

1 Temperature-dependence of the relationship between $p\text{CO}_2$ and dissolved organic carbon in
2 lakes

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19 Abstract

20 **The relationship between the partial pressure of carbon dioxide ($p\text{CO}_2$) and dissolved organic**
21 **carbon (DOC) concentration in Brazilian lakes, encompassing 194 lakes across a wide latitudinal**
22 **range in the tropics, was tested. Unlike the positive relationship reported for lake waters, which was**
23 **largely based on temperate lakes, we found no significant relationship for warm low-latitude lakes,**
24 **despite very broad ranges in both $p\text{CO}_2$ and DOC. These results suggest substantial differences in**
25 **carbon cycling in warm lakes, which must be considered when up scaling limnetic carbon cycling to**
26 **global scales.**

27

28 1.Introduction

29 Lakes cover less than 2% of the continent's surface [Downing et al., 2006; McDonald,
30 2012], but play a significant role in the global carbon (C) cycle [Cole et al., 1994; 2007; Tranvik
31 et al., 2009], contributing significantly to C burial and emissions to the atmosphere [Cole et al.,
32 2007; Downing et al., 2008 and Tranvik et al., 2009]. Dissolved organic carbon (DOC)
33 represents a major C pool in lakes, with both autochthonous and allochthonous contributions
34 [Xenopoulos et al., 2003; Duarte and Prairie, 2005; Duarte et al., 2005; Sobek et al., 2005; Cole
35 et al., 2007; Prairie 2008; Marotta et al., 2009; Tranvik et al., 2009; Larsen et al., 2012],
36 supporting heterotrophy tactility [Sobek et al., 2007] and affecting key biological and physico-
37 chemical processes involved in C cycling [Steinberg et al., 2006]. Large inputs of terrestrial
38 organic C and its subsequent mineralization have been suggested to be a major driver of CO₂
39 supersaturation commonly encountered in lakes [Xenopoulos et al., 2003; Duarte and Prairie,
40 2005; Duarte et al., 2005; Sobek et al., 2005; Cole et al., 2007; Prairie 2008; Marotta et al., 2009;
41 Larsen et al., 2012].

42 The mechanistic connection between DOC and heterotrophic CO₂ production is believed to
43 underpin the significant positive relationship between *p*CO₂ and DOC reported in comparative
44 analyses [Houle, 1995; Sobek et al., 2005; Larsen et al., 2012]. However, recent analyses have
45 revealed that the relationship between *p*CO₂ and DOC in lake waters is regionally variable and
46 not universal [Lapierre and del Giorgio, 2012]. Hence, relationship between *p*CO₂ and DOC
47 reported in comparative analyses based on data sets dominated by temperate and high-latitude
48 lakes may not be extrapolated for all kinds of lakes, mainly because of the tropical warm lakes
49 are generally underrepresented in global caught [Raymond et al., 2013].

50 One of priority for comparative study is the latitudinal variance, where lake temperature,
51 ice cover and mixing regime will differ and these climatically driven processes, in turn, should
52 strongly influence OC cycling [Hanson et al., 2015]. At low latitudes, warm conditions over the
53 whole year may impose intrinsically faster rates of C cycling in terrestrial [Ometto e al., 2005]
54 and aquatic [Marotta et al., 2009; Marotta et al., 2010] ecosystems compared to the low rates
55 characteristic of temperate systems in winter. High temperatures affect heterotrophic activity and
56 the associated mineralization rates of organic matter in soils [Davidson et al., 2006], waters
57 [López-Urrutia et al. 2007; Wohlers et al. 2008; Regaudie-de-Gioux and Duarte 2012] and
58 aquatic sediments [Wadham et al., 2012; Gudasz et al., 2010, Marotta et al., 2014]. An enhanced

59 heterotrophic activity in tropical ecosystems would support high fluxes of CO₂, leading to CO₂
60 enrichment in lake waters through inputs from in flowing waters and mineralization processes in
61 the water column and sediments.

62 A previous comparative analysis, characterized by a paucity of low latitude data, reported
63 *p*CO₂ in lake waters to be independent of temperature [Sobek et al., 2005]. However, a positive
64 relationship between temperature and *p*CO₂ was observed when subtropical and tropical
65 ecosystems were included in the analysis [Davidson et al., 2004; Marotta et al., 2009; Dillon et
66 al., 2010]. Hence, the relationship between lake *p*CO₂ and DOC could also be temperature-
67 dependent and, therefore, may differ between temperate and tropical lakes. Here, we test the
68 applicability of the relationship between *p*CO₂ and DOC, largely derived from north-temperate-
69 cold lakes [Houle, 1995; Sobek et al., 2005; Larsen et al., 2012], to tropical and subtropical lakes
70 in Brazil. Brazil has a large territory in the tropics, showing a high density of lakes and ponds
71 [Downing et al., 2006], with a diversity of conditions that render them appropriate to examine
72 general patterns [e.g. Marotta et al., 2009].

73

74 2.Methods

75 2.1.Study area and Lakes

76 Brazil extends from 5° 16' 20" North to 33° 44' 42" South, showing an area of
77 approximately 8,547,000 km² that represents half of South America and encompasses a high
78 diversity of low-latitude landscapes [Ab`Saber, 2003] predominantly located within tropical
79 latitudes. We conducted a survey of *p*CO₂ and DOC between 2003 and 2011 in surface waters of
80 166 permanent lakes from 0 to 33° of latitude across Brazil (Figure 1), yielding a total of 225
81 water samples. The lakes were sampled in representative biomes of Brazil: (1) Amazonia Forest
82 (Amazonia Biome, n = 65), (2) Pantanal Floodplain (Pantanal Biome, n = 29) and the (3)
83 Tropical (< 24° of latitude) and (4) Subtropical (> 24° and < 33° of latitude) Coasts, both in the
84 Atlantic Forest Biome (n = 35 and n = 37 lakes, respectively; Figure 1). These biomes follow the
85 classification of the Brazilian Institute of Geography and Statistics for biomes (IBGE 2004,
86 ftp://geofp.ibge.gov.br/mapas_tematicos/mapas_murais/biomas). Our data set encompasses a
87 broad inter-lake heterogeneity (n=166) for *p*CO₂ and DOC simultaneously sampled among
88 Brazilian biomes and along the latitudinal gradient, independent of the year's season.

89 The Amazonian Forest biome is formed by the most extensive hydrographic network of the
90 globe, the Amazon River basin that occupies a total area about 6.11 million km² from its
91 headwaters in the Peruvian Andes to the mouth in the Atlantic Ocean (ANA – www.ana.gov.br).
92 The Amazon Forest is the Brazilian biome characterized by higher mean annual precipitation
93 (approximately 2200 mm) coupled to warm mean air temperatures around 25°C and high cloud
94 coverage and humidity with low fluctuations over the whole year [Chambers, 1999]. We
95 sampled a wide variety of lakes, characteristic of different areas of the Amazonian Forest,
96 encompassing “clear” (low DOC and suspended solids), “white” (low DOC and high suspended
97 solids) and “dark” (high DOC and low suspended solids) lakes.

98 The Pantanal Floodplain is the world’s largest tropical freshwater wetland, extending
99 across an area of about 150,000 km² between 16° and 20° S and 58° and 55° W [Por, 1995].
100 Annual averages temperature and precipitation are approximately 22 °C and 1,000 mm,
101 respectively [Mariot et al., 2007], with a strong seasonality and subsequent variation in the
102 flooded area [Junk and Nunes da Cunha, 2005]. The high-water period occurs during the rainy
103 summer (usually from September to December), and low waters typically during the dry winter
104 (from March to July) [Hamilton, 2002].

105 The Atlantic Forest biome extends along a broad latitudinal belt between 5° and 30° S from
106 subtropics to tropics and a narrow longitudinal section between 55° and 56° W, occupying an
107 area of 1.11 million km² along the Brazilian coast (IBGE-www.ibge.gov.br). This biome is
108 characterized by numerous shallow coastal lakes receiving high inputs of refractory organic
109 matter [Farjalla et al., 2009] derived from the typical open xerophytic vegetation on sandy soils,
110 where water retention is low [Scarano, 2002]. The mean air temperatures vary from 27° C in
111 winter to 30° C in summer at the tropical coast [$< 24^\circ$ of latitude; Chellappa et al., 2009] and
112 from 17 and 20° C at the subtropical coast [$> 24^\circ$ of latitude; Waechter, 1998]. The mean annual
113 precipitation reaches 1,164 mm [Henriques et al., 1986] and 1,700 mm [Waechter, 1998] in the
114 tropical and subtropical Brazilian coast respectively. This biome is also characterized by
115 strong seasonality, with rainy summers and dry winters [Chellappa et al., 2009].

116

117 2.2 Sampling Design and Analytical Methods

118 Our sampling design encompassed the most representative Brazilian biomes from tropical
119 and subtropical coastal areas to tropical and subtropical forests (Amazon and Atlantic Forest)

120 and inland wetlands (Pantanal), with the intra-lake heterogeneity and seasonal fluctuations
121 randomly assessed and further integrated by means of each ecosystem. We joined 194 lakes,
122 including 166 from our own survey plus 28 from the published literature. The values reported
123 here represented, on an opportunistic manner, daily averages (N= 4 or 5 samples) for a given
124 year season or/and one sampling time over different seasons, which were also both integrated by
125 means of each lake.

126 pH, salinity and temperature in waters were measured *in situ*. pH was determined using a
127 pH meter (Digimed – DM2) with a precision of 0.01 calibrated with standard solutions of 4.0 and
128 7.0 units of pH before each sampling hour. Temperature and salinity were measured using a
129 Thermosalinometer (Mettler Toledo - SevenGo SG3) coupled to a probe inLab 737 previously
130 calibrated with 0.01M KCl. Surface lake waters for total alkalinity and DOC analyses were
131 collected taking care to avoid bubbles at about 0.5 m of depth using a 1L Van Dorn bottle.
132 Alkalinity was determined in the field by the Gran's titration with 0.0125 M HCl immediately
133 after sampling [Stumm and Morgan, 1996]. Water samples for DOC were pre-filtered (0.7mm,
134 Whatman GF/F) and preserved by acidification with H₃PO₄ 85% to reach pH < 2.0 in sealed
135 glass vials [Spyres et al., 2000]. In the lab, DOC was determined by high-temperature catalytic
136 oxidation using a TOC-5000 Shimadzu Analyzer. *p*CO₂ concentrations in surface waters were
137 calculated from pH and alkalinity following Weiss [1974], after corrections for temperature,
138 altitude and ionic strength according to Cole et al. [1994].

139 Aware of the difficulties in determining the *p*CO₂ in lakes with high contribution of
140 organic compounds [Wang et al., 2013] and also the possible overestimation due to the method
141 of TA and pH rather than direct measurements of *p*CO₂ [Abril et al., 2015], we tested the
142 relationship of *p*CO₂ and DOC considering the raw data and after correcting the contribution of
143 organic acids on TA and subsequent *p*CO₂ data, using the fitted linear regression for the medians
144 and averages values of the relative difference between calculated and measured *p*CO₂ with
145 ranked pH and DOC values, according the data disposable of Abril et al., [2015] (Figure 3 and 4,
146 more detail in support material).

147 2.3. Statistical Analyses

148 The variables *p*CO₂ and DOC did not meet the assumptions of parametric tests even after
149 logarithmic transformations [Zar, 1996], as data were not normally distributed (Kolmogorov-
150 Smirnov, *p* < 0.05) and variances were heterogeneous (Bartlett, *p* > 0.05). Therefore, we used

151 medians and non-parametric tests to compare these variables among biomes (Kruskall-Wallis
152 followed by Dunn's multiple comparison post hoc test, $p < 0.05$). The linear regression equations
153 were fitted to compare our results with previous studies from Sobek et al., [2005]. Statistical
154 analyses were performed using the software Graphpad Prism version 4.0 for Macintosh
155 (GraphPad Software, San Diego, CA).

156 3.Results

157 The lake waters surveyed were warm across all biomes (median 25-75% interquartile
158 range = 27.5°C , 25.2 – 30.1), but colder in subtropical coastal lakes (23.4°C , 20.0 – 26.2)
159 compared to Pantanal and Amazonian lakes (29.5°C , 27.7 – 31.4 and 29.4°C , 27.6 – 31.0,
160 respectively; Dunn's test, $p < 0.05$, Figure 2a). DOC concentrations were consistently high (6.3
161 mg C L^{-1} , 4.3 – 11.9) for all Brazilian biomes, but significant lower in the Amazonian Forest (3.8
162 mg C L^{-1} , 2.7 – 5.8) compared to the tropical coast (13.4 mg C L^{-1} , 6.1 – 32.8; Figure 2b; Dunn's
163 test, $p < 0.05$). Most lakes (approximately 83% of raw data) showed surface waters
164 supersaturated in CO_2 relative to atmospheric equilibrium ($p\text{CO}_2$ in atmospheric equilibrium of
165 $403\mu\text{atm}$, according Tans and Keeling 2014; data available in
166 www.esrl.noaa.gov/gmd/ccgg/trends/global.html#global), with much higher $p\text{CO}_2$ values in
167 Amazonian lakes (7,956 μatm , 3,033 – 11,346) compared to subtropical coastal lakes (900 μatm ,
168 391.3 – 3,212; Figure 2c; Dunn's test, $p < 0.05$).

169 The $p\text{CO}_2$ in surface waters of Brazilian lakes was independent of DOC concentrations
170 (Linear regression for raw data, $p > 0.05$, Figure 3a). After correcting our data and Sobek data
171 with the contribution of organic acids on TA and subsequent $p\text{CO}_2$ data, using the fitted linear
172 regression for the median values of the relative difference between calculated and measured
173 $p\text{CO}_2$ with pH, both groups continuous with the same pattern observed before (not significant
174 relationship for Tropical data ($p > 0.05$, $n = 194$) and positive relationship for Sobek dataset
175 ($p\text{CO}_2 = 45,70 \pm 1,84 \times \text{DOC} + 623,7 \pm 18,83$, $R^2 = 0,12$, $p < 0,0001$, $n = 4433$), figure 4a and
176 4b).

177 Even after correcting our data and Sobek data with the contribution of organic acids on
178 TA and subsequent $p\text{CO}_2$ data, using the fitted linear regression for the averages values of the
179 relative difference between calculated and measured $p\text{CO}_2$ with pH and medians and average
180 values with DOC, we continuous not observing a positive relationship between $p\text{CO}_2$ and DOC
181 for Brazilian data (see more detail in support material). The range of $p\text{CO}_2$ for a similar DOC

182 range in Brazilian lakes was larger than that reported by Sobek et al., [2005] for data set
183 dominated by high-latitude cold lakes, despite the number of lakes in their data set being
184 much larger.

185

186 4. Discussion

187 The Brazilian lakes sampled here were characterized by a prevalence of CO₂
188 supersaturation, consistent with general trends for lakes [e.g. Cole et al., 1994, Algesten et al.,
189 2005] and earlier reports for tropical lakes [Marotta et al., 2009]. The very high *p*CO₂ observed
190 here, in median 900 and 8300 μatm for subtropical and Amazon lake waters (respectively) are
191 consistent with those reported earlier for the Amazon River and tributaries (2,000 - 12,000 μatm;
192 Richey et al., [2002]), Amazon floodplain lakes (3,000 - 4,898 μatm; Rudorff et al., [2012]),
193 Pantanal lakes and wetlands (2,732 - 10,620 μatm; Hamilton et al., [1995]), coastal lakes (768 -
194 9,866 μatm; Kosten et al., [2010]; 361 - 20,037 μatm; Marotta et al., [2010b]), and global values
195 for tropical lakes (1,255 - 35,278 μatm; Marotta et al., [2009]), reservoirs (1,840 μatm;
196 Aufdenkampe et al., [2011]) and wetlands (3,080 - 6,170 μatm; Aufdenkampe et al., [2011]).

197 The not significant (Figure 3a and 4a) or weakly negative relationship (support material)
198 between DOC and *p*CO₂ reported here for warm-low latitude lakes contrasted with significant
199 positive relationships derived from previous datasets dominated by high-latitude lakes [Houle,
200 1995; Prairie et al., 2002; Jonsson et al., 2003; Sobek et al., 2005; Roehm et al., 2009; Lapiere
201 and del Giorgio, 2012; Larsen et al., 2012]. The results presented show that warm-low latitude
202 lakes range widely in *p*CO₂, reaching very high values, but tend to have comparatively more
203 uniform DOC concentrations.

204 Tropical conditions based on higher annual temperatures and solar incidence typically
205 increases the aquatic primary productivity activity [Paerl and Huisman 2008] that releases into
206 waters the DOC produced by the CO₂ uptake of algae and submerged plants [Staehr and Sand
207 Jansen 2007], that can withstand a negative variation in the *p*CO₂ with an increase in the DOC
208 concentration. The contrasting not-significant or weak negative relationship between *p*CO₂ and
209 DOC in warm Brazilian lakes here with respect to that positive relationship for cold lake waters
210 from the data set of Sobek al. (2005), suggests a temperature dependence of the *p*CO₂ and DOC
211 correlation in global lakes.

212 In conclusion, the finding that $p\text{CO}_2$ does not increase with DOC concentration in
213 Brazilian tropical lakes rejects the hypothesis that DOC serves as a universal predictor for $p\text{CO}_2$
214 in lake waters [Larsen et al., 2012]. Even discounting a possible artifact of the method that could
215 be causing an overestimation in the values of $p\text{CO}_2$, or considering the contribution of organic
216 acids on the alkalinity, the pattern of no relationship between DOC and $p\text{CO}_2$ in the Tropical
217 lakes was strongly confirmed. Despite limitations in the method of measuring the $p\text{CO}_2$, our
218 work is important because it adds to the literature a data set about DOC and $p\text{CO}_2$ of tropical
219 lakes so far not included in the global calculations until now. Therefore, our results suggest
220 potentially important latitudinal differences from depositional aquatic environments, whose
221 causes still need to be better addressed to improve accuracy of global C cycle models.

222

223 Authors Contribution

224 All authors contributed to the study design, interpreted data and wrote or commented the
225 manuscript. L. P. and H. M. performed the sampling and sample analyses.

226

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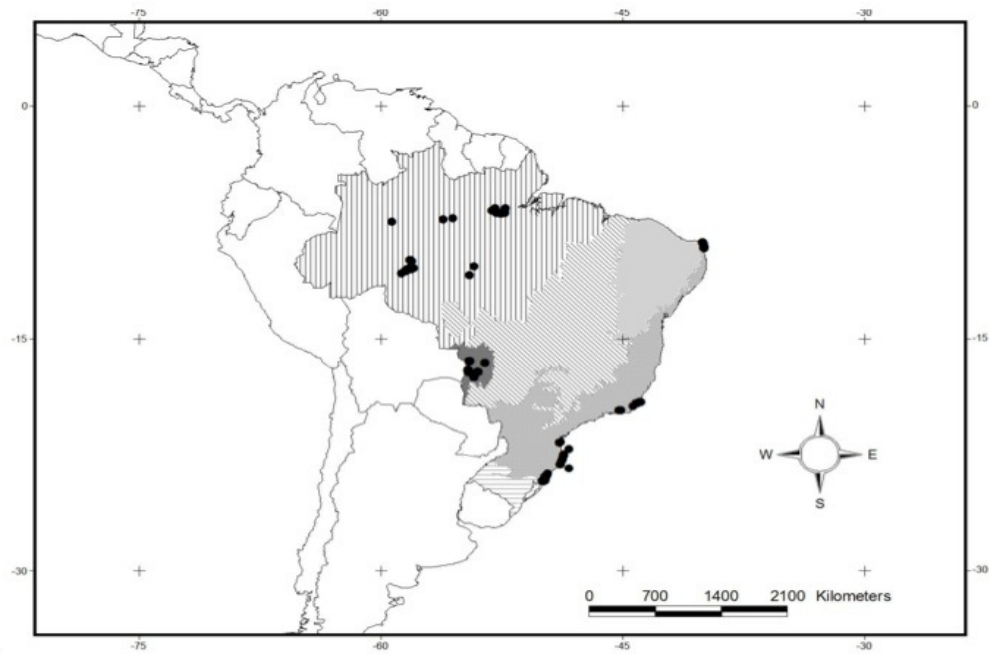
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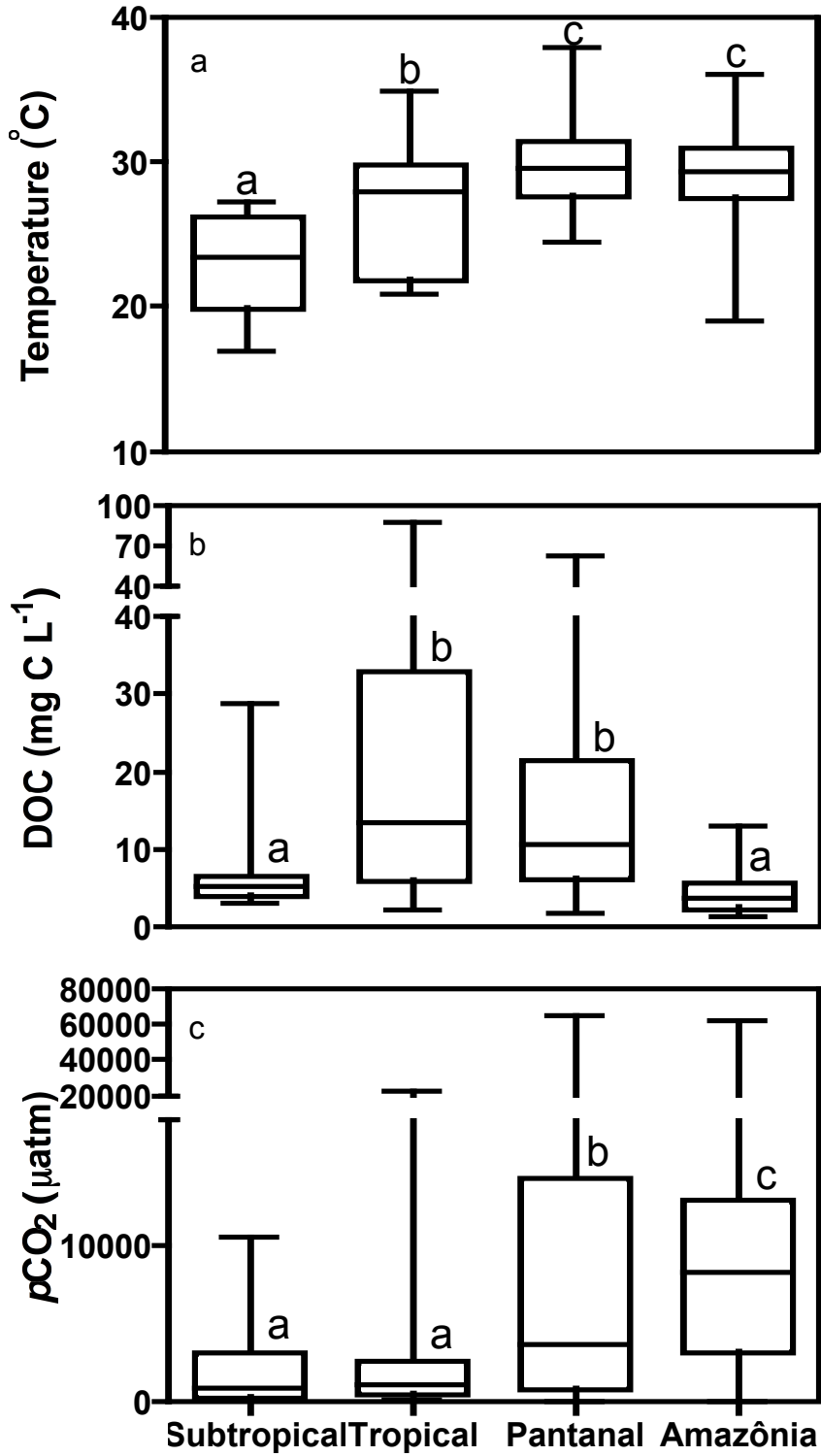
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430 Figure 1. Geographic location of Brazilian lakes sampled at different biomes (IBGE 2004,
431 available in ftp://geoftp.ibge.gov.br/mapas_tematicos/mapas_murais/biomas): Amazonia Forest
432 (vertical lines), Pantanal Floodplain (dark gray), and Atlantic Forest (gray; Tropical and
433 Subtropical costal lakes).



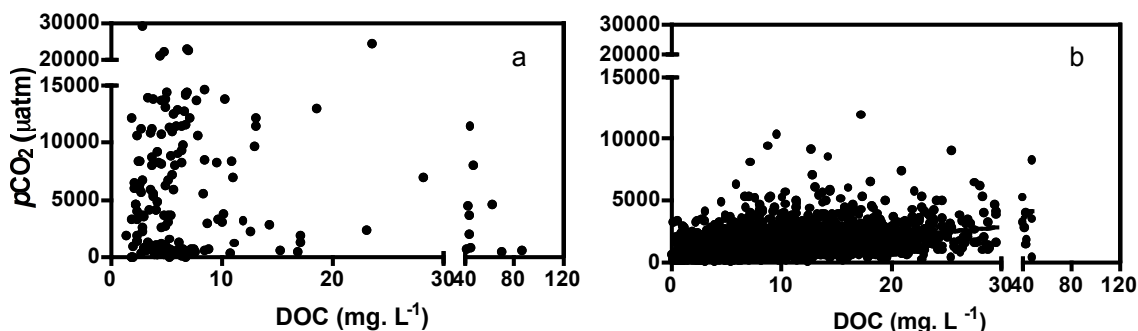
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436 Figure 2. Values of (A) temperature (°C), (B) DOC concentrations (mg C L⁻¹) and (C) pCO₂
 437 concentration (µatm) of Brazilian lakes sampled from different biomes, as defined by (SUBT)
 438 Subtropical Coastal lakes (n = 37), (TROP) Tropical coastal lake (n = 63), (PANT) Pantanal
 439 Floodplain (n = 58) and (AMAZ) Amazonia Forest (n = 67). The line depicts the median. The
 440 boxes show the quartiles, and the whiskers mark the 10% and 90% percentiles. Different
 441 lowercase letters near the boxplot indicate significant statistic differences between the groups
 442 (Kruskall-Wallis followed by Dunn`s multiple comparison post hoc test, p < 0.05).

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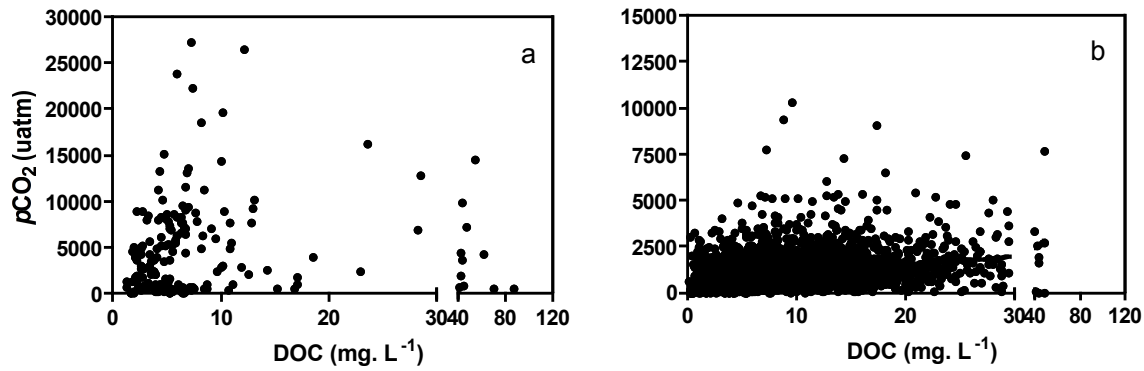
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446 Figure 3. The relationship between pCO₂ values and DOC concentrations for surface lake waters
 447 at (a) warm low latitudes from our compilation, and (b) cold high latitudes from the data set of
 448 Sobek et al. (2005). Each circle represents integrated values for each lake (see details in the
 449 Methods section). The solid line represents the fitted linear regression equation for cold
 450 lakes ($pCO_2 [\mu atm] = 2.67 + 0.414 \log DOC [mg C L^{-1}]$; $R^2 = 0.26$; $p < 0.05$, $n = 4554$). A non-
 451 significant linear regression was observed for warm low-latitude lakes ($p > 0,05$, $n = 194$).

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454 Figure 4: The relationship between $p\text{CO}_2$ values and DOC concentrations for surface lake waters
 455 after correcting the contribution of organic acids on TA and subsequent $p\text{CO}_2$ data, compiled
 456 as described in Figure 3 and using corrections from the fitted linear regression for the median
 457 values of the relative difference between calculated and measured $p\text{CO}_2$ with pH (see methods
 458 for details; data for corrections available in Abril et al., 2015). The solid line represents the fitted
 459 linear regression equation for cold high-latitude lake waters ($p\text{CO}_2 = 45,70 \pm 1,84 \times \text{DOC} +$
 460 $623,7 \pm 18,83$, $R^2 = 0,12$, $p < 0,0001$, $n = 4433$). A non-significant linear regression was observed
 461 for warm low-latitude lakes ($p > 0,05$, $n = 194$).

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