingu. Watercolour, according to Junk et al. (2011).

channel had below equilibrium concentrations of CO_2 . These low pCO_2 values occurred mainly in the sub-basins Içá-Putumayo, Jundiatuba, Purus, Tapajos, and Xingu during low-waters (Figure 2). Most rivers were not sampled during the low and high-water seasons, hampering the comparison of pCO_2 values between the two stages on a sub-basin scale. However, there were some exceptions: in the Tapajos, Xingu, and Purus rivers and in the main stem, several river stretches were sampled at different water stages. Comparing the nearby locations sampled during different periods generally showed lower pCO_2 during the low-water (LW) as compared to the high-water (HW) stage (Figures 1 and 2).

Of the variables we tested, using the individual data points, we only found highly significant correlations between pCO_2 and the organic carbon density in the soil ($r=0.38$, $p<0.001$, $n=417$; Figure 3a) and NPP ($r=0.12$, $p=0.009$, $n=407$) but the linear relation is weak (Figure 3b). Without the pCO_2 values calculated based on DIC values below the detection limit, the linear relations are not significant ($p=0.242$, $n=370$ for carbon density in the soil and $p=0.881$, $n=360$ for NPP). The relationship between pCO_2 and the soil organic carbon density is strongest during the LW stage

($n=266$) when pCO_2 tended to be lowest in areas with low soil organic carbon density (Figure 3a). A considerable share of the samples that had DIC concentrations below the detection limit was taken during the LW stage in areas with low soil organic carbon density, particularly in the Tapajos and Xingu subbasins. The calculated pCO_2 values here are low and, at the same time, overestimated (see method section). Excluding them from the analysis removes many low pCO_2 values, resulting in a non-significant linear regression ($p=0.299$, $n=219$). When categorized by stream order, the highest stream orders tended to have higher pCO_2 values than the lower stream orders (Figure 4).

At a sub-basin scale, we found that during HW, similar to the analysis based on the individual sampling points, pCO_2 was positively correlated to the organic carbon density in the soil ($r=0.95$, $p<0.001$, $n=7$) and to NPP ($r=0.79$, $p<0.018$, $n=7$). In addition, pCO_2 was positively related to the percentage of the sub-basin area consisting of floodable areas ($r=0.79$, $p=0.018$, $n=7$). During LW, pCO_2 was only correlated to the organic carbon density in the soil ($r=0.82$, $p<0.001$, $n=13$). NPP and soil organic carbon were also strongly

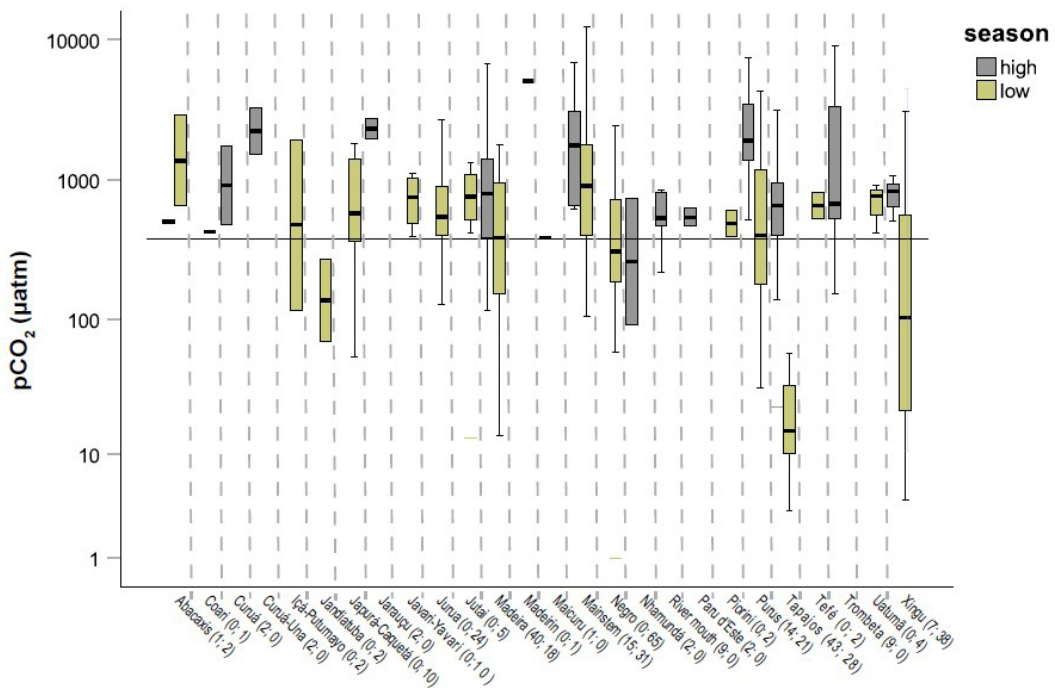


Figure 2. Partial CO_2 pressure (pCO_2) in the different sub-basins during high and low-waters. The number of locations sampled during high and low-waters, respectively, are given in parentheses. Only the sub-basins with n equal to or larger than four were used in the sub-basin correlation analysis. The horizontal line is the pCO_2 in water in equilibrium with the atmosphere. Boxes depict the 25% intervals around the median (black line), and whiskers represent the 25th and the 75th percentile.

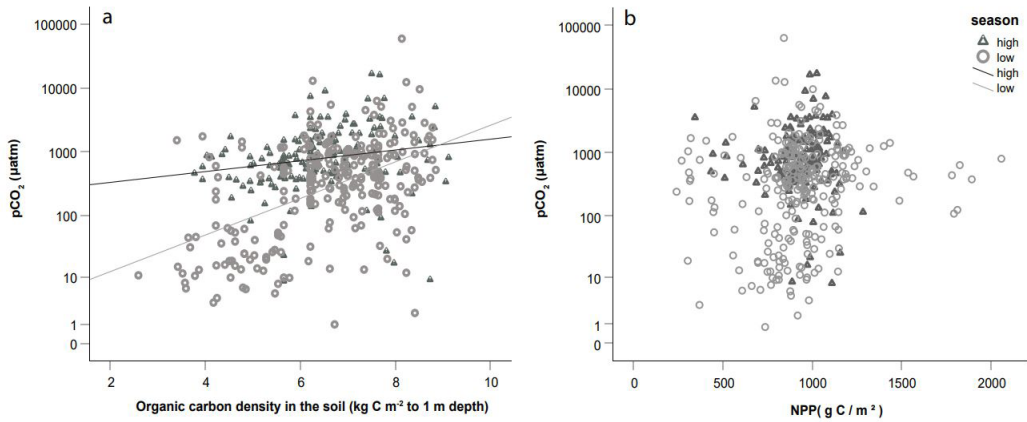


Figure 3. (a) Relation between partial CO₂ pressure (pCO₂) and organic carbon density in the soil. The relation is stronger during low-waters [$\log(\text{pCO}_2) = 0.5 + 0.29 \cdot \text{Csoil}$; $p < 0.001$; $R^2 = 0.25$, $n = 262$; light line] than during high-waters [$\log(\text{pCO}_2) = 2.4 + 0.08 \cdot \text{Csoil}$; $p = 0.021$; $R^2 = 0.03$, $n = 157$; dark line]; the overall relation is $\log(\text{pCO}_2) = 1.2 + 0.22 \cdot \text{Csoil}$ ($p < 0.001$; $R^2 = 0.14$, $n = 417$; not shown). Note that when samples below the detection limit were removed, the overall relation ($p = 0.242$) and the relation during low-water ($p = 0.299$) were not significant. (b) Relation between pCO₂ pressure and terrestrial net primary production, NPP (net ecosystem production). Linear model not shown ($R^2 < 0.02$).

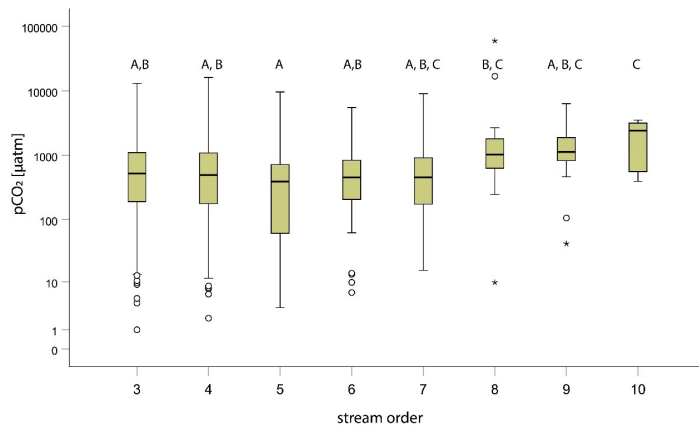


Figure 4. Relation between the mean soil organic carbon density and mean annual net primary production (NPP) in sub-basins with at least 4 sample points during the high or low water period (i.e., the sub-basins used for the correlation analysis in the main text) (Pearson correlation: $r = 0.77$, $p < 0.001$, $n = 14$).

co-correlated (Pearson correlation: $r = 0.77$, $p < 0.001$, $n = 14$).

Oxygen saturation ranged from 43% to 120%, with the lowest percentage of saturation measured during HW (Figure 5). Overall oxygen saturation levels tended to be lower during HW (Figure 5a). However, it should be noted that the high and low-water sampling locations are not evenly distributed over the basin and the observed tendency may therefore also be – partially – caused by spatial differences. Most of the sampling locations (66%) had O₂ concentrations in equilibrium with the atmosphere (i.e., between 90 and 110%). pCO₂ and O₂ saturation were negatively correlated ($r = -0.21$, $p < 0.0001$; $n = 361$; Figure 5b and for the

dataset without the DIC values below detection limit $r = -0.17$; $p = 0.002$; $n = 314$). Focusing on the locations not in equilibrium with the atmosphere, we found that most locations (76%) had above atmospheric pCO₂ values and below atmospheric O₂ concentrations (Figure 5b). Two percent of the sampling locations had above atmospheric concentrations of O₂ and below atmospheric pCO₂. Seven percent was over saturated with both gases. About 15% of the locations had below equilibrium concentrations of CO₂ and O₂.

4. Discussion

Our data show high spatial variability in pCO₂ across the Amazon basin. In line with

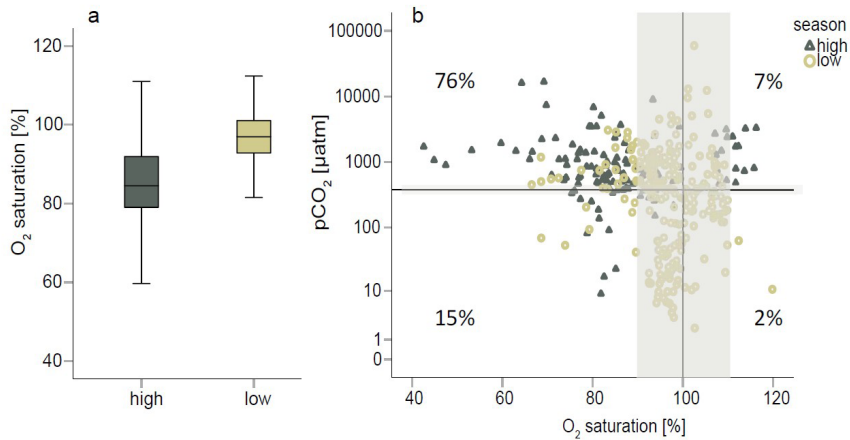


Figure 5. Oxygen saturation of the water in Amazonian rivers sampled during the high and the low-water stages (a). Partial CO₂ pressure (pCO₂) versus oxygen saturation in Amazonian rivers during high and low-water levels (b). The vertical and horizontal black lines depict the oxygen concentration and the pCO₂ in equilibrium with the atmosphere. Shaded area depicts CO₂ and/or O₂ concentrations +/- 20% and 10% of the equilibrium concentration, respectively. The percentages mentioned in the quadrants reflect the share of the total number of data points outside the shaded areas (n=121).

our first hypothesis, we found most rivers to be supersaturated with CO₂. Below equilibrium concentrations, however, were more widespread than anticipated (partially refuting hypothesis 2). Below-equilibrium concentrations occurred in several tributaries, particularly during low-water periods.

Our dataset is unprecedented concerning its spatial scale and the inclusion of difficult-to-reach Amazon tributaries. We found concentrations up to two orders of magnitude higher than the equilibrium concentration, despite the likely narrowing of the concentration range due to our sample preservation method (see Methods). The range of our pCO₂ values corresponds with what others have reported (e.g., Richey et al., 2002; Rasera et al., 2013; Abril et al., 2014; Borges et al., 2015). Also, in agreement with previous studies, we found generally lower pCO₂ values at low-water and higher values during the high-water period (e.g., Rasera et al., 2013; Scofield et al., 2016; Amaral et al., 2019). Furthermore, in parallel with earlier reports, we generally found relatively high pCO₂ values in the main stem compared to the tributaries, e.g., Sawakuchi et al. (2017), but see Amaral et al. (2019). They found relatively higher values in some of the tributaries of the Negro River system. Yet, the variation between tributaries was high, and some (e.g., Purus River, Figure 2) had pCO₂ values like the main stem. Across all sub-basins, pCO₂ values tended to be higher in streams with a higher order (Figure 4).

Lower than equilibrium concentrations of CO₂ mainly occurred in the upper part of the Tapajos and Xingu rivers, regions with relatively low organic carbon density in the soil. These rivers are known for their clear waters (Junk et al., 2011; Sioli, 1984). The high water transparency in these rivers may enable aquatic primary production. Indeed, abundant growth of submerged macrophytes has been observed in streams entering the clear water rivers (Junk, 1983). However, benthic and pelagic photoautotrophs (algae and cyanobacteria) may also contribute to aquatic primary production in these rivers. For instance, in the middle stretch of the Xingu River, high chlorophyll concentrations (annual average ~ 15 µg L⁻¹) have been observed (unpublished data V.H.). We, therefore, speculate that the below saturation pCO₂ levels that we observed there might be related to aquatic primary production. This postulation is also made in a recent global riverine study comparing day and night-time and clear and black water CO₂ emissions (Gómez-Gener et al., 2021).

Substantial aquatic primary production may result in high water column O₂ concentrations. We found many locations near and above equilibrium O₂ concentrations, especially during the low-water stage (Figure 4), when primary production may be highest. High O₂ concentrations coinciding with low CO₂ concentrations would be an even stronger indicator of primary production rates overruling respiration rates. This situation, however, only occurred at a limited number of

locations. Above equilibrium concentration of both CO₂ and O₂ occurred more frequently. This condition can be readily explained by high primary production combined with the inflow of CO₂-rich water or CO₂ anaerobic production.

Arguably, O₂ and CO₂ concentrations are influenced not only by the processes mentioned but also by the gas exchange velocity. Furthermore, the negative relationship between CO₂ and O₂ concentrations that would be expected when metabolic activities within the river are the primary driver of gas concentrations may be blurred by the conversion of CO₂ to HCO₃⁻ and the O₂ consumption by non-CO₂ producing processes, such as iron and sulfur oxidation (Richey et al., 1988). These processes may explain coinciding below equilibrium concentrations of CO₂ and O₂. While O₂ concentration is, therefore, a tricky indicator for the importance of primary production, more direct evidence regarding the importance of primary production comes from the stable isotope composition of O₂. Stable isotope analysis of O₂ in samples taken in white water rivers in the state of Acre (located in the western part of our study area) during the low-water stage indicated aquatic primary production as the main process regulating metabolic processes (Ellis et al., 2012).

Below equilibrium concentrations of CO₂ were not restricted to the southeast of the Amazon basin. Below equilibrium CO₂ concentrations were also found at locations situated more to the North and East, particularly in white and clear waters (Figure 1). The locations where below equilibrium concentrations were found were predominantly sampled during the low-water season; oxygen concentrations at these locations were near equilibrium and tended to have a high pH, possibly pointing to high primary production. A noticeable impact of the primary production on O₂ and CO₂ concentrations in rivers in Amazonian rivers corroborates with earlier studies (Wissmar et al., 1981; Scofield et al., 2016). Importantly, we may have underestimated the occurrence of CO₂ under saturation as several rivers were only sampled during the high-water season (Figure 1).

Despite the higher-than-expected prevalence of waters with below equilibrium pCO₂ values, we found most locations in most rivers – including the main channel of the Amazon and Solimões Rivers, the rivers Negro, Purus, Trombetas, Curuá and Jaruaçu, and the Amazon River mouth – were supersaturated with CO₂ (Figure 2). These high pCO₂'s lead to intense CO₂ outgassing, as reported

earlier (Richey et al., 1990, 2002; Rasera et al., 2013; Raymond et al., 2013; Sawakuchi et al., 2017).

pCO₂ was strongly correlated with soil organic carbon density and terrestrial net primary production. This hints at an essential contribution of organic carbon from uplands and floodplains fuelling aquatic respiration, as also discussed by others (Richey et al., 2002; Grace & Malhi, 2002), thereby enhancing pCO₂. Although pCO₂ was not significantly related to DOC in our dataset, this may be readily explained by the variation in DOC quality and degradability in Amazonian rivers (Mayorga et al., 2005; Ward et al., 2013). Bulk DOC concentrations are, therefore, not a reasonable proxy for aquatic mineralization. Our sub-basin aggregated data showed a positive relationship between the mean pCO₂ and the percentage of the watershed that floods during high waters. This underlines the importance of floodplains as sources of riverine CO₂ (Abril et al., 2014; Borges et al., 2015). Finally, the positive relation between pCO₂ and the inter-related variables net primary production and organic carbon density in the soil may also be caused by high soil respiration in organic carbon-rich soils (Davidson & Janssens, 2006) and subsequent flow of CO₂ rich water to the rivers (Johnson et al., 2008; Davidson et al., 2010).

Our pCO₂ data confirmed consistent temporal variation. In the rivers where we have pCO₂ data in both the low and high-water periods, pCO₂ tended to be lower during the low-water season (Figures 1 and 2). This confirms our expectations and concurs with the studies on pCO₂ time series that show a strong positive relationship between water level and pCO₂ (Almeida et al., 2017). This variation has been attributed to increased input of labile carbon from floodplains and lateral inflow of CO₂ derived from plant roots and microbial respiration (Devol et al., 1995; Richey et al., 2002; Rasera et al., 2013; Abril et al., 2014). Especially in the more transparent and shallower waters, however, relatively low pCO₂ levels during the low-water season may also result from the enhanced primary production in this period due to higher light availability in the water column and low flow velocities.

5. Conclusion

In summary, we conclude that supersaturation with CO₂ occurs in most rivers, but several tributaries are undersaturated. Our unique mapping of riverine pCO₂ in the Brazilian part of the Amazon

basin confirms earlier findings and our expectations about the prevalence of high CO₂ concentrations. However, the occurrence of below equilibrium concentrations of CO₂ was more widespread than anticipated. The surface area of the rivers in the sub-basins where we found CO₂ under saturation only represents a minor fraction of the total Amazonian river water surface. For example, the floodable areas in the Tapajos and Xingu basins comprise only 2.8 and 4.6% of the total floodable area in the entire basin (Melack & Hess, 2010). Under saturation in these sub-basins will, therefore, not strongly impact Amazonian river CO₂ efflux estimates based on data from a limited (primarily supersaturated) part of the basin extrapolated to the surface water area of the entire basin. We argue, however, that more work is needed to pinpoint the processes driving the CO₂ under saturation as its occurrence in several rivers and sub-basins shows that Amazonian rivers can play different roles in the regional carbon cycle. We assert that quantification of the role of aquatic primary production in the Amazonian riverine carbon cycle would fill an important knowledge gap.

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Data availability

Data can be accessed using this link: <https://doi.org/10.17026/dans-zmd-stsg>

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