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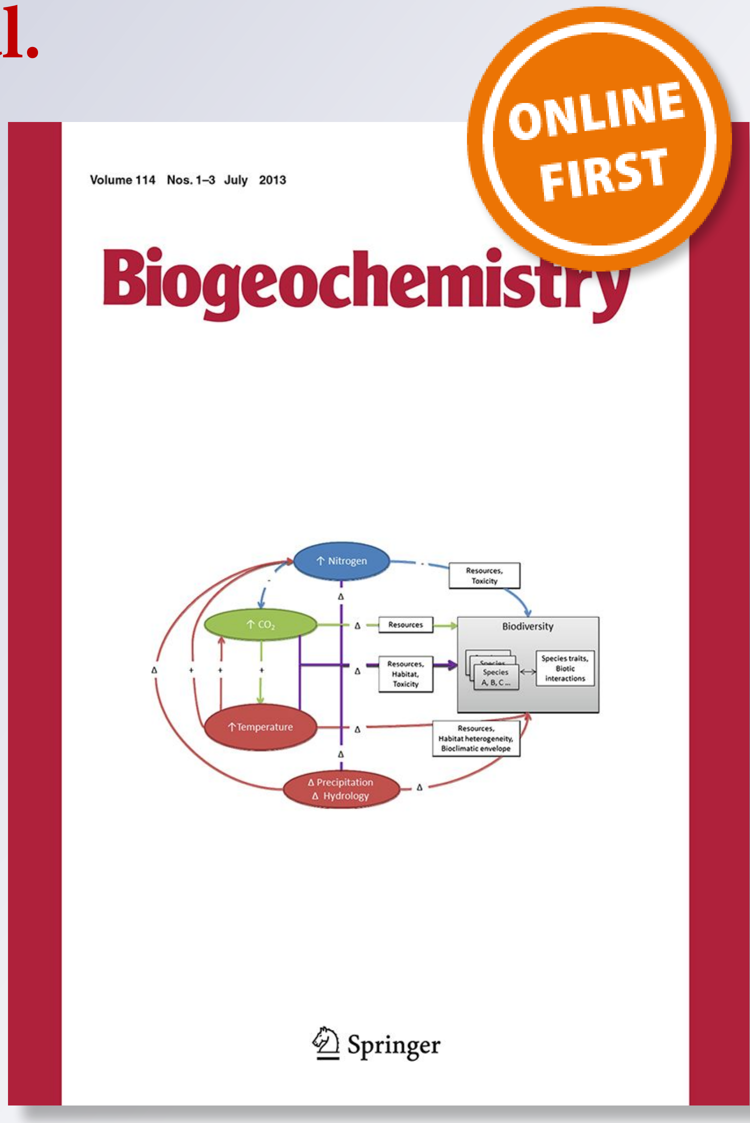

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Abstract Different sources and processes contribute to pCO_2 and CO_2 exchange with the atmosphere in the rivers and floodplains of the Amazon basin. We measured or estimated pCO_2, CO_2 fluxes with the atmosphere, planktonic community respiration (PCR), and environmental and landscape variables along the Negro and Amazon-Solimões rivers during different periods of the fluvial hydrological cycle. Values of pCO_2 ranged from 307 to 7527 µatm, while CO_2 fluxes ranged from − 9.3 to 1128 mmol m^{-2} d^{-1} in the Amazon-Solimões basin. In the Negro basin, pCO_2 values ranged from 648 to 6526 µatm, and CO_2 fluxes from 35 to 1025 mmol m^{-2} d^{-1}. In a general linear model including data from Negro and Amazon-Solimões basins, seasonal and spatial variation in flooded vegetated habitat area, dissolved oxygen, depth and water temperature explained 85% of surface pCO_2 variation. Levels of pCO_2 varied with inundation extent, with higher pCO_2 values occurring in periods with greater water depth and inundation area, and lower dissolved oxygen concentrations and water temperatures. In a separate analysis for the Amazon-Solimões river and floodplains, ecosystem type (lotic or lentic), hydrological period, water temperature, dissolved oxygen, depth and dissolved phosphorus explained 83% of pCO_2 variation. Our results

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demonstrate the influence of alluvial floodplains and seasonal variations in their limnological characteristics on the pCO_2 levels in river channels of the lowland Amazon.

Keywords Hydrological periods · Floodplains · Carbon cycle · Carbon dioxide outgassing · Tropical freshwaters

Introduction

Global and regional carbon balances are influenced by inland waters, as these aquatic ecosystems produce, receive, transport and process organic and inorganic carbon (Cole et al. 2007; Aufdenkampe et al. 2011). River systems can be sources of carbon dioxide (CO_2) to the atmosphere as they are often supersaturated in CO_2, and tropical rivers are globally important CO_2 sources (Richey et al. 2002; Raymond et al. 2013; Borges et al. 2015a; Melack 2016). However, the relative contributions of CO_2 produced in river channels and that derived laterally from river floodplains to pCO_2 and CO_2 emissions remains uncertain (e.g., Borges et al. 2015b; Teodoru et al. 2015; Liu et al. 2016).

The heterotrophic nature of river systems was suggested by the river continuum concept, which predicts that respiration of organic carbon (OC) will outpace OC production in upper and lower reaches of rivers (Vannote et al. 1980). The flood pulse concept added a lateral component to the river continuum concept by including the aquatic terrestrial transition zone (ATTZ) to river functioning (Junk et al. 1989; Ward and Stanford 1995; Junk and Wantzen 2004; Thorp et al. 2006). In reaches where in situ OC production is low, external inputs of carbon often dominate inputs, fueling heterotrophic activity and CO_2 outgassing in these rivers (Vannote et al. 1980; Wissmar et al. 1981; Abril et al. 2013; Butman et al. 2016). In general, inputs OC and CO_2 to rivers can include: (i) CO_2 from upland streams and groundwater, (ii) OC from aquatic and terrestrial primary producers, (iii) respired CO_2 from benthic communities and other aquatic heterotrophs, and iv) CO_2 from root respiration of flooded emergent vegetation. OC and dissolved CO_2 derived from these sources can be transported laterally and downstream to river channels and contribute to heterotrophy in riverine systems. However, the sources and processes contributing to pCO_2 and CO_2 evasion are likely to vary among river basins and require further examination.

The rivers and floodplains of the Amazon basin release large amounts of CO_2 to the atmosphere (Richey et al. 2002; Melack 2016). pCO_2 is often inversely related to dissolved oxygen (DO), reflecting its source from aerobic respiration in Amazon waters (Richey et al. 1988; Devol et al. 1995; Scofield et al. 2016; Amaral et al. 2018). Several studies suggest that OC produced by autochthonous primary producers, mainly within fringing floodplains, is a major source OC and that planktonic oxidation of this labile OC is an important process generating the excess of CO_2 that is transported by the Amazon River and its tributaries (Quay et al. 1992; Waichman 1996; Mayorga et al. 2005; Ellis et al. 2012). Other results emphasize terrestrially derived OC and the rich diversity of organic compounds that vary in their availability to biological processing (Ertel et al. 1986; Hedges et al. 1986, 1994; Mayorga et al. 2005; Ward et al. 2013, 2016). Bioassay experiments conducted with Amazon River water indicate that oxidation of refractory OC occurs and can make a significant contribution to riverine CO_2 (Ward et al. 2013, 2018). Additional sources of CO_2 input to Amazonian waters include root respiration from inundated vegetated habitats in the ATTZ (Melack and Forsberg 2001; Engle et al. 2008), groundwater (Rudorff et al. 2011; Call et al. 2018) and soils in upland catchments (Johnson et al. 2008). Photo-oxidation appears to be a minor contributor to OC degradation and CO_2 production in Amazon rivers (Amon and Benner 1996; Remington et al. 2011; Amaral et al. 2013), although it can enhance the microbial pathway of OC oxidation (Amado et al. 2006; Amaral et al. 2013).

At a regional scale, outgassing and pCO_2 are related to flooded area and associated inundated vegetation (Richey et al. 2002; Abril et al. 2013; Borges et al. 2015b). Mass balance computations indicated that a source of labile OC was needed to sustain the respiration measured in river channels and suggested the importance of lateral fluxes of labile OC from the ATTZ areas (Richey et al. 1990). The ATTZ's importance was reinforced by studies demonstrating that OC from C4 plants, mainly growing in the ATTZ, is oxidized efficiently (Waichman 1996; Engle et al. 2008; Melack and Engle 2009). Abril et al. (2013), using a simple one-dimensional model, demonstrated that dissolved CO_2 is laterally exported to the Amazon River channel and transported hundreds of kilometers within the river.

Understanding CO_2 dynamics in the Amazon basin is challenging due to the continental extent and heterogeneity of fluvial environments and the diversity of CO_2 sources and CO_2 generating processes. Identifying factors influencing these dynamics will contribute to understanding of the role of the Amazon River system in regional and global carbon cycles and potential responses to climatic changes. Our study incorporated a series of cruises in different seasons over long reaches of rivers using a design similar to that of the CAMREX project (Richey et al. 1990). We combined field measurements of CO_2 concentrations, planktonic community respiration (PCR) and environmental variables, together with calculated CO_2 fluxes and remotely sensed wetland composition and flooding patterns to investigate the drivers of CO_2 dynamics in contrasting floodplains and river channels of Amazonian river systems. We examined the Amazon-Solimões River, as the main stem of the Amazon River upstream of Manaus is called the Solimões River in Brazil, in addition to its tributaries: Japura, Jurua, Purus and Madeira River. These rivers all have high sediment and inorganic solute loads (Gibbs 1967), and extensive fringing floodplains occupied by abundant floodable forests and herbaceous aquatic macrophytes (Junk et al. 2011; Hess et al. 2015). We also sampled the Jutai tributary of the Solimões River and the previously under-sampled Negro River and 21 of its tributaries characterized by high amounts of dissolved organic carbon, low pH, low suspended sediment concentrations and low inorganic solute concentrations (Moreira-Turcq et al. 2003). Floodable forests are abundant in the floodplains of these tributaries, but herbaceous aquatic plants are not.

We aimed to identify the factors regulating the CO_2 dynamics in contrasting river by considering environmental parameters, planktonic respiration, and inundation characteristics. We hypothesize that CO_2 dynamics in the lowland Amazon River system is strongly influenced by inputs of CO_2 from the ATTZ. Seasonal changes in depth and inundation area are expected to influence planktonic metabolism due to effects on temperature, DO concentrations and OC inputs from aquatic and upland sources. While we expected CO_2 dynamics to vary among tributaries and seasonally, our results from this multi-river study reveal similar basin-wide controls of CO_2 dynamics in the central lowland Amazon.

Methods

The study was performed in the lowland central Amazon basin with sampling sites in the Amazon-Solimões and Negro rivers as well as tributaries of these rivers and lakes bordering the Solimões River (Fig. 1). Sampling sites in the Negro and Amazon-Solimões rivers are called mainstem, while rivers that feed these main channels are called tributaries, and open water areas on the floodplains are called lakes. The distribution of the sampling sites are as follows: Negro mainstem (4), Negro tributaries (21), Solimões mainstem (6), Amazon mainstem (below Negro and above Madeira) (1), Solimões tributaries (4), Amazon tributary (1, Madeira below S7), lakes along Amazon-Solimões mainstem (9). Additional information is provided in Scofield et al. (2016) for the Negro basin and in Barbosa et al. (2016) for the Amazon-Solimões sites.

We measured water depth, surface pCO_2, dissolved oxygen (DO), pH and water temperature (Temp), and collected surface water for determination of planktonic community respiration (PCR) and concentrations of chlorophyll-a (Chl-a), dissolved organic carbon (DOC), total suspended solids (TSS), total dissolved nitrogen (TDN), and total dissolved phosphorus (TDP) in all environments. River discharge was also measured at all lotic sites. Most measurements and all samplings were made between 0800 h and 1800 h near the center of river channels and in open water habitats in lakes. Depth, velocity and discharge measurements in rivers were made on longitudinal transects through sampling sites. Measurements and sampling were performed in four periods of the hydrological cycle in the Amazon-Solimões basin: low-water (LW), high-water (HW), early falling-water (EFW) and late falling-water (LFW), and during two periods in the Negro basin (LW and HW) (Fig. 2).

To determine the pCO_2 concentrations in the Amazon-Solimões basin, we used the same methodology as Scofield et al. (2016) used in the Negro basin. Briefly, we collected 20 mL of water between 0.15

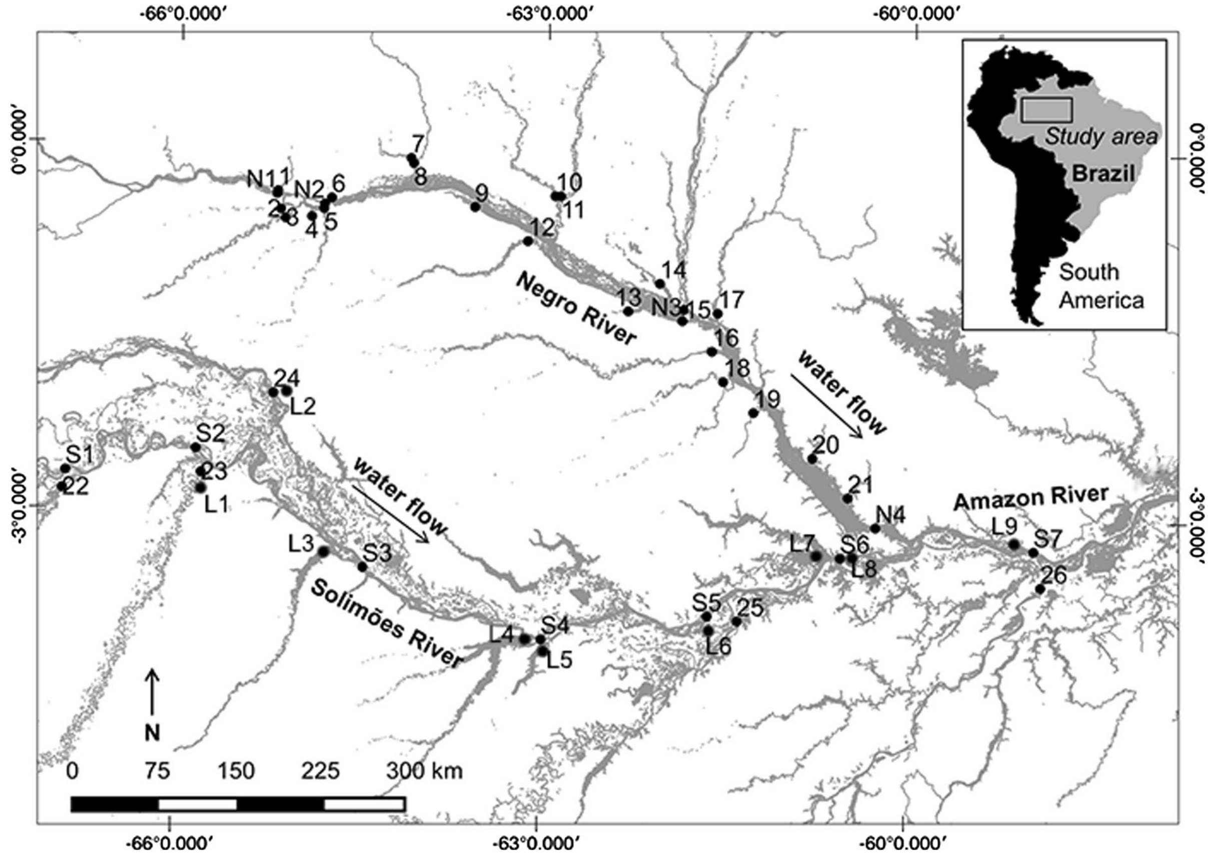

Fig. 1 Map showing sampling sites (n = 46) in the lowland Amazon basin. N1–N4 represent points in Negro river mainstem and S1–S7 represent points in Amazon-Solimões river mainstem. The tributaries in the Negro basin are: Marauia (1), Tea (2), Uneiuxi (3), Aiuanã (4), Urubaxi (5), Darahá (6), Preto (7), Padauari (8), Arirahá (9), Aracá (10), Demeni (11), Cuiuni (12), Caurés (13), Jufari (14), Branco (15), Unini (16), Jauperi (17), Jaú (18), Puduari (19), Apuaú (20) and Cuieiras (21). The tributaries in the Amazon- Solimões Basin are: Jutaí (22), Juruá (23), Japurá (24), Purus (25), and Madeira (26), L1-L9 represent lake sampling points in the Amazon- Solimões basin: Paupixuna (L1), Curupira (L2), Tefé (L3), Coari (4), Mamiá (L5), Ananás (L6), Cabaliana (L7), Calado (L8) and Tia Dora (L9)

and 0.3 m below the surface with 20 mL polyethylene syringes and carefully transferred these samples to rubber-stoppered 30 mL glass vials, that were sealed, injected with an additional 10 mL of atmospheric air and shaken vigorous for 60 s to equilibrate (Cole et al. 1994). The equilibrated air was then collected and analyzed with a portable infrared gas analyzer (IRGA) (EMG-4 Environmental Gas Analyzer for CO_2, PP-Systems) to determine CO_2 within a few hours after collection. At the time of IRGA readings the CO_2 concentration in atmosphere was also determined. At each point we collected 3 water samples for CO_2 determination and averaged the values. Values of pCO_2 in the Negro basin were previously reported in Scofield et al. (2016). However, the reported pCO_2 values were underestimated by approximately 30% due to over pressurization caused by the injection of the extra 10 mL of atmospheric air just before equilibration. These values were corrected here and are now approximately 30% higher than those reported in Scofield et al. (2016).

PCR was determined following DO consumption over 48 h in 20 mL borosilicate vials gently filled with unfiltered water from the sampling sites. Four replicate vials were incubated in an insulated box in the dark at ambient temperature. Oxygen was measured using a Clark-type sensor (OX-N, Unisene) connected to a picoamperimeter (PA 2000, Unisense) following Briand et al. (2004). Sensor sensitivity was $< 2\%$, and response time was < 10 s. PCR rates were calculated by averaging the changes in DO with time for the four replicates.

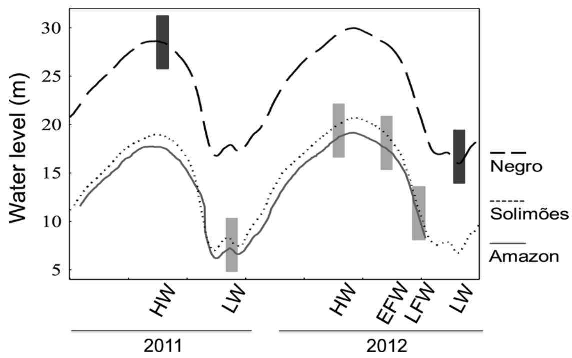

Fig. 2 Variation in the water level of the Negro, Solimões and Amazon rivers measured at the Manaus, Manacapuru and Jatuarana stations, respectively data from ANA, 2013/http://www.snirh.gov.br/hidroweb/). Black and grey rectangles indicate sampling periods in the Negro and Amazon- Solimões basins, respectively, during low-water (LW), high-water (HW), early falling-water (EFW) and late falling-water (LFW)

We measured discharge, depth and current speed using an acoustic Doppler current profiler (ADCP; RD Instruments, broadband, 600 kHz, with a bin size of 0.5 m). Average channel depth was calculated by dividing the total cross-sectional area by the river width observed on each ADCP transect. At each sampling point, at 0.3 m below the surface, we measured pH (Orion Star, Thermo Scientific; precision of 0.1, calibrated with 4.0 and 7.0 standards), conductivity (Orion Star, Thermo Scientific; accuracy of 1 µS cm^{-1}), temperature and DO concentrations (YSI 95 with thermistor (0.2 °C accuracy) and polarographic oxygen sensor (0.2 mg L^{-1} accuracy)). Water collected at 0.3 m in 5 L plastic bottles was analyzed for TSS by weighing suspended sediments collected on pre-weighed 0.5 µm cellulose acetate membrane filters (Meade et al. 1985). Chl-a was collected on 0.7 µm pre- combusted (1 h at 450° C) glass fiber filters (Whatman GF/F) less than 8 h after sampling and determined spectrophotometrically after extraction in hot ethanol following Lorenzen (1967). We used the filtrate of the Chl-a analysis to measure (i) TDN, by high temperature combustion (720 °C) and catalytic oxidation (Total Nitrogen Module—TNM-1, Shimadzu), (ii) TDP, after persulfate digestion, with the molybdenum blue method (Golterman et al. 1978) and (iii) DOC, by high temperature combustion (680 °C) and catalytic oxidation followed by non-dispersive infrared detection (TOC-V Shimadzu). Wind speed was measured using a portable anemometer (Kestrel 200 wind meter) held at 2 m above the water surface, facing the wind for 5 min and recording the average speed registered during this period, following the method described by Alin et al. (2011). Wind speed was normalized to a height of 10 m above the water using equations given in Scofield et al. (2016).

We calculated CO_2 fluxes for all campaigns and estimated total flooded area and flooded vegetated area near all stations sampled during the HW and LW periods in the Amazon-Solimões and Negro basins. CO_2 fluxes were estimated from measured CO_2 concentrations in water and air and k_{600} values derived from the literature. For lotic sites, k_{600} was calculated using a wind-based equation proposed by Alin et al. (2011), while for lentic sites equations proposed by MacIntyre et al. (2010) were applied. The lotic relationship of Alin et al. (2011) was:

$$K_{600} = 4.46 + 7.11 \times U_{10}, \quad (1)$$

where K_{600} is the k value normalized to a temperature of 20 °C and U_{10} is the wind speed at 10 m height, estimated from measured wind speed at 2 m. U_{10} was used in order to compare our results with those from other lotic studies in the Amazon and because Barbosa et al. (2016) reported no significant relation between current speed and K values in our study region. The model by MacIntyre et al. (2010) was chosen for lentic sites because it considered the effect of heat gain and loss on turbulence and outgassing, in addition to wind, and is given by the equation:

$$K_{600} = 2 + (2.04\ U_{10}) \quad (2)$$

Further details of these calculations are given in Scofield et al. (2016).

We used classified images from Hess et al. (2015) to determine the extent of flooded vegetated area and total flooded area upstream of our lotic sampling sites during high and low water periods. We assumed that these wetlands were a major source of labile DOC and pCO_2 to the river channels (Mayorga et al. 2005; Abril et al. 2013), and that the importance of the source diminished with distance from the measurement point due to cumulative downstream emission losses. Habitat data were integrated in a 100 km semicircular buffer, upstream of each river sampling point. This buffer size was chosen based on the predictions of a one-dimensional model for the advective transport of dissolved CO_2 in river channels, presented by Abril et al. (2013). Total flooded area was the sum of the extent from all flooded vegetation and non-vegetation classes in the calculated buffer extracted from Hess et al. (2015) for each sampling site and period.

Statistical analysis

CO_2 fluxes and pCO_2 levels were compared spatially and temporally. First, we compared mainstem with tributary stations for the Negro basin at LW and HW periods, and mainstem, tributaries and lakes for the four hydrological periods investigated for the Amazon-Solimões basin. Second, we compared CO_2 fluxes and pCO_2 levels between periods of the hydrological cycle for each environment type (mainstem, tributaries and lakes). Finally, we compared mainstem and tributaries stations of the Negro basin with similar stations of the Amazon-Solimões basin for a given LW or HW period. For the Negro basin, environment type and periods were compared with unpaired and paired t tests, respectively. For the Amazon-Solimões mainstem and its tributaries we used ordinary one-way ANOVA with Tukey's post hoc tests for multiple comparisons, when comparing environment types for a given period of the hydrological cycle. Repeated paired measurements (RM ANOVA) with Tukey's post hoc test for multiple comparisons were used for seasonal comparisons of pCO_2 and CO_2 fluxes for each of the environment types. Comparisons between similar environment types between Negro and Amazon- Solimões basins were done with an unpaired t test for each period of the hydrological cycle. All tests were done after testing for normality and homoscedasticity. The distributions of pCO_2 and CO_2 fluxes were non-normal and were log transformed for use in the cited tests. We utilized medians for comparisons between sites and periods in the text, since our dataset was non-normally distributed, but for comparative purposes we also reported mean values of pCO_2 and CO_2 fluxes, as it is more commonly reported in the literature.

We used generalized linear models to evaluate the simultaneous effects of factors influencing CO_2 concentrations measured in our study. These analyses were performed using the package nlme (Pinheiro et al. 2015). We evaluated the main and interactive effects of river basin (categorical factor: Negro, Amazon-Solimões), sampled period (categorical factor: LW and HW), environment type (categorical factor: tributaries, mainstem) and environmental variables (continuous variables: community respiration, DOC concentration, dissolved oxygen concentration) on pCO_2 concentrations. To meet normality and homoscedasticity assumptions, pCO_2 values were log-transformed. We built models containing all variables and interactions between variables and used an averaging procedure to identify the best fitting model (functions "aictab" and "evidence" in the aiccmodavg package; Mazerolle 2015). Best fitting models were those that had the lowest AICc scores, while showing high explanatory power (Burnham and Anderson 2004). Additionally, we ran generalized linear models using only the Amazon-Solimões dataset with four sampled periods (categorical factor: HW, LW, EFW, LFW) and three environment types (categorical factor: lakes, tributaries, and mainstem) to specifically evaluate the main predictors of pCO_2 in this basin. In the best fitting models, we performed contrast analyses among categories within categorical factors using the package lsmeans (Lenth and Herva 2015). All statistical analyses and graphics were done in the R programming language (R Core Team 2016) or with GraphPad Prism (Version 7.01).

Results

Physical and chemical conditions are described first, followed by a succinct summary of pCO_2 and CO_2 fluxes. Statistical differences among pCO_2 and CO_2 fluxes in different sites are blended into these sections. Finally, statistical relations between environmental conditions and pCO_2 are presented.

We only describe here the variables that were important to our statistical models (see below). A summary table with results from the other ancillary variables measured in the study is given at Supplementary material Tables 1 and 2. Water depths followed the river hydrograph with greater depths occurring from May to July. In the Negro basin, surface temperatures ranged from 25 to 30 °C with a median of 27.8 °C during HW and from 27.7 to 31.5 with a median of 29.9 °C during LW. In both periods, tributaries and mainstem had similar median temperatures (unpaired t test, $p > 0.05$). Dissolved oxygen varied from 1.2 to 5.3 mg L^{-1} with a median of 2.7 mg L^{-1} during HW when only tributaries were measured and from 4.1 to 7.4 with a median of

Table 1 Carbon dioxide concentrations and dynamics in the Negro River system

Environment type	Environment	pCO_2 (µatm)		CO_2 flux (mmol m^{-2} d^{-1})		Respiration (µM d^{-1})	
		LW	HW	LW	HW	LW	HW
Main channel	Negro 1 (N1)	1114*	2117*	142	308	5.7	2.0
	Negro 2 (N2)	1174+	2382+	168	82	–	20.4
	Negro 3 (N3)	991	3018	158	185	8.0	1.0*
	Negro 4 (N4)	923	3391	145	1025+	–	–
Tributaries	Aiuana (4)	2373+	3945	192	186	2.3	14.7
	Apuaú (20)	1456	2118	287	285	–	22.4
	Aracá (10)	1721	2867	129	333	–	–
	Arirahá (9)	1441	3449	119	215	10.9	26.9
	Branco (15)	641*	2848	72	207	–	20
	Caurés (13)	991	3156	170	313	10.1	14.4
	Cuieiras (21)	2052	4257	102	158	–	–
	Cuiuni (12)	1508	4477	94	762	13.2	36.5
	Darahá (6)	1859	2311	146	80*	–	–
	Demini (11)	1137	3579	72	665	29.2+	31.0
	Jaú (18)	1676	6528+	211	654	15.5	16.4
	Jauperi (17)	1178	4643	112	191	8.6	44.8+
	Jufari (14)	645	2758	35*	467	–	6.3
	Marauia (1)	1648	1328*	132	81	16.8	8.0
	Padauari (8)	1576	2620	157	93	14.2	25.8
	Preto (7)	1916	2808	61	267	15.2	29.4
	Puduari (19)	1439	2639	253	437	1.3*	40.1
	Tea (2)	1585	3852	106	325	10.7	n.d
	Uneiuxi (3)	1536	3110	134	238	15.0	n.d
	Unini (16)	1298	5615	90	860	11.8	8.7
	Urubaxi (5)	2139	3452	293+	153	5.1	11.0
	Median/Mean	1456/1441	3110/3331	134/143	267/343	11/11	16/18

Carbon dioxide partial pressure (pCO_2) in surface water, carbon dioxide fluxes (CO_2 flux) estimated using equation in Alin et al. (2011), and community respiration for the main channel and tributaries stations of the Negro River basin, during the periods of low water (LW) and high water (HW). "n.d" represent not detectable. "–" represents data not available due to analytical problems, "*" represents the lowest value, and "+" the highest value. Same numbers of sampling sites in Fig. 1 (between parentheses in the "Environment" column)

6.2 mg L^{-1} during LW when median DO values were similar between tributaries and mainstem stations (unpaired t test, $p > 0.05$). TDP values at HW ranged from 0.1 to 5.1 µM with a median of 0.5 µM, while LW values ranged from below detection to 0.9 µM with a median of 0.2 µM. TDP values were similar between tributaries and mainstem sites (unpaired t test, $p > 0.05$).

At the Amazon-Solimões sites surface water temperatures varied from 25.8 to 34.2 °C, with a median of 29.8 °C. Median temperatures were higher in the lakes than mainstem, but similar to tributaries (one way ANOVA, Tukey's post hoc test, $p < 0.05$), with the overall extreme values recorded at lake sites; the highest value (34.2 °C) during LFW (Tefé L.) and the lowest (25.8 °C) during the EFW period (Paupixuna L.) DO concentrations were similar for lakes, mainstem and tributaries (one way ANOVA, $p > 0.05$) with DO lake values ranging between 1.9 mg L^{-1} (Cabaliana L., HW) and 8.3 mg L^{-1} (Mamia L., LW), mainstem sites from 1.4 mg L^{-1} (Solimões 5 R., HW) to 6.7 mg L^{-1} (Amazonas R., LW), and those in

Table 2 CO_2 concentrations and dynamics in the Solimões/Amazonas River system

	Environment	pCO_2 (µatm)				CO_2 flux (mmol m^{-2} d^{-1})				Respiration (µM d^{-1})			
		LW	HW	EFW	LFW	LW	HW	EFW	LFW	LW	HW	EFW	LFW
Main channel	Solimões (S1)	1720	3405	1562	1137	68	632	146	194	24.8	33.7	33.0	34.3+
	Solimões (S2)	1315	4745	2422	1225	36	1128+	141	188	36.3	25.2	20.8	28.5
	Solimões (S3)	961	4432	2934	1383	99	311	512	127	24.7	9.1	21.7	16.8
	Solimões (S4)	1249	3009	2634	1957	122	355	206	274	42.9	18.5	18.6	9.1
	Solimões (S5)	967	3368	2634	2766	23	956	659	473	19.2	24.5	20.4	14.7
	Solimões (S6)	1666	3279	2974	2582	238+	578	439	707	54.4	17.8	33.4+	10.2
	Amazonas(S7)	1030	3339	3368	3509	219	847	770	440	49.2+	9.7	–	–
Tributaries	Japurá (24)	921	2285	2918	1720	35	213	806+	102	19.3	9.8	16.2	14.6
	Juruá (23)	1262	2936	3957	1616	34	512	327	94	30.1	23.5	30.4	19.5
	Jutaí (22)	1078	4715	3572	1010	134	271	218	71	1.2*	28.5	12.8	20.3
	Madeira (26)	773	2002	1955	1205	15	183	319	82	28.3	29.3	23.5	8.0
	Purus (25)	1050	3319	4573	5648+	80	369	714	742+	7.8	15.6	21.2	17.9
Lakes	Ananás (L6)	2593	3198	2839	4921	39	241	134	279	12.7	46.2+	22.7	25.2
	Cabaliana (L7)	1006	3215	4034	5173	12	74	88	117	84.9+	12.7	19.6	3.6
	Calado (L8)	878	2946	2288	4315	20	152	104	234	39.9	13.2	26.3	4.3
	Coari (L4)	933	1449*	927*	822	23	54	16*	16	55.4	1.5*	11.8	2.6*
	Curupira (L2)	2719+	1915	4918	3475	44	91	233	164	9.2	9.4	15.6	31.5
	Mamiá (L5)	307*	1856	2612	1799	– 9*	51*	123	111	21.4	3.1	27.6	11.7
	Paupixuna (L1)	2168	4861+	7527+	–	32	353	176	–	34.0	24.6	–	–
	Tefé (L3)	952	2070	1108	440*	50	51*	23	2*	8.0	8.0	7.1*	6.1
	Tia Dora (L9)	1054	3040	3232	3526	71	191	104	95	45.9	2.8	–	–
	Median/mean	1050/1267	3198/3114	2918/3095	1878/2511	39/66	271/363	206/298	145/226	28.3/31	15.6/17.5	21/21	14.7/15.5

Carbon dioxide partial pressure (pCO_2) in surface water, carbon dioxide fluxes estimated using equation in Alin et al. (2011), for main channel stations, and in MacIntyre et al. (2010) for lakes, and community respiration, for the lakes of the Solimões basin, during the periods of low (LW), high (HW), early falling (EFW), and late falling water (LFW). "–" represents data not available due to analytical problems. "*" represents the lowest value, and "+" the highest value. Same numbers of sampling sites in Fig. 1 (between parentheses in the "Environment" column) tributaries varying from 0.7 to 7.2 mg L^{-1}. Median TDP values for mainstem, tributaries and lakes were similar (0.5 µM for mainstem sites and 0.4 µM for tributaries and lakes). TDP values ranged from 0.1 µM (Amazonas R., LW) to 1.8 µM (Solimões 4 R., HW) in the mainstem, 0.04 µM (Jutaí R., EFW) to 1.2 µM (Purus R., HW) in tributaries, and between 0.1 µM (Cabaliana L., LW) and 1.9 µM (Ananas L., HW) in lakes. Most sampled lakes were thermally and chemically stratified during high and falling water periods.

Total flooded areas and flooded vegetated areas were higher near the Amazon-Solimões sites than in the Negro basin during both LW and HW periods (unpaired t test, $p < 0.05$) (Fig. 3). The median flooded area during LW was almost four and three times lower than the median during HW for the Negro and Amazon-Solimões sites, respectively (unpaired t test, $p < 0.05$) (Fig. 3). Median flooded vegetated habitats areas were four times lower during LW than HW (unpaired t test, $p < 0.05$). Median flooded vegetated areas for tributaries were lower than those for mainstem sites at the Negro basin (unpaired t test, $p < 0.05$), being 71% lower during HW and 79% lower during the LW. For the Amazon-Solimões sites median flooded vegetated habitats were similar (unpaired t test, $p > 0.05$) between tributaries and mainstem stations when comparing these stations for a given period (LW or HW).

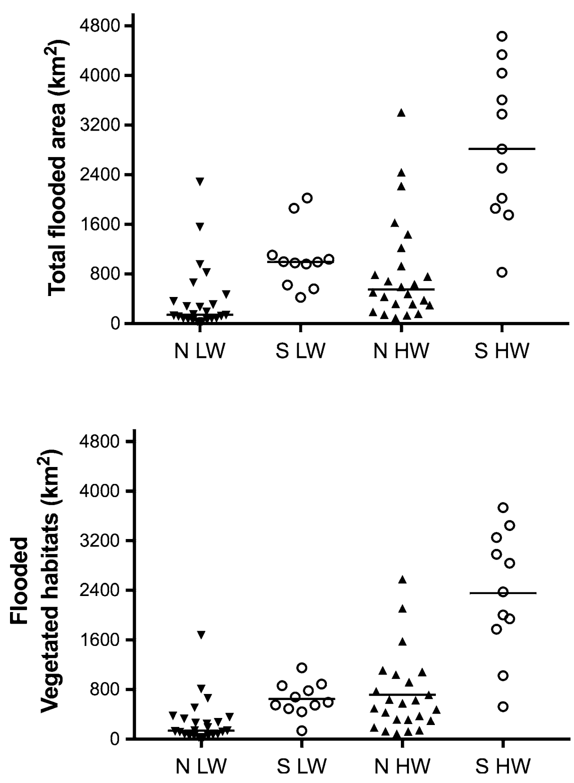

Fig. 3 Total flooded area (top panel), and total flooded vegetated area (bottom panel) in square kilometers calculated for a 100 km hemispherical buffers applied to the classified wetland vegetation maps of Hess et al. (2015), for sampling stations in the Negro (N) and Amazon- Solimões (S) basins during low water (LW) and high water periods (HW)

In the central lowland Amazon (all sites included), pCO_2 and CO_2 fluxes were higher during the HW period. pCO_2 in the Negro basin varied from 1328 to 6528 µatm during HW period, with a median (mean) value of 2700 (2727) µatm for mainstem and 3156 (3446) µatm for tributaries stations. During LW it varied from 641 to 2373 µatm and median (mean) pCO_2 values were 1052 (1050) and 1536 (15,150 µatm for mainstem and tributaries stations, respectively (Table 1; Fig. 4). Comparisons between mainstem sites and tributaries in the same hydrological periods did not differ significantly (unpaired t test, $p > 0.05$) for the Negro basin. However, seasonal comparisons (HW vs LW periods) were significant, with greater pCO_2 values registered during HW for mainstem and tributaries stations (Paired t test, $p < 0.05$). At the Amazon- Solimões sites, pCO_2 values (including all hydrological periods investigated) varied from 307 µatm (L. Mamia, LW) to 7527 µatm (L. Paupixuna, EFW). There were no differences between environment types for a given period of the hydrological cycle (one-way ANOVA, Tukey's post hoc test, $p < 0.05$) (Table 2; Fig. 4), as their median (mean) pCO_2 values were similar (mainstem 2608 (2408), lakes 2593 (2603) and tributaries 1978 (2426) µatm) (Table 2; Fig. 4). Seasonal comparisons of pCO_2 values for mainstem stations were lower at LW than during HW and EFW periods (RM ANOVA, Tukey's post hoc test, $p < 0.05$). Similarly, for tributaries and lakes, pCO_2 values during LW were lower than values measured during HW and EFW periods (RM ANOVA, Tukey's post hoc test, $p < 0.05$).

CO_2 fluxes in the Negro basin varied from 80 to 1025 mmol m^{-2} d^{-1} during HW and from 35 to 293 mmol m^{-2} d^{-1} during LW (Table 1). Differences in CO_2 fluxes between mainstem and tributaries were not observed for the Negro basin during LW or HW periods. When comparing between LW and HW periods for the same environment types, significant differences were noted for tributaries of the Negro

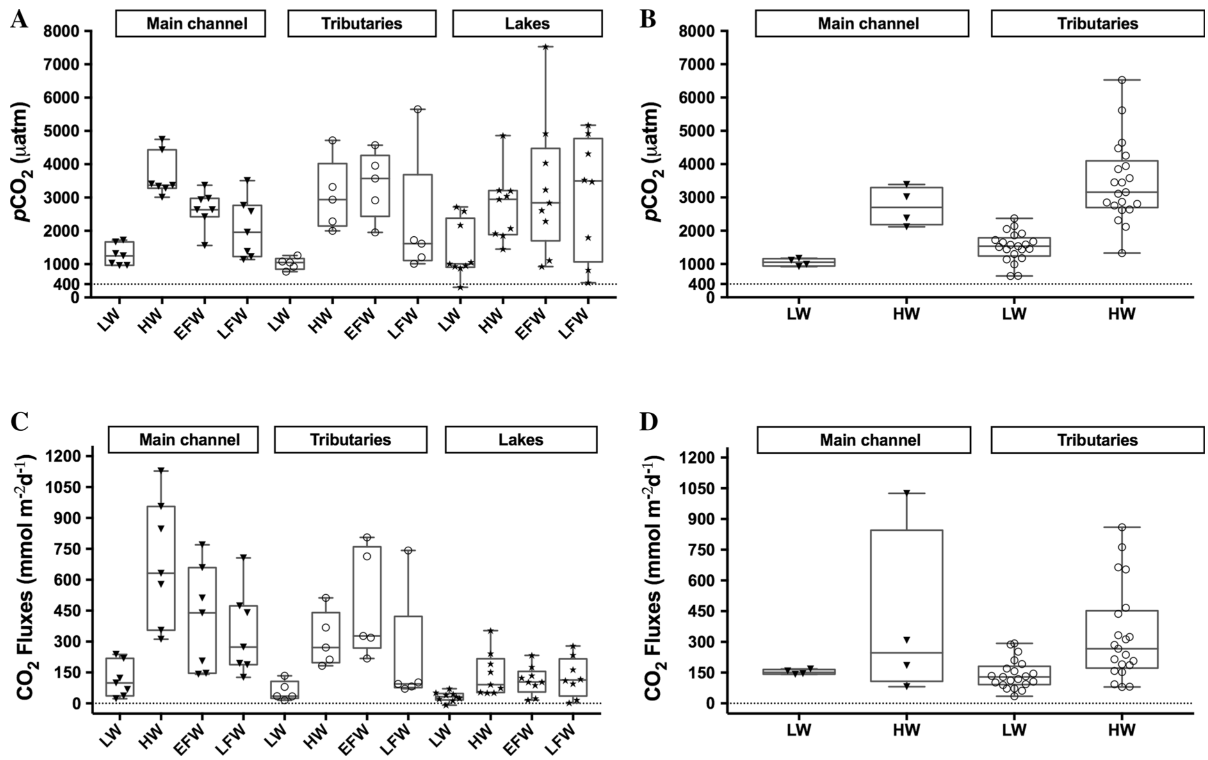

Fig. 4 Carbon dioxide partial pressure (pCO_2)—**a**, **b** Carbon dioxide fluxes to the atmosphere—(CO_2 fluxes). **c**, **d** in the floodplain lakes, tributaries and mainstem of the Amazon-Solimões river basins (**a**, **c**), during the low water (LW), early falling water (EFW), late falling water (LFW), and high water (HW) periods, and in the mainstem and tributaries stations of the Negro basin (**b**, **d**), during the LW and HW periods. The box mid-lines represent medians; the interquartile range (IQR) is represented by the lower and upper box boundaries, which denote the 25th and 75th percentiles, respectively; whiskers indicate correspond to the maximum and minimum. Symbols represent pCO_2 and CO_2 fluxes values for each sampled site

River with greater values during HW (paired t test, $p < 0.01$). For the Amazon-Solimões sites, CO_2 fluxes ranged from − 9.3 (L. Mamia, LW) to 1128 mmol m^{-2} d^{-1} (Solimões 2, HW). Seasonal comparisons for each environment type were significant for mainstem and tributaries, but not for lakes (Fig. 4). Median CO_2 fluxes were significantly lower during LW compared to the CO_2 fluxes measured during HW and EFW periods in mainstem and tributaries (RM ANOVA, Tukey's-posthoc, test $p < 0.05$) (Table 2; Fig. 4). Overall median (mean) CO_2 fluxes were more than three times higher in mainstem sites and two times higher in tributaries compared to lakes (292 (389), 198 (266) and 88 (102) mmol m^{-2} d^{-1}, respectively). Mainstem and tributaries had similar CO_2 fluxes during all periods investigated (Table 2; Fig. 4), and their CO_2 fluxes were significantly greater than the values measured in lakes during HW and EFW (ANOVA, Tukey's post hoc test, $p < 0.05$), (Fig. 4).

Comparisons between the Amazon-Solimões and Negro sites could only be made considering tributaries and mainstem stations during the LW and HW periods. Significant differences in pCO_2 and CO_2 fluxes were found when comparing similar environmental type (e.g., mainstem vs mainstem) between the Negro and Amazon-Solimões basins and for both periods of the hydrological cycle (unpaired t test, $p < 0.01$). During LW, CO_2 fluxes were four times higher and pCO_2 levels were 1.4 times higher in tributaries from the Negro basin when compared to the Amazon-Solimões sites. Conversely, during HW, median pCO_2 was 2.5 times higher and CO_2 fluxes were 1.2 times higher at the Amazon-Solimões sites (Fig. 4; Table 2).

Flooded vegetated habitat area within buffers ($t = 2.1$, $p < 0.05$), DO ($t = -11.4$, $p < 0.001$), water temperature ($t = -4.6$, $p < 0.001$) and depth (t = 2.8, p = 0.78) accounted for 85% of the variability in pCO_2 measured in the lowland Negro and Amazon-Solimões sites (GLM, adjusted $r^2 = 0.85$ $p < 0.01$) (Fig. 5). PCR did not contribute significantly to pCO_2 variation. At the Amazon-Solimões sites, DO (t = -8.5, $p < 0.001$) (Fig. 5), water temperature (t = − 2.9, $p < 0.01$) (Fig. 5), TDP (t = − 0.9, p = 0.38), the interaction between environment type (lentic or lotic) and hydrological period

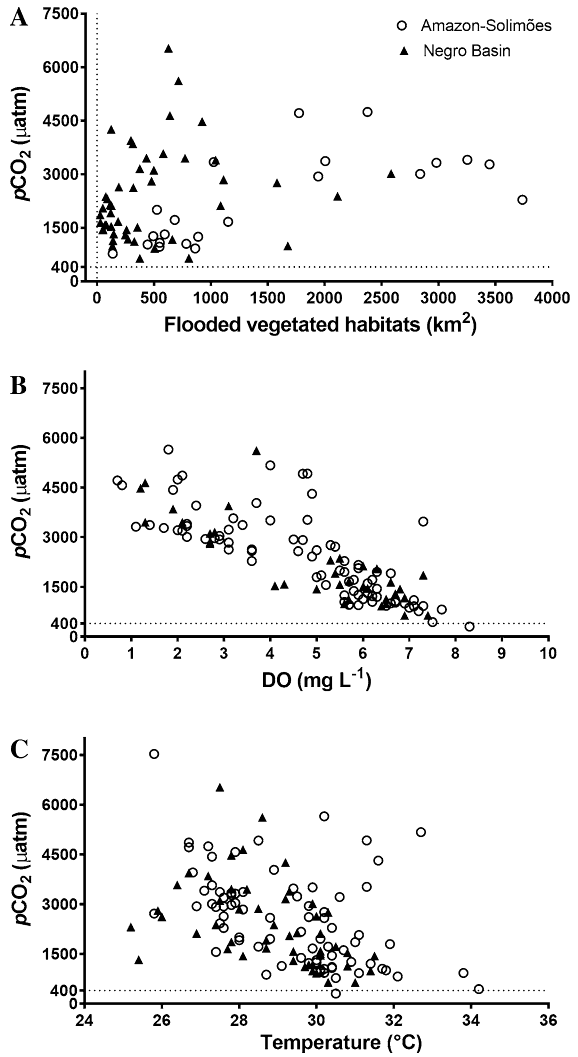

Fig. 5 Variation carbon dioxide partial pressure (pCO_2) as a function of: **a** flooded vegetated habitat area; **b** dissolved oxygen (DO), and **c** temperature, for each sampling station in Negro and Amazon-Solimões basins during the high and low water periods.) Variables presented in the figure are the ones selected in the general linear model (with $p < 0.05$) for the central lowland Amazon basin

(t = − 2.4, $p < 0.05$), and depth (t = 1.0, p = 0.31) explained 83% of the measured variation in pCO_2 (GLM, adjusted $r^2 = 0.83$, $p < 0.001$). All cited variables, except for TDP and depth, contributed significantly to the model ($p < 0.001$).

Discussion

The Amazon basin has large, heterogeneous and dynamic aquatic habitats, which vary seasonally in area (Hess et al. 2003, 2015). The inclusion of flooded vegetated area in our general linear model for pCO_2 variation supports the importance of these habitats for CO_2 dynamics in the central lowland Amazon. For instance, during the HW period, we found higher pCO_2 in mainstem stations of the Amazon-Solimões River and greater extent of total flooded area and flooded vegetated areas near these sites, when compared to Negro basin sites (Fig. 3). The importance of the flooded vegetated area for pCO_2 was also supported by the analysis of Borges et al. (2015b), who related differences in pCO_2 with the percentage of wetland vegetation coverage in rivers in the Congo and Amazon basins. The higher pCO_2 levels along the Amazon-Solimões mainstem during RW and HW may also reflect the abundance of floating herbaceous plants on its floodplains, a recognized source of OC and pCO_2 (Quay et al. 1992; Waichman 1996; Mayorga et al. 2005; Engle et al. 2008) that is largely absent on the Negro floodplain.

In the regression model for the Amazon-Solimões sites, depth, TDP and the interaction between environment type (lotic or lentic) and hydrological period contributed to the variation in pCO_2. The pCO_2 in river channels varied with hydrological period, with higher levels consistently occurring at HW. Median pCO_2 levels in lakes were more variable at HW, compared to other periods, and were only consistently low during LW (Table 2; Fig. 4). The low pCO_2 values observed in river channels during LW can be attributed, in part, to the reduction in flooded vegetated area on floodplains which is an important source of dissolved OC and CO_2 to these environments. Open water environments, which dominate the inundated portions of the floodplains at LW, often have abundant phytoplankton which can have a strong effect on community metabolism (Melack and Forsberg 2001; Abril et al. 2013; Forsberg et al. 2017; Amaral et al. 2018), as can be seen by the higher DO values observed during LW compared to the HW period (Supplementary Tables 1, 2), often reducing the CO_2 concentrations during this period. This may contribute to the lower levels of CO_2 transported from floodplains to rivers during this period (Moreira-Turcq et al. 2013) and may also explain the lower levels and variability of pCO_2 we encountered in lakes at LW (Fig. 4). The variable influence of phytoplankton in lakes could explain the greater variability of pCO_2 observed in other periods (Fig. 4), and at least part of the variability in TDP (Forsberg et al. 1988).

The negative correlation between DO and pCO_2 in our regression models likely reflects the effect of aerobic respiration as a source of CO_2 as reported for rivers of the Amazon basin (Richey et al. 1988; Devol et al. 1995; Scofield et al. 2016) and elsewhere (Liu et al. 2016; Borges et al. 2015a). Devol et al. (1995) demonstrated that pCO_2 and DO in the Amazon main channel do not vary as a simple function of in-channel volumetric respiration but also depend on channel depth, surface gas exchange and lateral inputs from adjacent floodplains. They found no significant variability in in-channel PCR and argued that most of the variation in gas concentrations was due to seasonal change in channel depth and floodplain inputs. Moreover, there are other processes that contribute to CO_2 production and DO consumption, in addition to planktonic community respiration, that vary seasonally with inundation. These processes include sediment respiration (Cardoso et al. 2014), methane oxidation (Barbosa et al. 2018), and root respiration by herbaceous and woody plants (Hamilton et al. 1995). Lateral export of dissolved CO_2 from fluvial wetlands to river channels has been demonstrated along the central Amazon main channel (Devol et al. 1995; Abril et al. 2013).

Ward et al. (2018) extrapolated results of PCR obtained from controlled incubations with river water to areal estimates of CO_2 production and argued that in-channel respiration is capable of sustaining the excess dissolved CO_2 often observed in Amazonian rivers as well as the CO_2 emitted by these systems. We did similar calculations based our estimates of PCR, channel depths at each site, and fluxes. At most sites in the Negro basin, PCR represented a fraction of the fluxes, though in four sites during high water areal PCR exceeded daily fluxes. This result suggests that additional sources of CO_2 are needed to support the pCO_2 and CO_2 fluxes measured in mainstem and tributaries stations of the Negro basin. A recent study of the lower reach of the Negro river (Call et al. 2018) demonstrated the importance of lateral inputs of CO_2 associated with groundwater to the Negro mainstem. In contrast, in most Amazon-Solimões sites, areal PCR exceeded the CO_2 fluxes. However, we caution that both our estimates and those of Ward et al. (2018) are based on extrapolations of very few PCR measurements and are being compared to short-term flux estimates that under-sample the temporal and spatial variability of these complex aquatic systems.

That PCR did not contribute significantly to our regression models may be related to our PCR protocol which is likely to have under-estimated respiration rates. We measured discrete DO changes in small stationary vials, incubated in the dark for 48 h. Water motions that maintain plankton in suspension during incubation have been shown to enhance respiration (Ward et al. 2018). DO changes at night by plankton exposed to light during the day can also be higher than those for plankton held in the dark for 24 h (Amaral et al. 2018). In an analysis of PCR in the Amazon-Solimões mainstem and associated tributaries, Benner et al. (1995) concluded that bacterial respiration was carbon limited and depended on continuous inputs of labile OC.

The range of CO_2 fluxes reported here (Tables 1 and 2) is similar to that encountered in other studies that included sampling sites in the Amazon basin and elsewhere. The mean CO_2 fluxes of 541 mmol m^{-2} d^{-1} reported in Butman and Raymond (2011) for a variety of north temperate rivers in the USA is higher than the overall (both basins together) average values for tributaries (241 mmol m^{-2} d^{-1}) and mainstem stations (364 mmol m^{-2} d^{-1}) in our study. The fluxes measured in tributaries in our study are similar to those measured by Sawakuchi et al. (2017) in clear water tributaries (207 mmol m^{-2} d^{-1}), though clear-water mainstem values are considerably higher (596 mmol m^{-2} d^{-1}). From the CO_2 fluxes reported by Alin et al. (2011) we calculated an overall mean flux of 427 mmol m^{-2} d^{-1} for Amazonian river stations wider than 100 m, including the Purus, Negro, Madeira, Amazonas and Solimões rivers, during HW, RW and FW periods, which is comparable to the overall mean CO_2 flux of 389 mmol m^{-2} d^{-1} encountered for mainstem stations of the Amazon-Solimões river in our study. de Rasera et al. (2013) reported a higher mean CO_2 flux value in the lower Negro (LW and HW periods together, 512 mmol m^{-2} d^{-1}) compared to the overall mean CO_2 flux (277 mmol m^{-2} d^{-1}) encountered for mainstem stations of the Negro river basin in our study. Also, the mean CO_2 flux value of 474 mmol m^{-2} d^{-1} reported by de Rasera et al. (2013) for mainstem stations of the Solimões river is slightly higher than the mean value reported here. Abril et al. (2013) reported CO_2 fluxes ranging from 466 to 727 mmol m^{-2} d^{-1} during LW in the Amazon River, and HW in the Solimões River, respectively. Richey et al. (1990) reported an overall mean value of 432 mmol m^{-2} d^{-1} for Solimões mainstem stations sampled at different cruises representative of the distinct periods of the Amazonian hydrological cycle.

Our median CO_2 fluxes measured in lakes are in the range of CO_2 evasion rates reported in other studies of Amazon floodplain lakes. Our median values are two times higher than the 50 mmol $m^{-2}d^{-1}$ CO_2 fluxes reported during the LW period in Lake Camaçari (Polsenaere et al. 2013), and 1.25 times higher than the CO_2 fluxes estimated for floodplains in the central and low Amazon River (Richey et al. 1988). However, our median CO_2 fluxes for floodplain lakes were 50% lower those estimated by Devol et al. (1988) for the central Amazon basin, during the EFW period, using direct measurements with floating chambers. Also, our CO_2 fluxes were in general, more than three times lower than the CO_2 fluxes estimated in a seasonal study in L. Curuai, along the floodplain of the lower Amazon River (Rudorff et al. 2011). Rudorff et al. (2011) calculated pCO_2 by measurements of DIC and pH, and estimated k_{600} incorporating thermal effects in addition to wind in their calculations; the average k_{600} reported in the study was estimated to be more than two times higher than the median k_{600} of 5 cm h^{-1} calculated for lakes in our study, what is likely the cause of such differences.

The range of pCO_2 values (641 to 6528 µatm) encountered in our study for lotic sites, were in the range of the pCO_2 values reported in a global compilation of pCO_2 values from 6708 river and stream sampling sites, that reported a median pCO_2 value of 3100 µatm (Raymond et al. 2013). The average pCO_2 value of 1235 ± 515 µatm for mainstem stations investigated in the subtropical Yangtze River basin (Liu et al. 2016) is lower than the average pCO_2 value (2314 ± 1058 µatm) including all mainstem stations in our study. Our pCO_2 values varied greater seasonally than spatially (Fig. 4), in contrast to the trend reported in Liu et al. (2016) for the Yangtze river basin. These differences might be associated to the greater extent of floodplain environments present in our study sites, that are likely to contribute more CO_2 to the river channels, compared to the predominantly mountainous river sites in the Liu et al. (2016) study. Additionally, the changes in CO_2 dynamics influenced by the seasonal flood pulse (Junk et al. 1989) discussed above are likely to explain the greater seasonal differences in pCO_2 values encountered in our study.

Our pCO_2 values are also in agreement with values reported for Amazonian aquatic ecosystems as summarized in Melack (2016). Richey et al. (2002) reported an annual average pCO_2 value of 4350 ± 1900 µatm for mainstem stations, significantly higher than the average value encountered here for mainstem sites (2314 ± 1058 µatm). This difference is possibly related to the inclusion of up-river mainstem stations with higher pCO_2 values in the Richey et al. (2002) study. The range of pCO_2 concentrations (259 to 7808 µatm) reported by de Rasera et al. (2013) for seven rivers of the Amazon basin, including clear, black and white waters, is within the range of pCO_2 values reported here. The median pCO_2 values observed during HW at main channel stations (mainstem + tributaries) in the Amazon-Solimões (HW-3198 µatm) and Negro (HW-3110 µatm) systems were comparable to the mean pCO_2 value of 3317 µatm registered by Alin et al. (2011) at similar river channel stations (wider than 100 m) integrating different periods of the hydrological cycle.

We conclude that pCO_2 levels in the lowland Amazon vary in synchrony with the annual hydrological cycle of the river and directly with water depth. Fluctuations in the area of flooded vegetation on floodplains upstream from sampling sites was shown to be an important factor influencing CO_2 levels measured in river channels, confirming the functional role of the ATTZ in river metabolism. DO was also demonstrated an important factor explaining pCO_2 variability in river channels, reinforcing the importance of aerobic respiration in CO_2 dynamics. The fact that PCR, the presumptive source of CO_2 in the river channel, was not included in our statistical models highlights the need to better understand the spatial and temporal complexity of OC production and respiration in the fluvial ecosystem and the advective transport of

CO_2 and DOC between compartments. This will require novel experimental approaches that include a combination of laboratory and field measurements of metabolic, hydrodynamic and hydrological processes integrated into a coherent systemic context that considers the spatial and temporal variability of carbon sources, dynamics and fluxes.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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