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Do models of organic carbon mineralization extrapolate to warmer tropical sediments?

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Abstract

Freshwater sediments are important sites of organic carbon (OC) burial and mineralization. Previous studies indicate that warming can increase rates of OC mineralization, implying more CO_2 release from sediments and, consequently, less OC burial, but temperatures typical of tropical ecosystems are poorly represented in the models of temperature and OC mineralization. We measured OC mineralization rates in 61 Brazilian tropical systems, including rivers, streams, lakes, coastal lagoons, and reservoirs from different regions (Pantanal, Amazonia, Atlantic Forest, and coastal areas). Oxygen consumption and dissolved inorganic carbon production in sediment core incubations were used for estimating OC mineralization rates. Multiple regression models were used to investigate the importance of temperature and other variables to predict OC mineralization. The average OC mineralization rate for all systems was 1223 ± 950 mg C m^{-2} d^{-1}. Rates increased significantly with increasing temperature and varied across system types and regions. In addition, salinity, total nitrogen, and chlorophyll *a* were important factors controlling OC mineralization in tropical sediments. The pattern of increasing mineralization with temperature was remarkably consistent with theoretical and empirical expectations. The explanatory power of previous temperature vs. mineralization models is confirmed and enhanced by the addition of the tropical data that substantially extended the temperature range.

Sediments are recognized as important components of the carbon cycle at local and regional scales, as they are active sites of carbon storage and mineralization (Tranvik et al. 2009). In sediments of freshwater ecosystems, those processes are mainly regulated by the availability of electron acceptors (e.g., oxygen, nitrate, manganese, iron, and sulfate), mixing regimes, the quantity and quality of the organic carbon (OC), and temperature (Fenchel et al. 2012). In spite of the increasing efforts to understand the effects of each of those processes on carbon fluxes from freshwater ecosystems, uncertainties still remain, particularly concerning the potential effect of temperature (Gudasz et al. 2010).

Temperature modulates many biological processes, including the metabolism of organisms (Yvon-Durocher et al. 2010). Based on models predicting the effect of temperature on metabolic processes in sediments, increasing temperature leads to higher OC mineralization rates and, consequently, less carbon burial (Gudasz et al. 2010). However, most of the studies used to develop these models cover only a limited range of temperatures (range from all studies 0°C to 25°C) and poorly represent aquatic ecosystems in tropical areas, where water temperatures often exceed 30°C (Hamilton 2010). Other studies have noted that the effect of increasing temperature on OC mineralization may not be the same in tropical and in temperate aquatic ecosystems (Pace and Prairie 2005; Yvon-Durocher and Allen 2012). However, other factors besides temperature, such as nutrient and electron acceptor availability, may also control mineralization rates (Talling and Lemoalle 1998).

Tropical inland waters (defined as those systems between the Tropics of Cancer and Capricorn) have an uneven distribution over the landscape and are mostly floodplain lakes, rivers, streams, and reservoirs (Downing et al. 2006). Based on comparative studies, tropical aquatic ecosystems differ from boreal and temperate systems in the absence of a cold season, the occurrence of high temperatures and irradiation, the importance of polymictic stratification regimes, and, in the case of floodplains, large seasonal changes in water depth and flooded area (Talling and Lemoalle 1998). These ecosystem characteristics interact with biogeochemical processes that are predicted to be influenced by climate changes, such as global warming and altered precipitation regimes (Hamilton 2010). Projected future temperatures for South America include an increase in extreme temperatures, with accompanying extremes in precipitation (Marengo et al. 2009). The overall increase in global temperature is expected to cause changes in the metabolism of organisms, which has already been observed in temperate regions (Yvon-Durocher et al. 2010; Yvon-Durocher and Allen 2012). However, in tropical areas little is known concerning the direct effects of increasing temperature on biota and the feedbacks between biota and the climate (Hamilton 2010).

In this study, our goal was to determine the effect of temperature and other variables on OC mineralization rates in the sediments of tropical freshwater ecosystems in Brazil, thereby extending observations on the upper end of the temperature range of natural waters. We also compared

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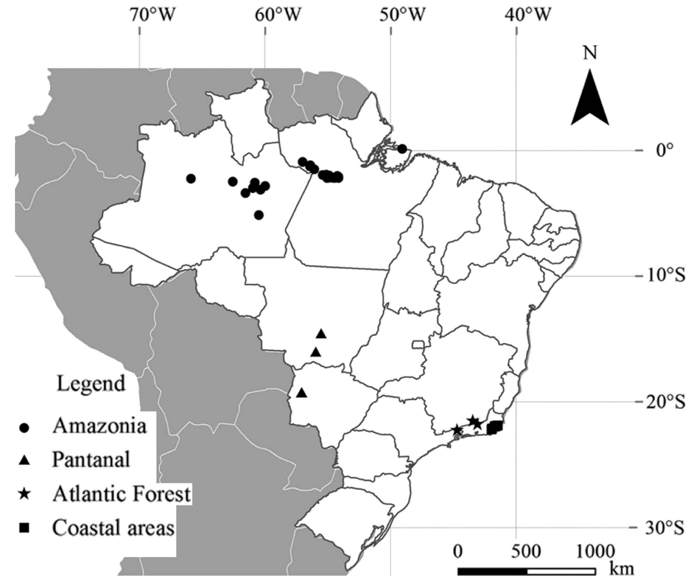

Fig. 1. Map of the 61 tropical Brazilian systems sampled in different regions.

our data to previous empirical and theoretical models relating temperature to carbon mineralization rates (Gudasz et al. 2010). Our results provide evidence that total nitrogen (TN), chlorophyll *a* (Chl *a*), and salinity are important drivers of OC mineralization in tropical sediments. Our data are consistent with theoretical and empirical predictions, and the addition of tropical data enhances the explanatory power of previous models.

Methods

Study sites—This study was conducted in 61 Brazilian tropical systems, including 3 reservoirs, 4 rivers, 2 streams, and 52 natural lakes. The systems have different morphometry and trophic conditions and are located in different Brazilian regions, encompassing three different biomes. These biomes are Amazonia, the Pantanal, and the Atlantic Forest (Fig. 1). The Atlantic Forest also includes coastal areas, but in this study they were analyzed separately due to the elevated salinity in these aquatic ecosystems.

Sediment sampling and incubation—Sediment cores were collected using gravitational sediment samplers (UWITEC® and Kajak) in the deepest and intermediate depth regions of the water body. In situ temperatures and oxygen concentrations were measured in the overlying water of the sediments in all cores in the field. Measurements were made right after the cores were brought from the bottom of the systems and removed from sediment samplers. The upper 10 cm were transferred to incubation cores (5.4 cm inner diameter and 60 cm height) without visible disturbance of the sediment structure. The incubation cores were then completely filled with water from the bottom of the sampling sites, collected with a Van Dorn sampler. The incubation cores were equipped with internal magnetic stirring devices to allow mixing of the overlying water without disturbing the sediment surface. Measurements of dissolved oxygen (DO), temperature, and pH were made in the water overlying the sediment. Aliquots of the overlying water were taken from each core to determine initial concentrations of dissolved inorganic carbon (DIC), total organic carbon (TOC), total carbon (TC), total nitrogen (TN), total phosphorus (TP), total suspended sediments (TSS), salinity, alkalinity, and Chl *a*. The cores were then sealed without headspace with an expandable polyvinyl chloride (PVC) stopper fitted with double o-rings and outlet tubing. The cores were maintained under in situ temperature and in the dark, to avoid primary production. The incubations varied from 4 h to 72 h. All cores were incubated in oxic conditions with initial DO concentrations in the overlying water of the sediment of approximately 7 mg L^{-1}. The effect of the duration of the incubations (4–72 h) was tested in a parallel experiment, performed in some of the systems studied. In this parallel experiment, we repeatedly removed cores for O_2 measurements every 4 h for 72 h. We noticed that the O_2 uptake in the cores during the different time intervals was linear, and rates measured in the different periods were not statistically different. We established that a minimum time of 4 h was enough to ensure a reliable measurement of the OC mineralization rates without affecting the results. As OC mineralization in the sediment is comprised of both aerobic and anaerobic processes that lead to the production of CO_2, we measured the net effect of all these processes as the DIC production in the overlying water of the sediment over time (methane production is excluded by this approach). When DIC data were not available, DO values were converted into carbon units based on a respiratory quotient of 0.9 (Granéli 1979).

Analytical methods—DO concentrations were measured with a picoamperimeter (Unisense® PA 2000), and pH was measured using a pH meter (Micronal B474). Water samples of the sediment were analyzed for DIC and TOC following sodium persulfate digestion on a Tekmar-Dohrmann TC analyzer (model Phoenix 8000). TC was calculated as the sum of DIC and TOC. TN and TP were analyzed according to the spectrophotometric method, TSS was determined gravimetrically according to the American Public Health Association (APHA 1998), and salinity was determined using a thermosalinometer (Yellow Springs Instrument, YSI-30). Alkalinity was analyzed by the titration method, with fixed endpoint titration, using 0.01 mol L^{-1} HCl, and Chl *a* was estimated fluorometrically after acetone extraction (Marker and Jinks 1982).

Data analysis—Differences in mean OC mineralization (measured as DIC production) across systems and across regions were tested using ANOVA, followed by Tukey's post hoc test using SigmaPlot (version 11.0). To investigate the relationships between OC mineralization rates and other explanatory variables, multiple regression models were developed. In this study the total number of samples (n = 392) includes multiple measurements made at each site (i.e., replicates). The multiple regression models were based only on the mean values found for each study site (n = 61). The potential explanatory variables included water depth,

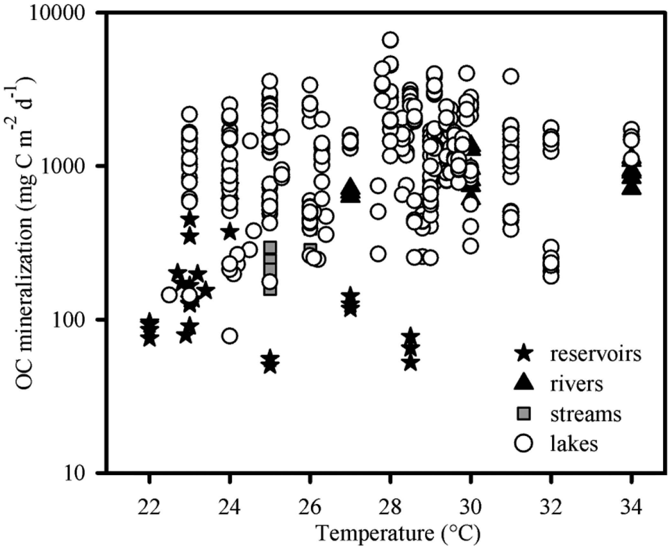

Fig. 2. Variability of OC mineralization rates measured in the sediment of different types of aquatic ecosystems in Brazil: reservoirs (n = 28 samples), rivers (n = 15), streams (n = 11), and lakes (n = 331). The y-axis of OC mineralization rates is represented on a log scale.

water temperature, pH, alkalinity, salinity, TSS, Chl a, and concentrations of TC, TN, and TP. The most parsimonious models were identified based on the Akaike information criterion corrected (AICc) for small sample size. We used a criterion of ΔAICc < 2 to separate models as most likely given the data. Regression analyses were performed with the software Spatial Analysis in Macroecology version 4.0 (SAM; Rangel et al. 2010). All data were $\log_{10}$ transformed.

The relationship between sediment OC mineralization and increase in temperature for the tropical systems considered in this study was compared to that from boreal and temperate ecosystems presented in Gudasz et al. (2010). The data from these two studies slightly overlap on the temperature scale in the region of 22°C to 27°C. We compared the temperature and OC mineralization relationships by plotting the data together and by assessing the similarities of the two regression models. The OC mineralization response to temperature was also expressed as Q_{10} values, i.e., the factor by which the rates increase when the temperature is raised by 10°C (Van't Hoff 1884). Q_{10} was calculated as follows:

$$Q_{10} = (Rt2/Rt1)^{(10/(t2-t1))} \quad (1)$$

where R is the OC mineralization rate at temperatures t1 and t2, and t2 > t1.

Results

The mean OC mineralization rate of all tropical systems was 1223 ± 950 mg C m^{-2} d^{-1}, with a large range between the minimum (50 mg C m^{-2} d^{-1}) and maximum (6607 mg C m^{-2} d^{-1}) rates. Temperature ranged from 22°C to 34°C (Fig. 2). Among the different types of aquatic ecosystems (Figs. 2, 3A), lakes had the highest OC mineralization rates (1363 ± 957 mg C m^{-2} d^{-1}) and reservoirs the lowest (183 ± 168 mg C m^{-2} d^{-1}). Rivers and streams had intermediate rates, 893 ± 231 mg C m^{-2} d^{-1} and 327 ± 126 mg C m^{-2} d^{-1}, respectively. Significant statistical differences were found among the mean log-transformed OC mineralization rates sorted by system type (ANOVA, p-value < 0.001), with lakes and rivers grouping

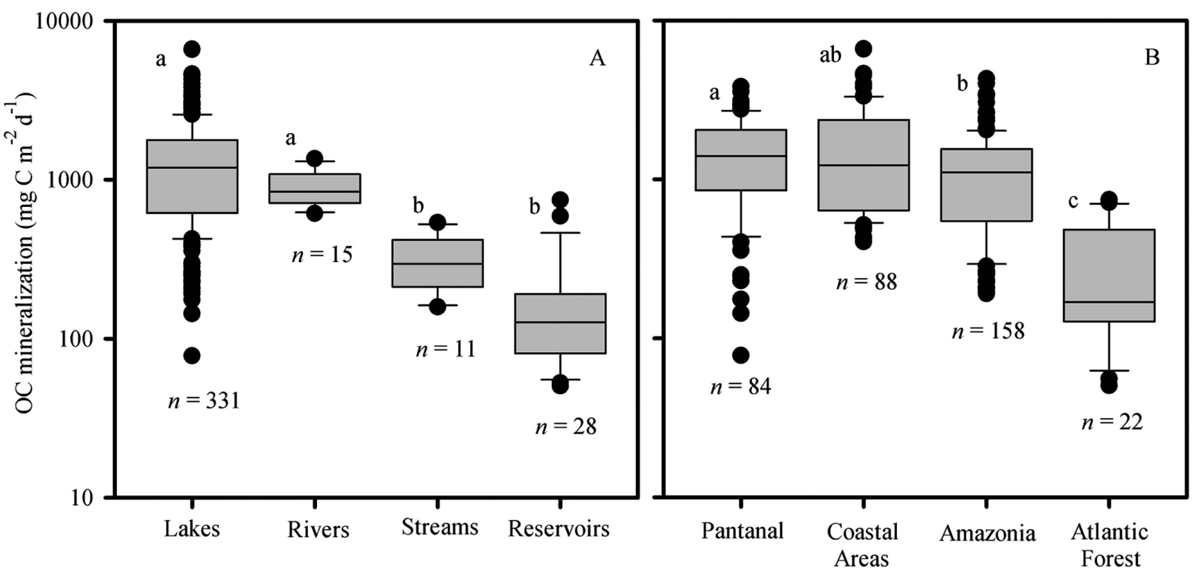

Fig. 3. OC mineralization rates measured in the aquatic sediments of different regions of Brazil. Box plots representing: (A) rates sorted by the different type of systems: reservoirs, rivers, streams, and lakes; (B) rates sorted by different Brazilian regions: Amazonia, Pantanal, coastal areas, and Atlantic Forest. The boundary of the box closest to zero indicates the 25th percentile, a line with the box marks the median, and the boundary of the box farthest from zero indicates the 75th percentiles. Error bars above and below the box indicate the 90th and 10th percentiles, and dark circles represent the outliers. The y-axis of OC mineralization rates is represented on a log scale. Different letters (a, b, c) represent statistical differences among the mean log-transformed OC mineralization rates (one-way ANOVA, Tukey's post hoc, $p < 0.001$).

Table 1. Results of the Ordinary Least Squares (OLS) Model Selection procedure, sorted by corrected Akaike Information Criterion (AICc), likelihood of the model (L(gi|x)), and Akaike weight (AICc Wi). Only results with delta AICc below 2 are shown. Best model (model 1) equation: $y = -1.81 + (2.681 \times \log_{10}$ (temperature)) + (0.316 × $\log_{10}$ (salinity)) + (0.372 × $\log_{10}$ (total nitrogen)).

Model	Variables in the model*	Variables selected	R^2	AICc	Delta AICc	L(gi|x)	AICc Wi
1	1, 2, 3, 4, 5, 6, 7, 8	2, 4, 5	0.670	6.773	0.000	1.000	0.220
2	1, 2, 3, 4, 5, 6, 7, 8	2, 4, 5, 8	0.694	7.759	0.986	0.611	0.135

* 1, system depth; 2, temperature of the water; 3, alkalinity; 4, salinity; 5, total nitrogen; 6, total carbon; 7, total suspended sediment; 8, Chl *a*.

together and having higher rates than streams and reservoirs (Fig. 3A). Among regions (Fig. 3B), systems in coastal areas had the highest OC mineralization (1602 ± 1273 mg C m^{-2} d^{-1}), whereas those in the Atlantic Forest had the lowest (289 ± 235 mg C m^{-2} d^{-1}) and systems in the Amazonia and the Pantanal had intermediate values (1176 ± 756 mg C m^{-2} d^{-1} and 1480 ± 840 mg C m^{-2} d^{-1}, respectively). These differences were also statistically significant (ANOVA, p-value < 0.001). Based on the Tukey test, there were three groups with highest mean values in the coastal areas and the Pantanal (Fig. 3B). The Pantanal data overlapped with Amazonia, and these values were distinctly higher than those from the Atlantic Forest (Fig. 3B).

The linear model selection analysis, used to investigate the relationships between OC mineralization rates and explanatory variables, generated 255 models (based on all possible combinations of the independent variables). Two of the 255 models attained the parsimonious cut-off criterion (ΔAICc < 2; Table 1). The first model ($R^2 = 0.67$, AICc = 6.77) included the variables water temperature, salinity, and TN, whereas the second model ($R^2 = 0.69$, AICc = 7.76) included water temperature, salinity, TN, and Chl *a.* The linear regression between the measured and predicted (most parsimonious model) OC mineralization rates provided a good fit and was unbiased, as suggested by a slope close to 1 (Fig. 4). The relationship between OC mineralization rates and temperature was positive and highly significant ($p < 0.0001$) based on the literature, this study, and all data sets combined (Table 2), despite the scatter in values for any given temperature (Fig. 5). The addition of tropical OC mineralization values substantially increased the r^2 (0.71) over that of the original model of Gudasz et al. 2010 ($p < 0.001$, $r^2 = 0.43$; Table 2). The tropical data also fit the range of Q_{10} values previously reported (Table 3).

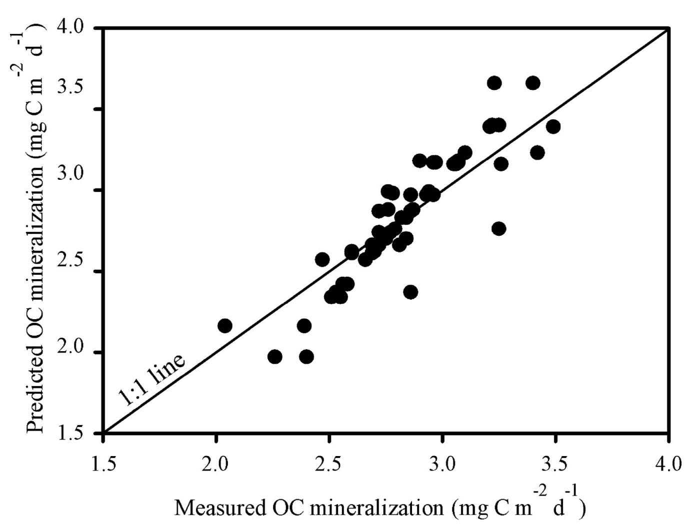

Fig. 4. The relationship between measured and predicted OC mineralization rate measurements based on the best AICc model (model 1, Table 1). The *x*- and *y*-axes representing OC mineralization rates are on a log scale.

Discussion

Increasing temperatures should lead to higher OC mineralization rates and, consequently, less carbon burial based on existing models (Gudasz et al. 2010). However, most prior studies included only boreal and temperate systems, rarely tropical systems. The most recent model of temperature dependence of OC mineralization in the sediments by Gudasz et al. (2010, *see* fig. 1a) included 574 measurements; none of those were from tropical systems. From our measurements of tropical systems in Brazil, we obtained 392 observations. The addition of these values to the model presented in Gudasz et al. (2010) confirmed the authors' conjecture of a linear increase in logged OC mineralization rates with increasing temperature (Fig. 5; Table 2), supporting extrapolation of the relationship into the higher temperature range. Further, based on the OC mineralization response to temperature expressed as Q_{10} values (*see* Eq. 1), our data were in accordance with values in the literature from different boreal and temperate aquatic ecosystems (Q_{10} between 2 and 3; Table 3).

Although mineralization rates of tropical systems in Brazil were, on average, higher than the rates reported by previous studies, rates varied among the different types of systems and regions (Figs. 2, 3). Reservoirs had the lowest, and lakes the highest, mineralization rates. Reservoir mineralization rates may be lower for several reasons: shorter water residence time of these systems; the lower effect of littoral zones because of large surface area to

Table 2. Parameters describing the regression between $\log_{10}$ OC mineralization (mg C m^{-2} d^{-1}) and temperature (°C) for literature data (Gudasz et al. 2010), this study (including all replicate values), and the two combined data sets (all data). Where $\log_{10}$ OC mineralization = intercept + slope × temperature (°C). Standard errors (SE) are given in parentheses. R^2 adj. = R^2 adjusted, n = sample size. For all regressions, $p < 0.0001$ (t-test).

Data source	Slope	Intercept	R^2 adj.	n
Literature	0.04(0.00)	1.63(0.02)	0.43	574
This study	0.04(0.01)	1.79(0.18)	0.10	392
All data	0.05(0.00)	1.52(0.02)	0.71	966

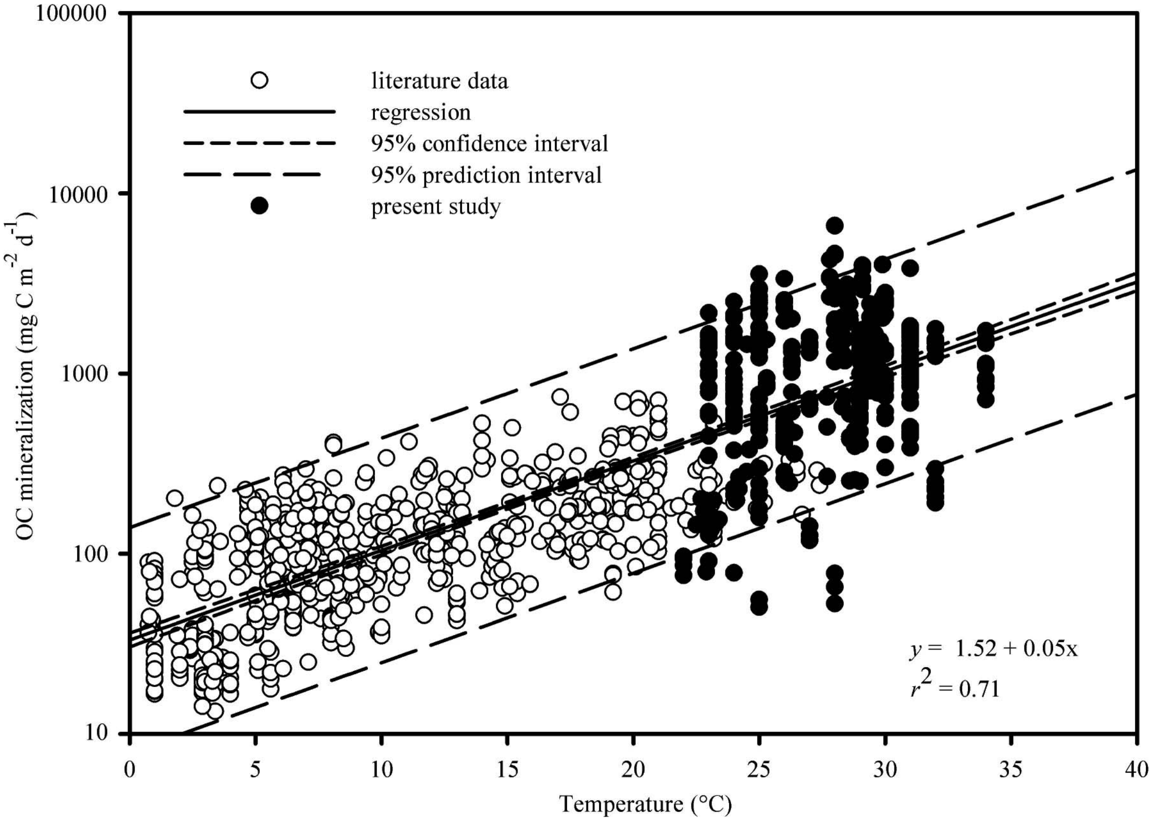

Fig. 5. The relationship between sediment OC mineralization rates and temperature in lake sediments. Data include values from the literature ($r^2 = 0.43$, $p < 0.0001$, $n = 574$; Gudasz et al. 2010) and the present study ($r^2 = 10$, $p < 0.0001$, $n = 392$). The regression for the two combined data sets is shown ($r^2 = 0.71$, $p < 0.0001$, $n = 966$). The y-axis of OC mineralization rates is represented on a log scale.

perimeter ratios; and the quality of the OC available for mineralization, which is potentially more processed due to partial mineralization prior to entry into the reservoir (De Junet et al. 2009). However, it is important to highlight that reservoirs had generally lower temperature ranges than other systems (Fig. 2), which makes it difficult to identify whether low temperatures, rather than differences between systems, contributed more to the low rates found. Lakes had a wide range of OC mineralization rates, and most were higher than in the reservoirs (Figs. 2, 3). The majority of the lakes studied are of coastal and riverine origins and are, therefore, shallow (< 5 m deep), with small to moderate surface areas (< 1 km² to 32 km²). It is likely that the morphometric characteristics of the sampled lakes, together with their light and mixing regimes, would favor primary production and, consequently, increase the

Table 3. Q_{10} values of benthic and pelagic respiration reported in prior inland water studies and calculated for this study.

System	Temperature range (°C)	Q_{10}	Reference
Lakes	2–12	7.6	Hargrave 1969
	20–20	2.2	
Lakes	5–10	2–3	Granéli 1978
	15–20	1.3–1.6	
Lakes	5–10	1.3–3.7	Granéli 1979
	10–15	1.6–3.4	
	15–20	1.7–3.6	
Lakes	10–20	1.9	den Heyer and Kalff 1998
Channel	−0.6–5.8	1.6–98	Kritzberg et al. 2010
Lakes, rivers, estuaries, and open ocean	0–30	2.5	Yvon-Durocher and Allen 2012*
Streams	5–25	1.9	Perkins et al. 2012
Lakes	0.7–21	3	Gudasz et al. 2010†
Lakes	0.8–27	1.9	Data compiled by Gudasz et al. 2010*
Lakes, rivers, streams, and reservoirs	22–34	2.5	This study

* Only inland water values were considered.
† Q_{10} values calculated for this study.

availability of labile OC from phytoplankton, macrophytes, and terrestrial plant matter to the sediment (Holmer 1996; den Heyer and Kalff 1998), which, in turn, would enhance mineralization rates.

Systems in the Atlantic Forest had the lowest mineralization rates, whereas systems in the coastal areas had the highest rates. The Atlantic Forest biome is composed of tropical moist forest that extends along the coast of Brazil (4° to 32° S). The precipitation in this area is on average 2000 mm per year, with mean annual temperature of 22°C (Ab'Saber 2006). The systems sampled in this biome included rivers, lakes, and reservoirs, all having a lower range of water temperatures (22°C to 27°C) in comparison to the other regions sampled (24°C to 34°C). We hypothesized that those lower temperatures contributed to the lower OC mineralization rates in the sediments of the region. In comparison with the Atlantic Forest, the systems in the coastal areas are mainly composed of coastal lagoons, located in northern areas of the state of Rio de Janeiro. The region is a mosaic landscape composed of shrub vegetation and flooded forest patches (Ab'Saber 2006). The climate of the region is tropical subhumid, with mean annual temperatures of 25°C and annual precipitation of 1165 mm. The systems sampled in this region had a water temperature range from 24°C to 31°C, very similar to the ones sampled in the Amazon (24°C to 34°C) and the Pantanal (26°C to 31°C) regions, but they also had higher salinity (15 ± 2) in comparison to the other systems (1 ± 1). We argue that, for the coastal lagoon systems, salinity, rather than temperature, was the most important factor controlling mineralization rates. In addition, it is important to highlight that high sulfate availability in the sediment of marine and coastal areas may also be an important factor that influences the higher OC mineralization rates observed (Fenchel et al. 2012). However, sulfate was not considered in our study, and its possible effect on OC mineralization requires further investigation.

Based on the AICc ranking (Table 1; Fig. 4), salinity, TN, and Chl *a* were the main driving factors of OC mineralization in addition to temperature for all the studied tropical ecosystems. The effect of salinity on freshwater organisms has been reported in the literature as an important biogeographic factor for selecting tolerant organisms with the capability of osmotic regulation (Marin et al. 2002). In general, our results showed that OC mineralization was higher in the systems in which salinity was also higher. Similar results were found by other studies with salinity gradients (Shultz and Ducklow 2000; Cottrell and Kirchman 2003). We hypothesize that salinity may cause a stress that increases respiration (OC mineralization) relative to growth. Evaluating the pure effect of salinity on OC mineralization rates is beyond the scope of our research, and we highlight this as an important issue for future studies.

Tropical freshwater ecosystems are often deficient in nitrogen (Talling and Lemoalle 1998). Higher temperatures in the tropics favor nitrogen fixation in the upper mixed layer of stratified water bodies, but they also favor higher rates of ammonification and denitrification in the water column and in the sediment, making the local nitrogen supply insufficient to account for nitrogen demand (Fenchel et al. 2012). Nitrogen is an important limiting nutrient to phytoplankton, and a deficiency of this resource would cause a reduction on primary production. A reduction in primary production would, in turn, reduce the amount of carbon that is transported from the water column to sediments, affecting the OC mineralization rates. Recently, experiments manipulating nitrogen in tropical coastal lakes showed that nitrogen can modulate CO_2 outgassing from lakes (Peixoto et al. 2013). This finding reinforces the importance of nitrogen as a limiting factor on the amount of CO_2 released from inland water bodies to the atmosphere.

The concentration of Chl *a* in the water column is related to the productivity of phytoplankton, which, in turn, is an important contributing pool of OC for the sediments. Chl *a* is related to the productivity of ecosystems, which is intrinsically related to nutrients, light availability, and temperature. Increases in temperature can cause an increase in the productivity of aquatic ecosystems (Yvon-Durocher et al. 2010) and can thereby affect processes in the ecosystem as a whole (Hamilton 2010). We hypothesize that higher temperatures, by favoring primary production, would consequently enhance the contribution of labile OC from phytoplankton to the sediment. Because the carbon coming from phytoplankton is preferentially degraded by microorganisms (Kritzberg et al. 2006), an increase in availability would cause an increase in sediment mineralization rates in freshwater sediment, as previously noted by Holmer (1996) for marine ecosystems. However, in spite of the positive relationship between Chl *a* and mineralization, this effect appears to be weak and possibly reflects correlations with other independent variables. By comparing the two best linear models (Table 1), the second model gained only 2% in explanatory power by adding Chl *a* (from $r^2 = 0.67$ to $r^2 = 0.69$). In this case, Chl *a* alone does not appear to exert a large control on mineralization rates, and the rates may be influenced by other variables, such as TN.

Based on this study, we conclude that OC mineralization models can be extrapolated to warmer tropical sediments. Also, based on our regression models, OC mineralization rates in tropical sediments are regulated by other local factors besides temperature, such as nitrogen availability, system productivity, and salinity. To understand the main factors regulating OC mineralization in the sediments, it is critical to improve predictions about sediment storage vs. mineralization of OC. Moreover, the understanding of these processes in tropical areas will increase the capability to predict the effects of global warming, particularly in the context of inland waters as sinks for OC.

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