Tropical forests as drivers of lake carbon burial

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A significant proportion of carbon (C) captured by terrestrial primary production is buried in lacustrine ecosystems, which have been substantially affected by anthropogenic activities globally. However, there is a scarcity of sedimentary organic carbon (OC) accumulation information for lakes surrounded by highly productive rainforests at warm tropical latitudes, or in response to land cover and climate change. Here, we combine new data from intensive campaigns spanning 13 lakes across remote Amazonian regions with a broad literature compilation, to produce the first spatially-weighted global analysis of recent OC burial in lakes (over ~50-100-years) that integrates both biome type and forest cover. We find that humid tropical forest lake sediments are a disproportionately important global OC sink of 7.4 Tg C yr\(^{-1}\) with implications for climate change. Further, we demonstrate that temperature and forest conservation are key factors in maintaining massive organic carbon pools in tropical lacustrine sediments.
Forests are major global atmospheric carbon (C) sinks\textsuperscript{1–4} of which a significant biomass fraction is transported by water flow into lacustrine sediments\textsuperscript{5–10} that represent temperature-sensitive organic carbon (OC) stocks that are vulnerable to greenhouse gas conversion\textsuperscript{11,12}. However, recent global estimates of OC burial in lakes\textsuperscript{8} have not considered biome type nor land use in datasets where low-latitude lakes are severely underrepresented, leading to uncertainty in current predictions of the effects of warming on large inland water C stocks. Given this lack of information, we sought to substantially increase the representation of tropical ecosystems over the previous efforts\textsuperscript{8,10}, and estimate recent sediment OC burial rates (~50–100 year range) in global lakes through a novel approach that integrates their areal distribution\textsuperscript{13} across biome types\textsuperscript{14} and land cover\textsuperscript{15}. In addition, their relationship with forest cover around lakes from the largest humid tropical forest in the world (i.e., the Amazon rainforest) was assessed using more accurate spatial analysis than previously reported for extensive low-latitude floodplains\textsuperscript{16}. Natural lakes cover approximately 2.67 million km\textsuperscript{2} or 1.8\% of the land surface area across nearly all climate zones\textsuperscript{13}. Lakes within watersheds are depositional environments with generally high recent OC burial rates\textsuperscript{8,17–19} playing an essential role in the global carbon C cycle\textsuperscript{5,7,20} that is disproportionate to their relatively small area. The role of lacustrine sediments as biosphere-atmosphere C sinks may be comparable to greenhouse gas emissions from inland waters\textsuperscript{8}. Along latitudinal gradients, previous studies have reported positive relationships between temperature and OC burial in lakes spanning polar to boreal\textsuperscript{18}, boreal to temperate\textsuperscript{19}, and temperate to subtropical\textsuperscript{17} biomes. Conversely, with the exception of temperate biomes\textsuperscript{19,21}, these initial efforts to determine global C accumulation in lake deposits have not considered remaining land cover across the world’s biomes\textsuperscript{17,18} with early efforts substantially underrepresenting low-latitude ecosystems. In extensive flooded areas within humid tropical forests, higher annual temperatures could actively stimulate both OC degradation\textsuperscript{11,12} and accumulation\textsuperscript{22}, increasing uncertainty about the role of temperature variations in determining sediment OC burial rates.

Here, our aim is to investigate recent global OC burial rates in lake sediments (over a ~50–100-year timeframe), integrating variations in global biomes, location in reference to natural or human-altered environments, and the relative area of forest cover near lakes within the Amazon. These results show that the conservation of the surrounding forests is positively related to the highest OC burial rates in lakes globally.

Results and discussion

A framework to estimate lacustrine C accumulation. In order to avoid bias due to large differences with OC accumulation estimated via other methods such as \(^{14}\) C dating and sediment traps, our dataset was restricted to rates derived from \(^{210}\)Pb dating methods, considered the most accurate method for secular dating\textsuperscript{23}. Despite the relative ~20\% decrease in the number of high-and medium-latitude lakes used in the latest review of OC burial rates\textsuperscript{10}, our efforts resulted in a proportionately larger tropical dataset from an extensive field survey of an additional 13 remote Amazonian lakes in combination with a literature compilation spanning other 43 from humid tropical forests. Accordingly, our new approach doubled the representation of warmer tropical lakes in a humid tropical forest when compared to previously reported, allowing a better representation of the global distribution of lacustrine OC burial rates along the latitudinal gradient (see details in Methods and Supplementary Material). Then, our spatial upscaling of OC accumulation was based on the latest review of global natural lake area (i.e., not including rivers, inundated floodplains or wetlands, streams, reservoirs, and artificial ponds)\textsuperscript{13}.

This updated dataset improves the representation of low-latitude environments for global upscaling of lake OC burial (Supplementary Table 1). Further, we analysed the potential terrestrial controls over OC accumulation in lakes by comparing OC accumulation rates in lake sediments with those of forests around the world\textsuperscript{11,14}, and by examining the relationship between recent OC burial in Amazon floodplain lakes with C dynamics in the surrounding non-flooded forests.

Global mapping of lake OC burial. Our results along the latitudinal gradient demonstrate consistently high recent OC burial rates in the humid tropical forest lakes, with an average (± standard error; SE) of 113.5 (±18.1) g C m\textsuperscript{2} yr\textsuperscript{−1}. In natural biomes in temperate, boreal or polar, and subpolar latitudes OC burial rates reached 38.9 (±8.4), 36.7 (±3.2), 15.4 (±3.9), or 10.9 (±2.7) g C m\textsuperscript{2} yr\textsuperscript{−1} respectively, while human-altered environments showed 47.6 (±3.1) g C m\textsuperscript{2} yr\textsuperscript{−1} independent of temperature variation (Fig. 1 and Supplementary Fig. 1). The observed higher lake OC burial rates in warm low-latitude biomes contribute to the climate-C-burial debate in global lakes, confirming prior findings on the likelihood of warming increasing C accumulation in lacustrine sediments\textsuperscript{17–19}. As biological remineralization and subsequent loss of large OC stocks to greenhouse gases with increasing temperature has also been reported\textsuperscript{11,12}, our findings demonstrate that both burial and degradation of OC may be enhanced in a warming world. Increases in OC inputs\textsuperscript{24} and burial\textsuperscript{18} in lacustrine sediments have been attributed to the enhanced production of aquatic and terrestrial biomass, which reach inland waters under warmer conditions. In turn, the refractory nature of terrestrial organic matter (OM)\textsuperscript{25,26}, coupled with high oxygen consumption in bottom waters and surface aquatic sediments in lakes surrounded by tropical forests\textsuperscript{27} typically leads to greater preservation of the OC pool in flooded areas\textsuperscript{26}. Significantly higher lake OC burial with increasing annual air temperature (p < 0.05, one-way ANOVA followed by the Tukey’s post hoc test; Fig. 2) and the resulting positive linear regression between both variables were observed only in natural biomes (p < 0.05; Fig. 3A) a trend that confirms prior regional studies at high and mid-latitudes\textsuperscript{17–19}.

Consistent with this, humid tropical forest lakes showed an average OC accumulation of ~23 and 8\% higher than eutrophic and hypereutrophic lakes at medium and high latitudes reported by Anderson et al.\textsuperscript{28} (see Supplementary Discussion for more details). This suggests that eutrophication and subsequent water contamination could be insufficient to offset reductions in recent OC burial in lakes surrounded by lower forest cover in tropical areas, even with the expected short-term increases of biomass inputs to inland waters following deforestation in the watershed\textsuperscript{21}. Although the relationship between long-term forest productivity and terrestrial C export to the aquatic ecosystem are well known\textsuperscript{24}, there are few studies assessing the effects of forest cover on OC burial in humid tropical lakes\textsuperscript{29}.

Our results indicated that warmer lakes had average OC accumulation rates ~3-fold higher in the Amazon Forest than tropical lakes under intense eutrophication in urban or cropland areas (366.2 ± 51.0 and 129.5 ± 12.9 respectively, N = 5 for each). Considering the observed relationship between lake OC burial and temperature (Fig. 3A), we estimated that recent C accumulation rates in warm lakes at human-altered biomes here (>18 °C) could be only ~50\% of those predicted in conserved areas, while the biomass sink in cold lakes were less sensitive to human alteration (~6 and 9 °C). This supports an integrative perspective on lake OC burial debate, in which both...
climate and land cover might control vast C stocks in lacustrine sediments around the world. The more intense OC burial in humid tropical forest lakes is due to the large organic inputs from highly productive terrestrial vegetation into flooded areas of this biome which fuel intense C cycling processes. The role of rainforests in promoting intense OC accumulation in warm lake sediments at low latitudes is also independently demonstrated by the positive linear regression between recent OC burial rates in Amazon lakes and the relative area of non-flooded forest cover in their surroundings \((p < 0.05, \text{Fig. 3; see details in Methods and Supplementary Material})\). Considering the \(\delta^{13}C\) values and C:N molar ratios for the major OM sources documented for the Amazon forest, both C3 soil and woody plants accounted for over 60% of the OM source to Amazon lake surface sediments (Fig. 3C). This higher participation of arboreal sources in lake OC burial might still be conservative since algae and C4 plants are more susceptible to mineralization before burying in deeper layers of aquatic sediments (see more details in Supplementary Discussion).

Tropical drivers of OC accumulation in lakes. Our data demonstrate that humid tropical Amazon forest lakes are burying approximately 15% more OC per unit area than previously reported, indicating that local lakes are destinations for significant proportions of the OM produced in the forest. The variation of recent OC burial rates in humid tropical forest lakes reached a SE of 3.835 \(g \text{ m}^{-2} \text{ yr}^{-1}\), which was from 4- to 14-fold higher than those observed in other natural and human-altered biomes. This finding demonstrates warmer tropical lakes contain a broader range of processes involved in C cycling (i.e., greater both C uptake and release rates) than those at higher latitudes. In contrast to the much higher average OC burial rates we observed in natural forest areas, the intense mineralization rates under higher annual temperatures and the lateral export to rivers have been considered important processes to reduce C accumulation in lakes after long-term deforestation in the humid tropics (i.e., declines in terrestrial OM sources). Specifically, our study design supports conclusions about the potential role of humid tropical forests on global C stocks in lacustrine sediments. Indeed, previous evidence has reported spikes of lake OC burial following the removal of forest in the watershed but clearly restricted to the initial period of logging in riparian regions (see Supplementary Discussion in Supplementary Material for more details). These contrasting processes of intense increases and decreases in inputs of terrestrial biomass under warm tropical conditions are therefore likely to contribute to the observed variability expressed as coefficient of variation (CV) or SE (Figs. 2, 3 and Supplementary Table 1) of OC burial in tropical lakes.

Overall, rates of recent OC burial observed in humid tropical forest lakes were among the highest in the world and comparable to other known productive ecosystems, within the same order of magnitude as those reported in seagrass meadows and saltmarshes or up to two times higher than in mangroves. Even assuming a much smaller area than other biomes (~3% of the global lake area. See details in Methods and Supplementary Material),
we found that humid tropical forest lacustrine sediments represent a disproportionately large C sink that accounts for ~10% of the annual C accumulation in lakes globally (Supplementary Table 2).

Applying our recent OC burial rates to global lake area resulted in an estimated global sink of 80 Tg C yr\(^{-1}\), which is equivalent to ~27% of estimated global carbon dioxide (CO\(_2\)) emissions from lake waters to the atmosphere (i.e., 292 Tg C yr\(^{-1}\))\(^{20}\). This estimate for tropical natural forest lakes may be an underestimate as we do not include data for calculating the contribution of all tropical and subtropical lakes (see details in Methods and Supplementary Material). The C sequestration rates in sediments may be even more important relative to atmospheric emissions, given that CO\(_2\) mineralization under higher temperatures\(^{11,12}\). Such deforestation-related mechanisms could lead to reductions or even negations of lake C burial that had been widely predicted under existing global warming scenarios\(^{8,17-19}\). These effects are most pronounced in the tropics, which account for around half of all increases in global net primary production (NPP) despite being only around 22% of the land area, highlighting the need to preserve tropical ecosystems, and the lakes they contain, merit specific attention\(^{30}\).

Given the need to limit climate change to within 1.5 degrees C of warming this Century, these newly-identified mechanisms of aquatic C loss in humid tropical forests present us with both a challenge and opportunity in tackling climate change. A challenge is that humid tropical forests are particularly vulnerable to ongoing regional land-use change\(^{37}\), and an opportunity in that the immediate implementation of conservation and afforestation programs focused on extensive tropical areas rich in lakes will likely arrest ongoing lake sediment C loss while restarting their globally important C sequestration function.

**Methods**

Sources and calculation of OC accumulation rates. A literature review and a wide field survey were conducted with the objective of finding direct measurements of recent OC burial rates, with major emphasis given to the inclusion of under-represented tropical lakes. A cross-reference search was performed using “Web of Science”, “Science Direct”, “Google Scholar”, and Ph.D. thesis platforms until December 2019. We created a dataset (\(N = 397\) lakes) from published literature, including three reviews\(^{28,29,39}\), 21 other papers, and three thesis (see all data and sources in the work dataset), which were combined with new records from our field surveys in 2014, 2015, and 2016 (\(n = 13\)) in a wide area of 580,000 km\(^2\) along a maximum distance of 1170 km (Supplementary Fig. 3, and work dataset). This approach increased by ~75\(^{10}\) and 130\(^{10}\) the number of tropical forests that are represented over previously published studies.

All data were based on estimations of OC burial using profiles of \(^{210}\)Pb, excluding other methodologies. Then, we provide data regarding the sediment OC mass accumulation rates. The \(^{210}\)Pb was measured by Alpha or Gamma-ray activity. \(^{238}\)Ra was measured through Gamma-ray and activities were determined through daughter peaks of \(^{214}\)Pb and \(^{214}\)Bi. The excess \(^{210}\)Pb (\(^{210}\)Pb\(_{ex}\)) activity is estimated by subtracting the \(^{228}\)Ra from the total \(^{210}\)Pb activity. The total \(^{210}\)Pb activity decay and \(^{210}\)Pb\(_{ex}\) were used to date sediment intervals through the constant rate supply (CRS),
and constant initial concentration (CIC) models$^{23,40}$ as the difference between both is negligible over the assessed timeframe (50–100 years)$^{35}$. The CRS model determined ~77% of the presented OC burial rates, and we used the CRS model for the sediment cores sampled here (Supplementary Fig. 4). Moreover, to avoid bias towards time periods with higher resolution, the $^{210}$Pb measurements were evenly distributed along the sediment profile. Then, the sediment mass accumulation rate (SAR) was determined as the product of sediment accumulation (cm yr$^{-1}$) and respective dry bulk density [g cm$^{-3}$] in each interval$^{42,43}$. The results are expressed as SAR [cm year$^{-1}$], dry bulk density [g cm$^{-3}$], and OC content (OC Burial [g C m$^{-2}$ yr$^{-1}$]: SAR [cm year$^{-1}$] × dry bulk density [g cm$^{-3}$] × [% OC/100]).

The whole-lake OC burial was then estimated by three alternative methods depending on the available data as described by Mendonça et al. (2017): (1) the average of such rates derived from two or more sediment cores sampled at different parts of a given ecosystem; (2) dividing the rate from a single core sampled in the preferential sediment deposition area by the sediment focusing factor (SFF) following Blas and Kalff (1995) when mean lake slope is measured; or (3) dividing the single rate by the SFF reported into groups according to lake maximum depth ($\leq$5 m, >5–10 m, >10–30 m, >30–90 m, and >90 m) when bathymetric data were not determined.

Concerning forest OC accumulation, we compiled the estimates of each compartment reported in a previous review: Soil Organic Matter, Living Biomass, Deadwood, Litter, and Wood product (Supplementary Table 2). The equatorial carbon in soil was not estimated by Pan et al. (2011), but we obtained it from Malhi and Grace (2000). Then, we also used the forest area inventory provided in Pan et al. (2011) but subtracted the tropical forest wetland area reported in Mitra et al. (2014). This approach based on the comparison of relatively longer periods (around 50–100 years) with forest OC accumulation rates (around 10 years) allowed more conservative estimates of lake OC burial, as non-mineralized fractions in terrestrial soils may continue to decay over time (i.e., resulting in an overestimation of these rates in the forest as related to the lake sediment).

### Our survey and chemical analyses.

Thirteen sediment cores (approximately 50–90 cm long; Supplementary Fig. 4) were sampled from the deepest area of each lake using a gravity core. The sediment cores were then sealed and cooled for transport. In the laboratory, cores were sectioned at 2 cm intervals; samples with known volumes were weighed and freeze-dried. The dry bulk density was...
calculated by dividing the dry weight of the sediment by the initial volume \(45\). The total organic carbon (total C) and the \(13C\) and \(15N\) isotopic compositions (groundwater and lake water) were analyzed in triplicate by a Thermo Fisher isotope ratio (Delta V IRMS) mass spectrometer. The analytical precision is \(1\%\), \(N = 0.1\%\), \(6\%\), and \(1.5\%\). The CRS model \(13C/13C\) dating was applied using all \(13C/13C\) measurements in each sediment core for the present study. All Amazon lakes here were situated in conserved areas during sampling (2007–2012), with the land around them ranging from 0 to 20 km2, and the immediate watershed cannot be delimited due to the low altitude. Accumulation in lacustrine sediments with non-fluvial terrestrial input sources into lakes situated in forested areas was determined in different sized buffers (3, 4, 6, 8, 12, and >15 km2, and >15°C) with different \(13C\) and \(15N\) ratios of Amazon lake surface sediments (0–6 cm samples) are the result of our survey and published data (\(N = 18\) and 54 lakes, respectively), following the boundaries of major OM sources\(46–49\).

**GIS dataset.** We used the HydroLAKES database\(13\) to determine natural lake areas around the world (see Supplementary Table 1). This model shows a total surface area of 2.67 \(\times 10^8\) km\(^2\), which was created by compiling, correcting, and unifying several near-global and regional datasets. The resulting map scale was estimated to be 1:100,000 and 1:250,000 for most lakes globally, with some coarser ones at 1:1 million. Each lake in this database was classified according to the respective biome.

Further, the seven categories of terrestrial world biomes here (i.e., (1) Humid tropical forest; (2) Other tropical and subtropical latitudes; (3) Temperate forest; (4) Boreal forest; (5) Other medium latitudes; (6) Subpolar and polar latitudes; and (7) Deserts) were extracted from a shape previously published\(14\) at various locations around the world (see Supplementary Table 1). This model shows a total surface area of 2.67 \(\times 10^8\) km\(^2\), which was created by compiling, correcting, and unifying several near-global and regional datasets. The resulting map scale was estimated to be 1:100,000 and 1:250,000 for most lakes globally, with some coarser ones at 1:1 million. Each lake in this database was classified according to the respective biome.

In relation to Amazon lakes here (Fig. 3B), we used ASAR global monitoring mode (available at https://earth.esa.int/handbooks/asar/CNTRDE-2-5.html) to determine flooded and non-flooded areas around each studied ecosystem. Then, non-flooded areas were classified into two categories (1) forest and (2) natural and anthropic field cover, using MODIS/Terra Surface Reflectance 8-Day L3 Global 500 m SIN Grid V006 (available at https://lpdaac.usgs.gov/dataset_discovery/modis/miis/products/table/mod09q1v006). Moreover, we selected MODIS and ASAR products from periods when the water level of the main river of each study Amazon study lake was close to the 23-year average (deviation of 15% \(\pm 8\%\); Supplementary Table 3), obtained from the full Brazilian National Water Agency dataset (available at http://www.uinfoshir.gov.br/hidroweb/publico/medicoes_historicas_abas.jsf). To perform the segmentation process of ASAR and MODIS products, an object-oriented classification method was implemented (see details on decision tree in Supplementary Fig. 5), using a multisresolution algorithm with scale parameters 10, and 0.2 of form and 0.8 of compactness. Finally, the relative area of non-flooded forest was determined in different sized buffers (3, 4, 6, 8, 12, and 18 km2; 0–6 cm lake at the same river floodplain (i.e., excluding the main river or its other margin)). This approach using buffers in ASAR and MODIS products is more appropriate in order to assess the potential catchment and terrestrial input sources into lakes situated in flat areas, such as inside the Amazon Forest where the immediate watershed cannot be delimited due to the low altitude. After analysing each sized buffer (Supplementary Fig. 7), we found that the 6 km\(^2\) area provided the best-fit relationship between recent OC burial in Amazon floodplain lakes and non-flooded forest area (higher \(r^2\) of linear regression, \(p < 0.01\); Supplementary Fig. 2). These results allowed us to identify trends of C accumulation in lacustrine sediments with non-flooded forest cover in the surrounding area.

**Comparisons with global lake C emission.** Raymond et al. (2013) consider reservoirs were treated as similar to natural lakes because their \(pCO_2\) has been shown to be elevated only during the initial ~15 years after impoundment. This paper estimates a global lake and reservoir surface area of 3.000,000 km\(^2\), of which 91.3% is lakes and 8.7% is reservoirs. Thus, we calculate 91.3% of 320 Tg C yr\(^{-1}\) around ~27% (or ~292 Tg C yr\(^{-1}\)) of our estimates.

**Statistics.** The OC burial log-transformed data met the assumptions of parametric tests\(7\); the data were not normally distributed (Kolmogorov–Smirnov, \(p < 0.05\)) and variances were heterogeneous (Bartlett, \(p < 0.05\)). Mean (Supplementary Table 4) and parametric tests were used to compare sampling groups (Kruskal–Wallis, \(p < 0.05\)). The same tests were performed in relation to temperature; however, in this case, the data were not log-transformed. Thus, we used one-way ANOVA followed by a Tukey post-test (significance \(p < 0.05\)) to compare conserved and human-altered areas. The stabilization of variance with the number of measurements randomly selected was reached (Supplementary Fig. 8).

**Data availability**

The data that support the findings of this study are available in the Supplementary Data.

Received: 26 September 2020; Accepted: 3 June 2022.
Published online: 13 July 2022

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**Acknowledgements**

This study was funded by grants from the Research Support Foundation of the State of Rio de Janeiro (FAPERJ, 203.304/2017, E.26/210.441/2021, E.26/211.329/2021 and E.26/ 201.118/2022) and the Council for Research and Scientific Development of Brazil (CNPq, 310152/2017-8, 203366/2019-0, and 314955/2020-0) to H.M. (Principal Investigator). H.M. was awarded by CNPq Research Productivity and FAPERJ Young Scientist of Rio Janeiro State fellowships. H.M and A.E.-P were recipients of FAPERJ Scientist of Our State fellowships. A.E.-P was supported by the funding agency Formas (2021-02429). L.A.-N. was recipient of Ph.d scholarship from FAPERJ “Student Grade 10” award. L.A.- N. (151237/2021-2) and F.M.-S. (152325/2020-4) were awarded by Postdoctoral fellowships from CNPq. R.L was supported by Serrapilheira Institute (Serra-1708-15159). C.J.S. and carbon burial analyses were supported by the Australian Research Council (LE14010083). The authors are grateful to the support from the Multi-user Facility for Gas, Water, and Sediment Geochemistry at the Fluminense Federal University (GASUFF).

**Author contributions**

H.M. and L.A.-N. designed and wrote most of the paper. H.M., L.A.-N., C.J.S., A.E.-P., P.F.M.-T., V.G., R.C.C., and R.C.A contributed to the main data interpretation. L.A.-N., H.M., R.C.A., C.J.S., and A.E.-P. constructed the figures. L.A.-N., H.M., C.J.S., L.S.M.S., P.F.M.-T., A.E.-P., R.C.C., L.S.M., T.F., and F.M.S. carried out field sampling or data compilation in the literature. L.A.-N., C.N.F., T.F., and F.M.S performed spatial analysis and statistics. L.A.-N., L.S.M.S., C.J.S., and R.C.A. did the chemical analysis. R.L. contributed to the overall scientific context. All authors contributed comments and input to this manuscript.

**Funding**

Open access funding provided by Linköping University.

**Competing interests**

The authors declare no competing interests.

**Additional information**

**Supplementary information** The online version contains supplementary material available at https://doi.org/10.1038/s41467-022-31258-8.

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**Peer review information** Nature Communications thanks the anonymous reviewer(s) for their contribution to the peer review of this work.

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