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A biogeochemical comparison of three representative lakes of Costa Rica

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ABSTRACT

Lakes are widely distributed across Costa Rica, from coasts to the highest elevation regions and located in the main terrestrial biomes, yet updated biogeochemical information about the main types of lakes is still lacking. We present comparative biogeochemistry (water chemistry, stable isotopes, and picoplankton) for a coastal lake (Lake Madre de Dios), a volcanic lake (Lake Barva), and a glacial lake (Lake Ditkevi). Sampling was conducted between February and November 2022, including dry and rainy seasonal conditions. Hydrological and chemical conditions were evaluated using water and carbon stable isotopes, dissolved organic matter, major ions, and microbiota analysis. Isotopic data on water ($\delta^2\text{H}$ and $\delta^{18}\text{O}$) and dissolved inorganic carbon ($\delta^{13}\text{C}_{\text{DIC}}$) confirmed lower evaporative losses for the maar and tarn lakes and productivity response to precipitation inputs. Excitation/emission matrices confirmed the prevalence of fulvic and humic acids in the coastal and glacial lakes, mainly aromatic proteins and soluble microbial byproducts in the volcanic lake. Picophytoplankton (PPP, $\sim 0.2\text{--}10\ \mu\text{m}$) was mainly represented by phycocyanin-rich picocyanobacteria in the 3 lakes, but maar and tarn lakes had greater representation of phycoerythrin-rich picocyanobacteria. We confirmed fluctuations in PPP cell abundance in the lakes was lower than in comparable temperate lakes. For other eutrophic lakes, abundance of picocyanobacteria dominated over picoeukaryotic algae. This work aimed to promote an ecosystem approach to study the biogeochemical functioning of tropical lakes using a combination of chemical, hydrological, and biological data and to provide baseline information for future studies (e.g., climate change and pollution impacts) on tropical lakes of Costa Rica.

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Introduction

Tropical lakes play a key role in the conservation and stability of local ecosystems and are highly significant because of the ecological, social, and economic services they provide (Horn 2017, Boëchat et al. 2019, Obrist-Farner et al. 2019, Deirmendjian et al. 2020). These freshwater ecosystems support a wide array of biodiversity and are home to countless species of aquatic plants, fish, and invertebrates, many of which cannot be found in other biomes on Earth. The intricate web of life and biogeochemical transformations sustained by these lakes contributes to global biodiversity and supply water resources to the surrounding population (Bogotá-Gregory et al. 2020, Giresse et al. 2023). Thus, the preservation and protection of these lake systems are imperative for promoting sustainable development and ensuring the well-being of both nature and people (Horn 2017, Ramírez et al. 2020).

The biogeochemistry of tropical lakes is a complex interplay of biological, physical, and chemical processes that shape the composition and dynamics of such

ecosystems. The unique characteristics exhibited by these lakes are due to warmer temperatures, higher solar radiation incidence, and usually higher levels of precipitation (Moser et al. 2019, Zhang et al. 2021a). The waters of these lakes are characterized by rapid nutrient cycling and microbial activity, which accelerate organic matter decomposition. These rapid biochemical transformations are related to higher concentrations of nutrients such as nitrogen and phosphorus, but the nutrient conditions make the surface water systems more susceptible to the occurrence of algal blooms and eutrophication, especially if the lakes are influenced by human activities such as agriculture, tourism, urbanization, and deforestation (Gagliardi et al. 2019, Jovanelly et al. 2020, Dubey et al. 2022, Fadum and Hall 2022). Thus, a better understanding of the biogeochemistry of tropical lakes, for instance, the relationship between the taxonomic and functional variations of the microbial communities and the physicochemical and environmental variables, may contribute to the characterization of their invaluable natural resources

and more effective conservation strategies and sustainable management (Lønborg et al. 2021, Johnes et al. 2023).

Although research on the biogeochemistry of tropical lakes has made significant progress in the past decades, gaps remain in our understanding of these complex ecosystems. For example, the role of aquatic microorganisms is not fully understood. We know microbes play a crucial role in nutrient cycling and organic matter decomposition, yet research focusing on the diversity, dynamics, and functional roles of microbial populations in these ecosystems is limited (Ávila et al. 2019, Rathour et al. 2020). The carbon dynamics within tropical lakes are also relatively understudied. More research about the sources, sinks, and transformations of carbon compounds in these aquatic systems could advance our knowledge of their contribution to regional and global carbon budgets (Savvichev et al. 2020, Díaz-Torres et al. 2022). Nutrient dynamics and the pathways and rates of nutrient inputs, transformations, and exports also need more comprehensive investigation. Overall, understanding how different land use practices and anthropogenic activities influence nutrient cycling is necessary for conducting nutrient enrichment and eutrophication studies (Guimarães-Nobre et al. 2020, Kraemer et al. 2020, Fadum and Hall 2023). In a regional tropical context, tropical lakes are also vulnerable to climate change-induced alterations in temperature, precipitation patterns, and extreme weather events, changes that generate habitat loss for many aquatic and terrestrial species; therefore, lake monitoring is relevant for wildlife preservation (Hansen et al. 2022). Investigating how these changes affect lake thermal stratification, nutrient cycling, and carbon dynamics is crucial for predicting future ecosystem shifts and climate change impacts (Moser et al. 2019, Pratihary et al. 2021).

We recognize most Central American lakes (including the Costa Rican lakes) lack consistent long-term monitoring to gather systematic data, limiting our ability to track trends and changes in biogeochemical processes over time. Many studies have focused on individual aspects of lake biogeochemistry but have not applied integrated approaches that consider the interconnections of physical, chemical, and biological processes within these ecosystems (Kumar et al. 2019, Guo et al. 2020, Manirakiza et al. 2022). Moreover, recent advances in technology have opened novel experimental approaches for studying the biogeochemistry of tropical lakes, including environmental metagenomic analysis, stable isotope analysis, spectroscopic characterization of dissolved organic matter (DOM), and biogeochemical modeling (Huguet et al. 2009, Guo et al.

2020, Tran et al. 2021). For instance, stable isotopes of elements like carbon, nitrogen, and oxygen can provide information about nutrient sources, cycling, and trophic interactions within tropical lakes, whereas the analysis of the fluorescence properties of DOM can provide information about the sources, transformations, quantity, and quality of organic matter within the lentic environment (Zsolnay et al. 1999, Bird et al. 2020, Zhang et al. 2021a, Yang et al. 2022). The analysis of the microbial communities present in the aquatic ecosystems is crucial to understanding how environmental variables affect the ecosystem services they provide, including nutrient cycling (Grossart et al. 2020). For this purpose, flow cytometry provides reliable, quantitative, high-throughput data on picophytoplankton (PPP) communities partly responsible for nutrient cycling (Ning et al. 2021). Thus, the initiation of long-term monitoring by implementing combined approaches of chemical, isotope, and biological techniques in these 3 different systems can help unravel the complex biogeochemical transformations related to nutrient cycling and carbon dynamics in tropical lakes under different conditions.

Here we present the first scientific information resulting from a comparative study based on monitoring of biogeochemical data during the dry and wet season conditions in 3 fundamentally different lakes of Costa Rica: a coastal lagoon with estuary conditions at 0 m a.s.l. and surrounded by wet forest, a volcanic/maar lake inside montane rainforest at 2860 m a.s.l., and a glacial/tarn lake at 3500 m a.s.l. in a subalpine rain páramo. We aimed to describe and compare water chemistry, stable isotopes of water ($\delta^{18}\text{O}$ and $\delta^2\text{H}$), and dissolved inorganic carbon ($\delta^{13}\text{C}_{\text{DIC}}$) with respect to DOM optical properties, DOM decomposition processes, and PPP abundance analysis in the lakes (chlorophyll, phycoerythrin, and phycocyanin pigment events). The analysis of chlorophyll, phycoerythrin, and phycocyanin is useful in this study because these pigments facilitate the identification and quantification of various types of PPP. Overall, chlorophyll can be utilized to measure the total biomass of PPP because it is present in all primary producers. Phycocyanin, which is mainly found in cyanobacteria, specifically indicates the abundance of cyanobacteria in PPP; however, phycoerythrin is typically used to estimate the abundance of red algae and serves as an indicator of these specific groups within the phytoplankton community (Stadnichuk et al. 2015). Although our study is restricted to 1 year and only 3 lakes in Costa Rica, we expect this contribution to help promote the implementation of an ecosystem approach to study the biogeochemical functioning of tropical lakes and aid in establishing and maintaining comprehensive

monitoring to provide essential insights into the impacts of climate and land use changes and pollution on tropical lakes of Costa Rica. We also consider our limnological study will be of interest to studies at other latitudes because of the unique ecological dynamics and biodiversity tropical environments it offers, including distinctive nutrient cycling, productivity, and species interactions, in ways distinct from temperate lakes.

Materials and methods

Study sites and design

The studied lakes are in the Caribbean domain of Costa Rica (Fig. 1a, Table 1). We selected 3 representative types of lakes at an elevation gradient from 0 to 3520 m a.s.l.: 1 coastal lake (Lake Madre de Dios, hereafter LMD), 1 volcanic or maar lake (Lake Barva, hereafter LB), and 1 glacial or tarn lake (Lake Ditkevi, hereafter LD). LMD is a salt-wedge estuary fed by 3 freshwater streams that enter the lake at the northern and southern margins. Unlike LB and LD, LMD is an elongated lake, 3.4 km long and 250 m wide, with a maximum depth of ~8.0 m (Fig. 1b, Table 1). The tidal variations in this lake are relatively small (<0.5 m). LB is in the Braulio Carrillo National Park (Barva sector) and is situated at the highest elevation (2860 m a.s.l.) of Barva Volcano in the Cordillera Central of Costa Rica (Umaña 1990, Horn and Haberyan 2016). This lake is an old crater, or maar, surrounded by a dense cloud forest that covers the inner and outer crater walls; it has a diameter of ~115 m and a maximum depth of 7.9 m (Fig. 1c, Table 1). The lake is also characterized by abundant input of allochthonous organic matter from the local forest, which favors the accumulation and dissolution of complex organic matter (e.g., humic-like substances). LD is a glacial lake located in the páramo ecosystem at the Chirripó National Park at 3520 m a.s.l. It has no human activity, except for visiting hikers, and is a protected area dedicated exclusively to conservation purposes. This tarn extends 1.66 ha, has a maximum depth of 8.2 m, and was reported to have clear waters and a low level of nutrients (Fig. 1c, Table 1; Esquivel-Hernández et al. 2018).

The meteorological conditions at the study sites correspond to 3 climatic zones: coastal wet forest (LMD), montane rainforest (LB), and subalpine rain páramo (LD; Holdridge 1978). The precipitation patterns at LMD and LB show no defined dry season (Fig. 2), unlike the rainfall variations at the Chirripó National Park where the well-defined dry season goes from December to April (Horn and Haberyan 2016). The typical

precipitation at the study sites ranges from 2500 to 3500 mm/yr and the average ambient temperature is 26.5 °C (LMD), 10.8 °C (LB), and 8.6 °C (LD).

Sample collection

We collected samples between February and November 2022 to include dry and rainy seasonal conditions. At LMD, sampling was conducted in March, June, August, and October 2022. Given the extension of LMD (3.4 km), samples were collected at 4 sites within the lake from a motorboat: (1) inlet of Madre de Dios river at the entrance of the lake (83.272613°W, 10.192905°N, 1 m a.s.l.); (2) at the inlet of Santa Marta pond (83.270342°W, 10.200083°N, 0 m a.s.l.); (3) at the center of the lake (83.272252°W, 10.208668°N, 0 m a.s.l.); and (4) at inlet of the Pacuare River (83.280116°W, 10.219730°N, 0 m a.s.l.). LB samples were collected in April, June, August, and October 2022 at the center of the lake from an inflatable boat (84.105438°W, 10.133852°N, 2815 m a.s.l.). Because of the remoteness of the LD study site, samples were only collected in February and November. Sampling at this lake was conducted on the southwestern bank of the lake (83.481035°W, 9.468190°N, 3517 m a.s.l.). We collected 31 lake composite water samples (LMD = 20, LB = 5, and LD = 6) for the analysis of fluorescence and optical properties of DOM, DIC, stable isotopes, and major ions. The PPP analysis was only conducted in composite samples of each lake (1 sample per sampling campaign). All samples were collected at the epilimnion (i.e., ~0.5–1 m below the surface). We also collected precipitation samples at each study site (LMD = 125, LB = 34, and LD = 57) for stable isotope analysis using passive Palmex collectors (Gröning et al. 2012) during the sampling period. These samples were used to construct the local meteoric water lines of each study site.

Samples for carbon and major ions were collected in pre-cleaned 30 mL glass amber bottles covered with aluminum foil to protect samples from solar/light radiation. Stable isotope samples were collected in 30 mL high density polyethylene (HDPE) bottles with plastic inserts to prevent evaporation. Sampling bottles were rinsed at least 3 times with the lake water before collection. During transportation and after filtering (0.45 µm polytetrafluoroethylene [PTFE] and/or polyvinylidene fluoride [PVDF] filtration), all samples were stored at <5 °C until analysis. Temperature (°C), hydrogen ion activity (pH), dissolved oxygen (DO, mg/L), and electrical conductivity (EC, µS/cm) of water samples were recorded at each lake using a field portable tester during the study period (Hanna Instruments HI98194, Ann Arbor, MI, USA).

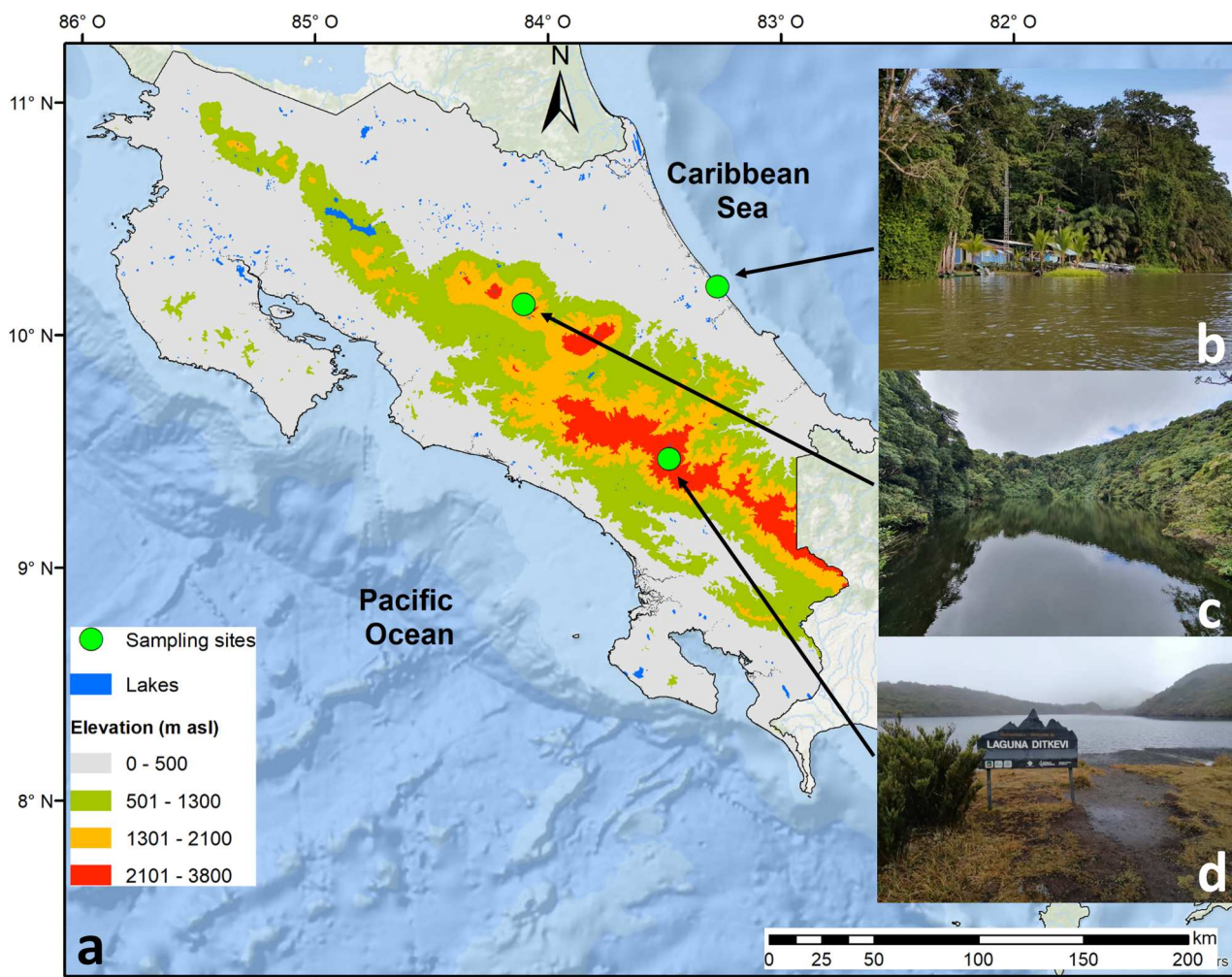


Figure 1. (a) Sampling sites across the elevation gradient of Costa Rica. Lake Madre de Dios (LMD) is located on the Caribbean coast (0 m), Lake Barva (LB) is in the Central Cordillera (~ 2800 m a.s.l.), and Lake Ditkevi (LD) is in the Talamanca Cordillera in southern Costa Rica (~ 3500 m a.s.l.). The distribution of other lakes across the Costa Rican territory is also shown. Photographs of the lake systems: (b) LMD, (c) LB, and (d) LD.

For the PPP analysis, water samples (1 L) were filtered using a 50 μm mesh. A volume of 9 mL of filtered water was combined in a 15 mL plastic tube with 1 mL of borate-buffered fixative solution with 10% formalin and 0.5% glutaraldehyde (100 mM sodium borate, pH 8.7). The fixed samples were incubated ~20 min in the dark, then distributed in 5 mL cryovials and quickly frozen in liquid nitrogen in the field. Samples were transported in liquid nitrogen to the laboratory and stored at -80°C until flow cytometry analysis, following the methodology described in Priyadarsini et al. (2023).

Ion and stable isotope ($\delta^2\text{H}$, $\delta^{18}\text{O}$ and $\delta^{13}\text{C}_{\text{DIC}}$) analysis

Ion chromatography (Thermo Scientific ICS-5000+, CA, USA) was used to analyze ammonium (NH_4^+), sodium (Na^+), potassium (K^+), magnesium (Mg^{2+}), calcium (Ca^{2+}), chloride (Cl^-), nitrite (NO_2^-), nitrate (NO_3^-), and sulfate (SO_4^{2-}). The detection limits for these ions were 0.02, 0.041, 0.05, 0.05, 0.07, 0.06, 0.07, 0.24 (expressed as NO_3^-), and 0.17 mg/L, respectively. To ensure the quality of the analysis, blanks and recovery standards were also included in each batch of

Table 1. Main characteristics of the 3 lakes, Lake Madre de Dios (LMD), Lake Barva (LB), and Lake Ditkevi (LD), included in this study.

Lake system	Longitude (degree)	Latitude (degrees)	Elevation (m a.s.l.)	Area (ha)	Maximum depth (m)	Temperature ($^\circ\text{C}$)	Electrical conductivity ($\mu\text{S}/\text{cm}$)	pH	Dissolved oxygen (mg/L)	Alkalinity (mg/L CaCO_3) ³
LMD	84.067° W	10.983° N	0–1	85	8.0	27.4	543	7.72	5.37	105
LB	84.105° W	10.134° N	2840 ¹	0.77 ¹	7.9 ¹	15.0	47	7.32	5.46	90
LD	83.480° W	9.468° N	3520 ²	1.66 ²	8.2 ²	11.5	23	7.71 ²	5.36	100

¹Horn and Haberyan (2016), ²Esquivel-Hernández et al. (2018); ³1 mg/L CaCO_3 = 0.02 mmol/L.

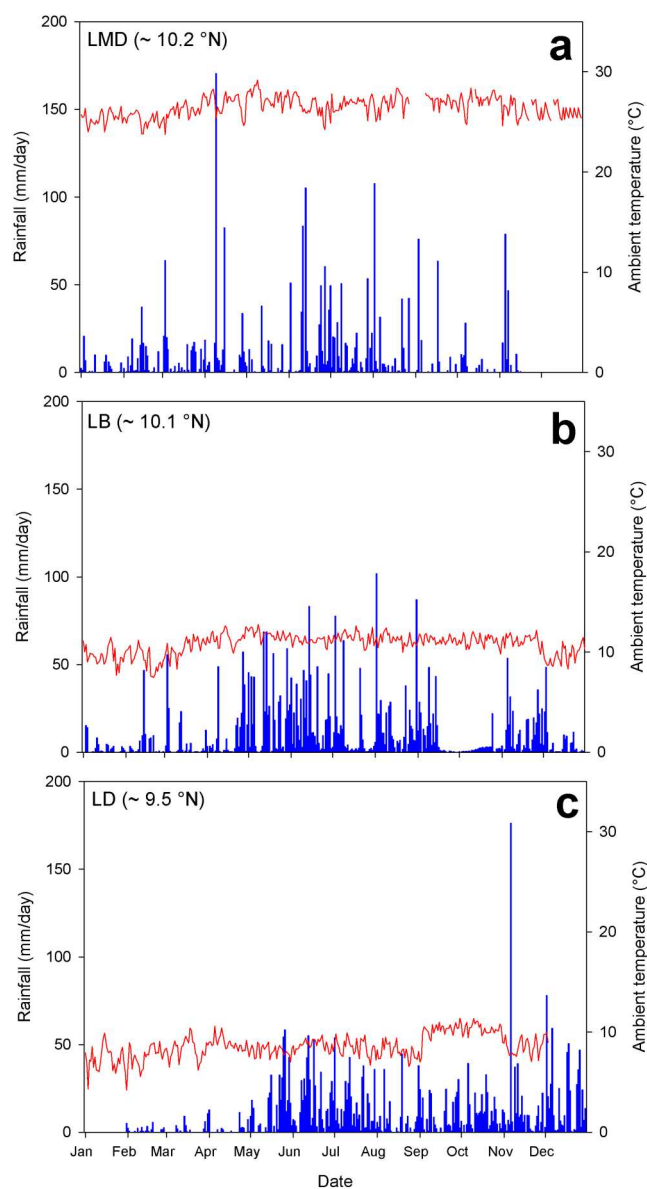


Figure 2. Time series showing representative precipitation (blue bars in mm/day) and daily ambient temperature (red lines in °C) at (a) Lake Madre de Dios (LMD), Caribbean Coast, (b) Lake Barva (LB), Braulio Carrillo National Park (Barva, Heredia), and (c) Lake Ditkevi (LD), Chirripó National Park.

samples. The total phosphorus concentration (P_{total}) in the lake water samples was analyzed based on the conversion of P compounds into orthophosphate, which was then determined by UV-Vis spectrophotometry following the 4500-P D, stannous chloride method outlined by the Standard Methods for the Examination of Water and Wastewater (APHA et al. 2023). The detection limit was estimated at 0.02 mg/L.

Lake water and precipitation samples were analyzed at the Stable Isotopes Research Group laboratory at the Universidad Nacional (Heredia, Costa Rica) using an IWA-45EP water analyzer (Los Gatos Research, Inc., California, USA) with a precision of $\pm 0.5\text{‰}$ for $\delta^2\text{H}$ and $\pm 0.1\text{‰}$ for $\delta^{18}\text{O}$ (1σ , $n = 5$). Calibrated secondary standards MTW (Moscow, Idaho tap water; $\delta^2\text{H} =$

-130.3‰ , $\delta^{18}\text{O} = -16.7\text{‰}$), USGS45 ($\delta^2\text{H} = -10.3\text{‰}$, $\delta^{18}\text{O} = -2.2\text{‰}$), and PGW (local groundwater; $\delta^2\text{H} = -52.6\text{‰}$, $\delta^{18}\text{O} = -8.4\text{‰}$) were used to normalize the results and to assess the quality and drift control procedures. $^{18}\text{O}/^{16}\text{O}$ and $^2\text{H}/^1\text{H}$ ratios are presented in delta notation δ (‰), relative to the VSMOW-SLAP scale.

The stable isotope composition of $\delta^{13}\text{C}_{\text{DIC}}$ and total alkalinity of filtered aliquots ($0.45\ \mu\text{m}$ PTFE) was analyzed using an automated DIC sample preparation system (Picarro AutoMate FX system, USA). A 10% phosphoric acid solution was injected into Exetainer sealed vials to release CO_2 from the sample. A stream of dry and ultra-pure nitrogen was bubbled through the acidified solution to flush the CO_2 from the vial headspace. The CO_2 was captured into gas sampling

bags of a Picarro Liaison™ Universal Interface before being analyzed using Cavity Ring Down Spectroscopy (CRDS, Picarro G2201-i). The instrument cavity and the gas sampling bag were purged with dry and ultra-pure nitrogen after each successive measurement. Calibration was done using the following standards: University of McGill, Canada: CO₂ mixing ratio = 1553 ppmv, δ¹³CO₂ = -43.15‰, Heredia's compressed air: CO₂ mixing ratio = 419.1 ppmv, δ¹³CO₂ = -10.09‰; NOAA gas standard: CO₂ mixing ratio = 394.85 ppmv, δ¹³CO₂ = -8.292‰. ¹³C/¹²C ratios in DIC are presented in delta notation δ (‰), relative to the Vienna Pee Dee Belemnite (VPDB) scale (Craig 1957). The corresponding uncertainty for δ¹³C in DIC is ±0.1‰ (1σ).

The total alkalinity of each sample (reported as mg/L CaCO₃) was also calculated from the average CO₂ concentration measured during the isotope analysis. The CO₂ concentration measured by the CRDS was standardized against Na₂CO₃ solutions (Sigma Aldrich, >99.0%, 5–200 mg/L). These standard solutions were analyzed following the same procedure described earlier. Given the small sample volume analyzed by this method, only water samples with total alkalinity >10 mg/L were quantified. A portable tester (Hanna Instruments HI775, USA) was also used to preliminarily estimate in situ the alkalinity in the field.

DOM optical properties

DOM excitation–emission matrices (EEMs, Coble 1996) were measured using a spectrofluorometer (Jasco FP8300, Tokyo, Japan) equipped with double monochromators both at the excitation and the emission sides. Excitation wavelengths were set up in the range of 200–450 nm with sequential increments of 5 nm with an integration time of 0.5 s and increments of 1 nm in the emission wavelength for the range of 280–550 nm. We also measured absorbance spectra in a range of 200–750 nm with increments of 1 nm using a spectrophotometer (Jasco VP7500, Tokyo, Japan) to inner-filter effect correction procedures, based on an approach described by Kothawala et al. (2013) and code-applied by Pucher et al. (2019). Spectral corrections and Ramman normalization for the EEMs were conducted with sample blanks using deionized water type I in each batch of samples under the same conditions (using quartz cells of 1 cm path length; Huguet et al. 2009).

Flow cytometry analysis for photosynthetic picoplankton (PPP)

For the identification of PPP, we applied the protocol described by Ning et al. (2021). Before the analysis, fixed water samples were defrosted in the dark. The

PPP community was analyzed using an Accuri C6 Plus Flow Cytometer (Becton-Dickinson Life Sciences, San Jose, CA, USA) equipped with a 488 nm blue laser and a 640 nm red laser (Tamm et al. 2018). Unstained samples were analyzed by attempting to maintain 2000 events/s at a fast flow rate (66 μL/s) for at least 3 min. The equipment was calibrated using BD CS&T RUO Beads. The following parameters of each event were recorded: side scatter (SSC), orange fluorescence related to phycoerythrin (FL2, 585/40 nm emission after blue light excitation); red fluorescence related to chlorophyll *a* (FL3, >670 nm emission after blue light excitation); and red fluorescence related to phycocyanin (FL4, 675/625 nm emission after red light excitation).

Data analysis

Simple linear regression analysis was used to construct the local meteoric water lines, the local evaporation line, and δ¹⁸O–δ²H plots of the isotopic composition of precipitation and lake water of each study site. Pearson's correlation analysis was calculated to identify potential relationships between water chemistry, stable isotopes of water (δ¹⁸O and δ²H), and δ¹³C_{DIC} in the lakes. We also applied a Kruskal-Wallis one-way analysis of variance (ANOVA) on ranks followed by Dunn's method to assess differences in the variables between sampling sites. Statistical analyses (α = 0.05) were performed using SigmaPlot software 11.0.

To better understand the hydrological status of the lakes, we estimated the evaporation (*E*) to inflow (*I*) ratios (*E/I*, in %) of LB and LMD using the stable isotope mass balance approach described by Gibson et al. (2016a, 2016b). Overall, the *E* from the lakes as a fraction of *I* is estimated based on the linear resistance model developed by Craig and Gordon (1965) for free-surface evaporation. Calculations were performed in the Hydrocalculator software (Skrzypek et al. 2015). The *E/I* ratios were calculated using the following equation:

$$\frac{E}{I} = \left(\frac{1-h}{h} \times \frac{\delta_{lake} - \delta_{rain}}{\delta^* - \delta_{lake}} \right) \times 100, \quad (1)$$

where *h* is the average local relative humidity (expressed as a fraction), δ_{rain} is the isotopic composition of precipitation, δ_{lake} is the average isotopic composition of lake water, and δ* is the limiting isotope composition enrichment (details in Gibson et al. 2016a). Overall, these first calculations of *E/I* values for LB and LMD are useful for comparing the evaporation conditions of these lakes with the well-established water isotope framework for LD (Esquivel-Hernández et al. 2018, 2022).

EEMs diagrams, presented following Chen et al. (2003) wavelength boundaries, were used as a qualitative tool for

assessing the principal sources of DOC in the water. The fluorescence index (FI; McKnight et al. 2001), the humification index (HIX; Zsolnay et al. 1999), and the autochthonous biological activity index (BIX; Huguet et al. 2009) were calculated using the *starD* package (Pucher et al. 2019), as were the data preparation and correction procedure, so our results may be useful for comparing DOC optical properties with other studies.

We used the C6 Plus Analysis Software (BD Biosciences, San Jose, CA, USA) for flow cytometry data acquisition. PPP was identified and enumerated in biplots of FL3 vs. SSC biplots using FlowJo software (Becton Dickinson). Phycoerythrin-rich picocyanobacteria (PE-Pcy) and phycocyanin-rich picocyanobacteria (PC-Pcy) cells (with FL2 and FL4 vs. FL3 biplots, respectively) were enumerated and expressed as total Pcy. When <10000 cells were gated, the cells were estimated as <10000. A comprehensive review of flow cytometry analysis in environmental microbiomes is available in Priyadarsini et al. (2023).

Results

Water chemistry

We found similar average pH values, DO, and alkalinity concentrations at the 3 sampling sites during the study period (Table 1). A further comparison for ion species, $\text{Ca}^{2+} + \text{Mg}^{2+}$, $\text{SO}_4^{2-} + \text{Cl}^-$, NO_3^- , and P_{total} , also indicated differences between the lake systems (Fig. 3). The median sum of $\text{Ca}^{2+} + \text{Mg}^{2+}$ in LMD (3.34 meq/L) was significantly higher ($p < 0.05$) than the values calculated for LD (0.57 meq/L) and LB (0.08 meq/L). We also found that the median sum of $\text{SO}_4^{2-} + \text{Cl}^-$ (6.81 meq/L) was significantly greater ($p < 0.05$) than the values estimated for LD (0.05 meq/L) and LB (0.04 meq/L). This significant difference at $p < 0.05$ was also verified for the median P_{total} (LMD = 5.92 $\mu\text{eq/L}$, LD = 1.7 $\mu\text{eq/L}$, and LB = 2.1 $\mu\text{eq/L}$). For the NO_3^- concentrations, LD showed a significantly higher median concentration (20.4 $\mu\text{eq/L}$) than the other 2 lakes (LMD = 8.08 $\mu\text{eq/L}$ and LB = 3.90 $\mu\text{eq/L}$, $p < 0.05$). We found that the NH_4^+ and NO_2^- concentrations were below the detection limit in all samples. At $p < 0.05$, we confirmed that Na^+ and K^+ concentrations measured at LMD were significantly greater than the corresponding values in LB and LD. As expected, given the EC values at LMD, the median Na^+ concentration (96.53 mg/L) was ~180 times greater in this lake than in the other 2 lakes, whereas the median K^+ concentration (4.68 mg/L) was ~10 times greater in LMD than in LB and LD. Overall, the Na^+ and K^+ concentrations at LB and LD were low; most samples had values below the detection limits.

Stable isotopes ($\delta^2\text{H}$, $\delta^{18}\text{O}$, and $\delta^{13}\text{C}_{\text{DIC}}$)

The local meteoric water line of LMD was $\delta^2\text{H} = 8.21 \times \delta^{18}\text{O} + 12.76\text{‰}$ ($r^2 = 0.992$, $n = 125$, $p < 0.001$), of LB was $\delta^2\text{H} = 7.86 \times \delta^{18}\text{O} + 13.49\text{‰}$ ($r^2 = 0.995$, $n = 34$, $p < 0.001$), and of LD was $\delta^2\text{H} = 8.00 \times \delta^{18}\text{O} + 13.79\text{‰}$ ($r^2 = 0.990$, $n = 57$, $p < 0.001$). The evaporation line of LMD for lake water was $\delta^2\text{H} = 6.49 \times \delta^{18}\text{O} + 4.14\text{‰}$ ($r^2 = 0.866$, $n = 30$, $p < 0.001$; Fig. 4b), of LB was $\delta^2\text{H} = 5.78 \times \delta^{18}\text{O} - 6.76\text{‰}$ ($r^2 = 0.672$, $N = 6$, $p < 0.01$), and of Ditkevi was $\delta^2\text{H} = 8.54 \times \delta^{18}\text{O} + 17.94\text{‰}$ ($r^2 = 0.941$, $n = 14$, $p < 0.01$) (Fig. 4a). Variations were found in the slopes of the evaporation lines of the 3 lakes (6.49–8.54; Fig. 4b). A comparison between the intercept values of the evaporation lines also confirmed that the evaporation effects in LB are better indicated in the water isotope composition of this lake (−6.76‰) than in the other lake waters (+4.14‰ for LMD and +17.94‰ for LD). Based on the stable isotope mass balance approach, we estimated that the *E/I* values for LB and LMD were 2.5% and 8.3%, respectively. The average *E/I* value for LD was recently estimated at $5.5 \pm 2.5\%$ (1σ) for the period 2015–2020 (Esquivel-Hernández et al. 2022).

A comparison of $\delta^{13}\text{C}_{\text{DIC}}$ and $\delta^{18}\text{O}$ values measured at each lake was useful to identify a potential relationship between the lake productivity and effective water/moisture input (Fig. 5). Overall, low $\delta^{18}\text{O}$ values are typical for areas with highly effective moisture (i.e., low evaporation/precipitation), whereas high $\delta^{13}\text{C}_{\text{DIC}}$ values indicate higher lake productivity (McKenzie 1985, Pérez et al. 2011). We found no statistically significant differences between the average $\delta^{13}\text{C}_{\text{DIC}}$ values of LB, LD, and LMD ($-14.8 \pm 5.6\text{‰}$, $-11.3 \pm 3.1\text{‰}$, and $-12.6 \pm 4.9\text{‰}$, respectively). However, the average $\delta^{18}\text{O}$ values of lakes LB, LD, and LMD were significantly different at $p < 0.05$ ($-6.82 \pm 0.95\text{‰}$, $-11.42 \pm 1.40\text{‰}$, and $-3.86 \pm 1.06\text{‰}$, respectively). At $p < 0.05$, the comparisons on ranks using Dunn's Method confirmed that $\delta^{18}\text{O}$ values were significantly different among the lakes. In LMD, we also identified a significant correlation between $\delta^{13}\text{C}_{\text{DIC}}$ and $\delta^{18}\text{O}$ values ($p < 0.05$; Fig. 5).

Fluorescence properties of dissolved organic carbon (DOC)

Based on the EEMs regions delimited by wavelength boundaries (Chen et al. 2003 and references therein), we found that the DOM in the lakes was influenced by different organic matter sources (Fig. 6). LMD reported moderate intensities in Regions V–III, but also with minimal signals in Regions I–II (i.e., aromatic proteins). In turn, LB made a minimal contribution to the region dominated by humic acid-like substances

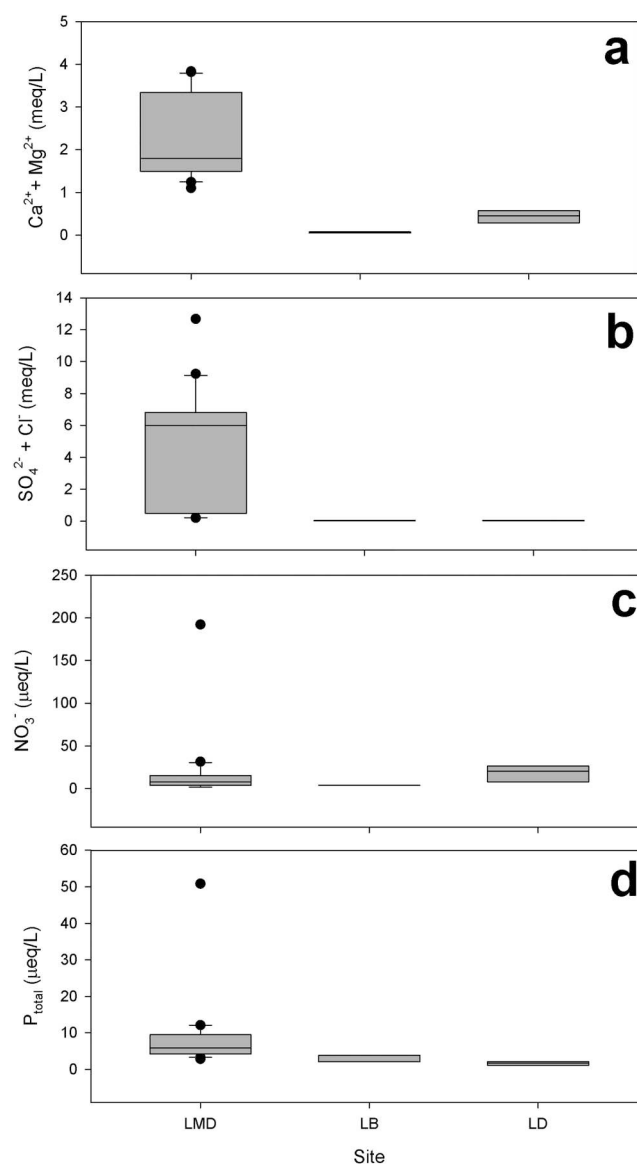


Figure 3. Box plots of chemical variables: (a) $\text{Ca}^{2+} + \text{Mg}^{2+}$, (b) $\text{SO}_4^{2-} + \text{Cl}^-$, (c) NO_3^- , and (d) P_{total} . Sampling site plots include 25th, 75th, median, and outliers.

(Region V) and in the fulvic acid-like region (Region III) and moderate intensity in the protein or microbial byproduct-like contents in the Region I-II and IV (Fig. 6, center panel). LD exhibited strong intensities in the region dominated by humic acid-like substances (Region V), followed by a moderate intensity in the fulvic acid-like region (Region III), with minimal influence of protein or microbial by-product-like contents in the Region I-II and IV (Fig. 6, left panel). We found significant differences between the fluorescence-based indices calculated for DOM as per sampling site (Fig. 7). At $p < 0.05$, the BIX value of LB (2.88 ± 1.55) was significantly greater than the BIX values of LMD and LD (< 0.7). The average FI value (2.00 ± 0.07) estimated for LMD was significantly greater than the FI values of LB and LD (< 1.7). The HIX indices also showed differences where

the average value (0.45 ± 0.16) of LB was significantly lower than the HIX values of LMD and LD (> 0.8).

Lake picophytoplankton (PPP)

Information on the abundance and population dynamics of PPP is relatively scarce in tropical freshwater systems (Shi et al. 2019), and thus PPP analysis results were disaggregated by month to better identify variations in the population abundance (Table 2). PPP was mainly represented by Pcy, mainly PC-Pcy, in all 3 lakes. For instance, PC-Pcy was the dominant type of PPP at LMD (Table 2), whereas LB had greater representation of PE-Pcy events in April, June, and October; PC-Pcy only dominated in August. At LD, we identified a seasonal variation of PE-Pcy of the most abundant type

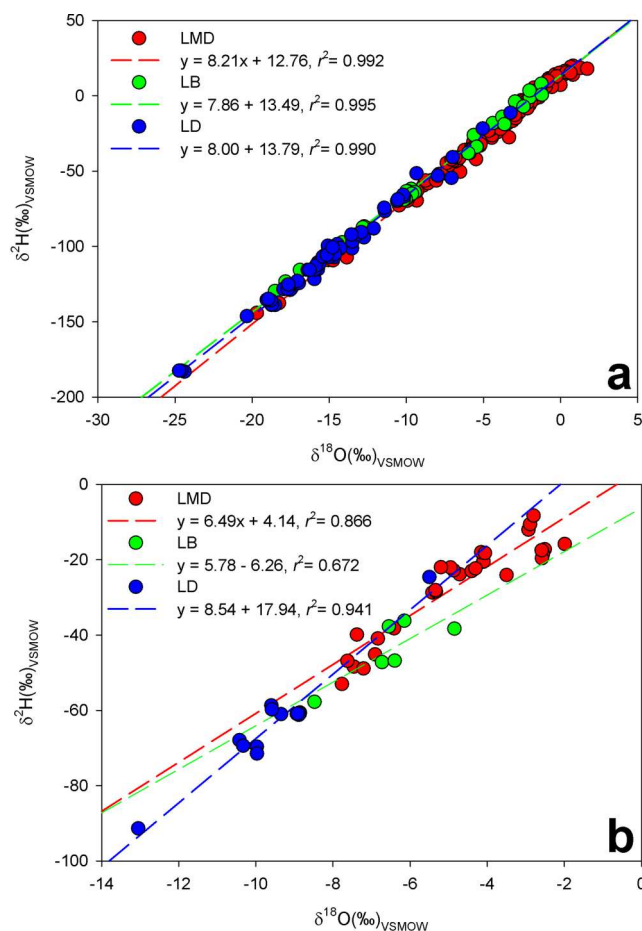


Figure 4. (a) Dual plot of $\delta^{18}\text{O}$ (in ‰ relative to the Vienna Standard Mean Ocean Water or VSMOW) versus $\delta^2\text{H}$ (in ‰ relative to the Vienna Standard Mean Ocean Water or VSMOW) in precipitation for Lake Madre de Dios (LMD), Lake Barva (LB), and Lake Ditkevi (LD). The local meteoric water lines estimated for each site are also reported. (b) Evaporation lines calculated for LMD, LB, and LD are shown as dashed lines.

of PPP in February, but PC-Pcy was most abundant in November (Table 2). The highest PPP cell abundance (cells/mL) was found in LB ($\text{Pcy} = 5.10 \times 10^5$), whereas the lowest count was measured at LD ($\text{Pcy} = 2.22 \times 10^4$). The magnitude of change between maximum and minimum concentrations of Pcy (cells per mL) was higher in LB (6 times) and LMD (5 times) compared to LD (3 times; Table 2). Overall, we found no significant correlation between the cell abundance in the lakes and the physicochemical variables (i.e., pH, EC, DO, and temperature). However, we preliminarily found that PPP abundance may be influenced by the precipitation inputs to the lakes because we registered lower cell abundances during higher monthly rainfall (Fig. 8). For instance, we observed a decrease in the PPP abundance at LMD and LB in June and August as a response to higher precipitation inputs (Fig. 7). At LD, we also verified a change in the PPP abundance (i.e., higher abundance in Nov than in Feb), probably related to the influence of dry and wet seasonal conditions in this study site. However, the short duration of our

monitoring and the different sampling periods included in this study must be considered when interpreting these results.

Discussion

Hydrological and chemical status

The evaluation of continental waters (e.g., lakes) is generally challenging because the hydrology and chemistry of these systems are influenced by factors like precipitation inputs, hydrological processes, local geology, topography, orography, climate, and anthropogenic influence (Pérez et al. 2011, Boëchat et al. 2019, Guimarães-Nobre et al. 2020). However, this task is even more difficult in tropical regions (e.g., Costa Rica) because of the lack of systematic monitoring and the complex biogeochemical processes controlling energy and mass fluxes in these lacustrine systems. Our results indicated that the hydrology and chemistry of LMD, a coastal lake, differed from mountain lakes like LB and LD in 2 key

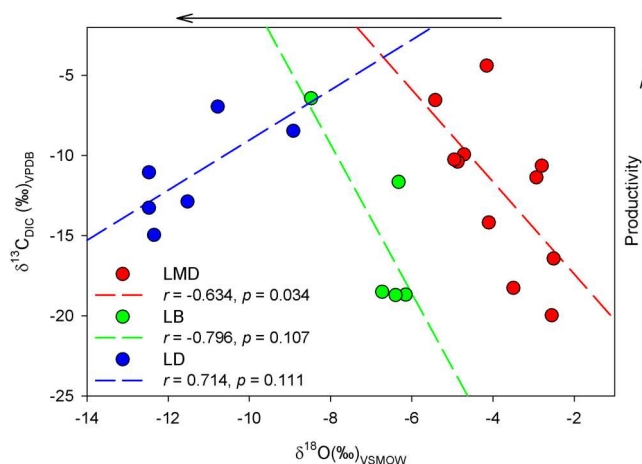


Figure 5. The dual plot of $\delta^{13}\text{C}_{\text{DIC}}$ (in ‰ relative to the Vienna Pee Dee Belemnite, or VPDB) and $\delta^{18}\text{O}$ (in ‰ relative to the Vienna Standard Mean Ocean Water or VSMOW) in lake water for Lake Madre de Dios (LMD), Lake Barva (LB), and Lake Dítkevi (LD) reflects the input of effective moisture (i.e., precipitation-evaporation) and carbon productivity. The red, blue, and green dashed lines show the best linear trends between the water and carbon isotopic values of LMD, LB, and LD, respectively. The corresponding Pearson coefficients and p values are also reported.

aspects: a higher concentration of ions (e.g., Na^+ , K^+ , Ca^{2+} , Mg^{2+} , SO_4^{2-} , and Cl^-) and higher evaporation losses (i.e., a higher E/I value). The higher ion concentrations were probably related to the regular input of salt water from the Caribbean Sea to LMD. Overall, lake waters reflect neutral waters ($\text{pH} \sim 7$), typical DO concentrations (~ 5 mg/L), and good buffer capacity (100 mg/L CaCO_3). In turn, EC values and temperature were significantly higher in LMD than in the other lakes, which probably indicates a higher input of salt

water and higher solar radiation given its location on the Caribbean coast of Costa Rica. However, our chemical data for LMD were comparable with the ion concentrations reported for Laguna Zent, located ~ 20 km south of LMD (Horn and Haberyan 2016). Thus, we most likely collected water samples above the halocline of this lake during the study period. The different concentrations of NO_3^- and P_{total} in the lakes are worth noting. Overall, we reported low NO_3^- and P_{total} concentrations, indicating no eutrophication at these

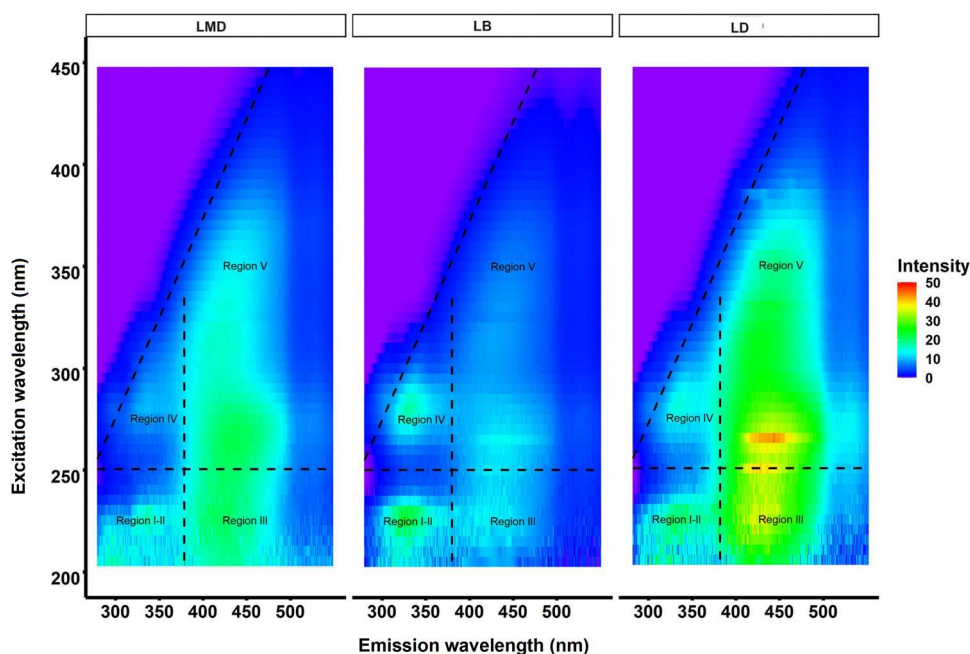


Figure 6. Combined fluorescence excitation/emission matrices (EEMs) per sampling site. EEM regions were defined as: Region I-II = aromatic proteins, Region III = fulvic acid-like substances, Region IV = soluble microbial byproduct-like substances, and Region V = humic acid-like substances (Chen et al. 2003 and references therein).

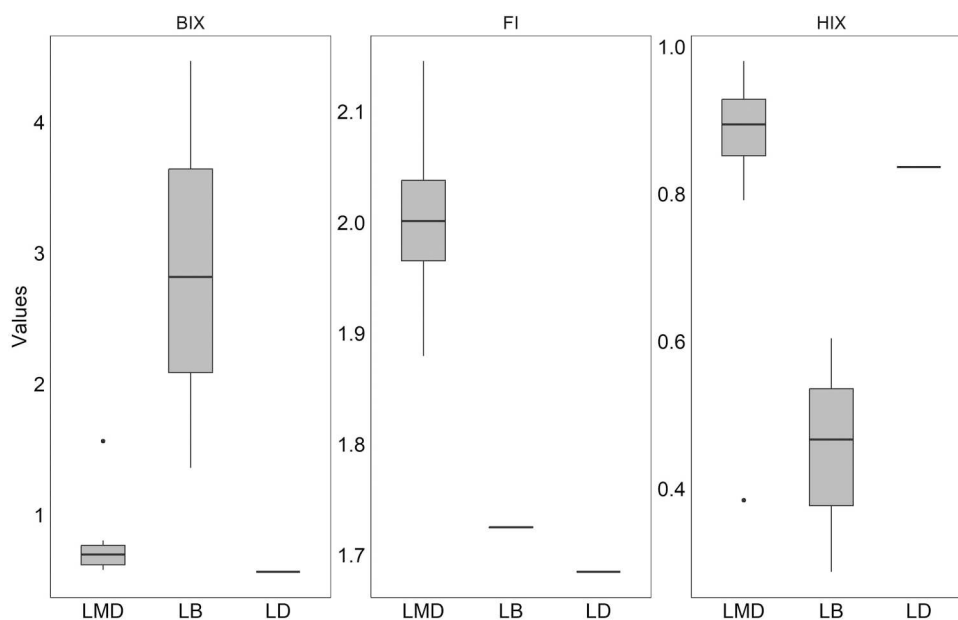


Figure 7. Fluorescence-based indices calculated for dissolved organic matter as per sampling site. (a) Autochthonous biological activity index (BIX) (Huguet et al. 2009), (b) fluorescence index (FI) (McKnight et al. 2001), (c) humification index (HIX) (Zsolnay et al. 1999).

lakes. However, the higher P_{total} concentrations found at LMD can reflect more eutrophic waters and are possibly related to the input of fertilizers from intensive agriculture in the catchment (e.g., banana and pineapple plantations; Arias-Andrés et al. 2018). In turn, the higher NO_3^- concentration in LD than in the other lakes is probably related to the low biochemical activity of the high-elevation and glacial lakes of Chirripó (Horn 2017). Thus, denitrification of the mineralized organic matter from the adjacent soils and páramo vegetation seems to be less effective in this lake, which leads to higher nitrate concentrations than in LMD and LB.

Regarding the hydrological status of the lakes, the higher E/I value estimated for LMD was mainly related to (1) higher solar radiation, (2) higher water temperature, and (3) lower precipitation inputs during the study

period. No differences were found in the relative humidity at the sites (average range 85–90%). However, annual precipitation recorded at the lake catchment of LMD was lower (2578 mm) than the corresponding values registered at the catchments of LB and LD (3568 and 3392 mm, respectively). Overall, the local meteoric water line intercepts at these sites were $>10\text{‰}$, reflecting the input of recycled water vapor (Froehlich et al. 2008). The median $\delta^{18}\text{O}$ values of precipitation also indicate that precipitation at LMD is mainly generated from a mixture of Caribbean water vapor and local moisture (-4.21‰), whereas the precipitation in LB and LD is related to orographic distillation (-9.08‰ and -14.86‰ , respectively). Differences in the hydrology of the 3 lakes could influence their evaporation losses. The slopes of LMD and LB indicate evaporation effects (i.e., values <8), whereas the slope >8 and intercept >10 of LD probably indicates the input subsurface water and recycled precipitation to this lake during the study period (Clark and Fritz 1997, Jasechko 2019). In general, LB can be considered a terminal waterbody because it has continuous water inflow from precipitation and runoff but no water output (Gibson et al. 2016a). LB's waters also were reported as poor in dissolved minerals and with pH values in the range of 5.5–7.5 (Umaña 1990). Thus, the isotopic composition of LB's water mostly reflected the input of rainfall to the lake, which underwent evaporation throughout the study period (slope ~ 6 and intercept $\sim -6\text{‰}$). Unlike LB, LMD and LD are throughflow lakes with continuous water inflow and shorter outflow and residence times of

Table 2. Picocyanobacteria (Pcy) monthly abundance in the lakes (Lake Madre de Dios [LMD], Lake Barva [LB], and Lake Ditkevi [LD]) during the study period. PC = phycocyanin-rich, PE = phycoerythrin-rich.

Lake system	Month	Pcy ($\times 10^4$ cells/mL)	Pcy (log cells/mL)	Dominant types of bacteria
LMD	March	27.8	5.4	PC-Pcy
	June	5.10	4.7	PC-Pcy
	August	6.14	4.8	PC-Pcy
	October	19.4	5.3	PC-Pcy
LB	April	2.45	5.4	PE + PC-Pcy
	June	18.0	5.0	PE + PC-Pcy
	August	3.08	5.5	PC-Pcy
	October	51.0	4.7	PE + PC-Pcy
LD	February	5.62	5.7	PE + PC-Pcy
	November	2.22	5.3	PC-Pcy

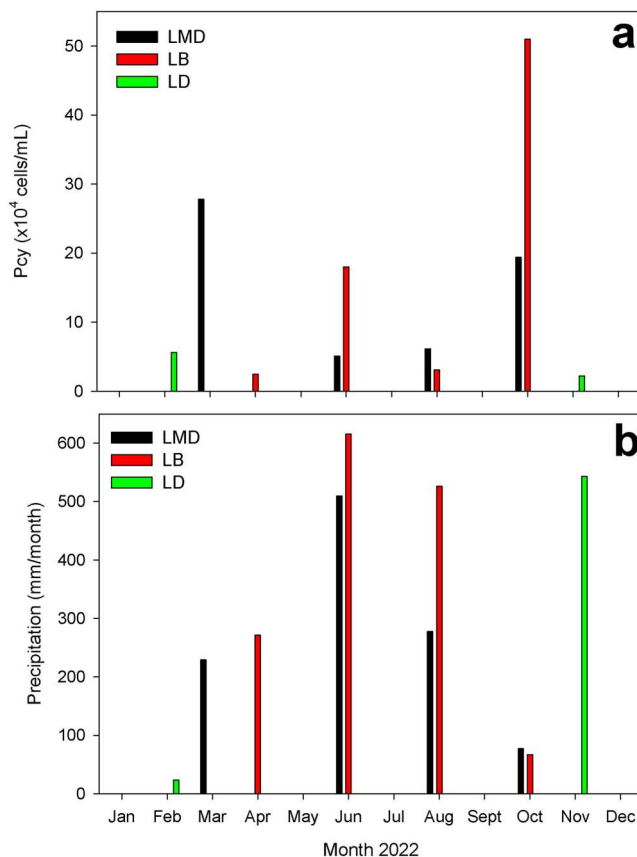


Figure 8. (a) Monthly abundance of picophytoplankton (Pcy) in Lake Madre de Dios (LMD), Lake Barva (LB), and Lake Ditkevi (LD). (b) Monthly precipitation (mm/month) registered at the lake catchment of LMD, LB, and LD during the study period.

water than LB. In both lakes, precipitation and runoff contributed to water inflow, but the lake catchment of LD had more rapid hydrological responses, mostly during the wet season, because of the steep slopes of the páramo (Esquivel-Hernández et al. 2018). However, LD was disconnected from the catchment during the dry season of Chirripó (Dec–Apr), and the lake may have undergone significant evaporation. In addition to the lake water temperature, solar radiation, and precipitation, the greater evaporation losses calculated for LMD were also related to the greater area of the lake, ~50 and 100 times greater than LD and LB, respectively (Vystavna et al. 2021).

Lake carbon cycle and picophytoplankton abundance

The availability of stable isotope information of DIC and the optical properties of DOM are useful to better understand the carbon sources and the potential relationship with the photosynthetic processes represented by the phytoplankton of the studied lakes. Carbon-13 is an excellent tracer of the evolution of DIC in surface waters because of the large isotopic variations in the

different carbon sources (Pawellek and Veizer 1994, Clark and Fritz 1997, Horgby et al. 2019). Overall, the observed changes in the $\delta^{13}\text{C}_{\text{DIC}}$ values of the lakes indicated changing conditions in the lake productivity as a response to water input. Even though the correlation coefficients calculated for these isotopic parameters were not significant (i.e., $p > 0.05$) for LB and LD, the observed trend suggested that LB responded like LMD to the effective water input. We identified a significant correlation between $\delta^{13}\text{C}_{\text{DIC}}$ and $\delta^{18}\text{O}$ values for LMD, indicating a higher productivity in the lake after effective water inputs (McKenzie 1985). In turn, lake productivity of LD seemed to decrease after the effective water input. Moreover, the indirect proportional relationship between the $\delta^{13}\text{C}_{\text{DIC}}$ values and $\delta^{18}\text{O}$ values observed at LMD and LB indicated that lake productivity was enhanced during drier periods. Under these conditions, solar radiation and lake water temperature will typically increase, and the photosynthetic activity in the lake will be higher. Unlike LMD and LB, the relationship between the $\delta^{13}\text{C}_{\text{DIC}}$ values and $\delta^{18}\text{O}$ values was directly proportional in LD. We consider that these changes were not directly related to the lake productivity but to the input of DIC from the lake catchment.

Thus, during the wetter periods, the low $\delta^{13}\text{C}_{\text{DIC}}$ values (up to $\sim -20\text{‰}$) mostly reflected the dissolution of soil CO_2 in the lake (Pawellek and Veizer 1994).

The characterization of DOM can serve to identify its origin, allochthonous (i.e., terrestrial and anthropogenic) or autochthonous (i.e., aquatic), but also to evaluate the nutrient sources for microbes, namely the primary productivity of the lower food web in the lakes (Deirmendjian et al. 2020, Minor and Oyler 2023). Our results also indicated that DOM in the lakes reflects different sources and decomposition processes. In terms of EEMs and fluorescence-based indices, LMD showed similar behavior to LD (HIX ~ 1 and, BIX < 0.75), but the origin of the organic matter fluorescence was mainly related to the microbiological activity in this coastal lake (FI > 1.9). At LB, the fluorescence-based indices demonstrated that the organic matter originated from biological or aquatic bacteria sources (BIX > 1 and HIX < 4), although the FI index (~ 1.7) also suggested a mixed origin of DOC from terrestrial and microbial sources. However, we hypothesized that the major proportion came from bacterial origin because of the higher intensities in the respective region. The FI values for LD, (1.6–1.8) were also in the range reported for other tropical waters (Sánchez-Murillo et al. 2022) and suggested possible mixing of DOC sources (terrestrial and microbial). This finding was also verified by the other 2 fluorescence-based indices values; LD exhibited low autochthonous biological activity (BIX < 0.6 , Huguet et al. 2009) but higher humification processes (HIX > 0.8). Of the 3 studied lakes, LD showed a more diverse composition of DOM and more intense fluorescence (i.e., higher concentrations). However, DOM seems to be dominated by recalcitrant organic matter (i.e., humic and fulvic acids), although DOM input from the adjacent soils is likely given the presence of aromatic proteins and soluble microbial byproduct-like substances. Because DOM is an important carbon source for bacterial growth and reproduction, microbial degradation and utilization do not seem to greatly affect the fate of DOM in this glacial lake (Zhang et al. 2021b). The optical properties of DOM in LB indicated that the organic matter in the lake is dominated by aromatic proteins and soluble microbial byproduct-like substances. As a result of the low temperature of lake water ($\sim 15\text{ °C}$) and the high input of allochthonous organic matter from the nearby forest, the dissolution of humic and fulvic acids seem to be restricted to the deepest water of the lake, confirming the temperature stratification reported by Umaña (1990). Thus, DOC concentrations in the surface water of LB are probably lower than in the bottom, as indicated by the less intense fluorescence. The DOM fluorescence in LMD is mainly

due to the presence of humic and fulvic acids. Unlike LD and LB, the higher water temperature and lake productivity control the decomposition of DOM at LMD, and thus the concentration of aromatic proteins and soluble microbial byproducts are lower than in more recalcitrant organic matter (Ávila et al. 2019, Begum et al. 2023).

The influence of lake type and land use on the sources of DOM and mineralization processes is important. Among the study sites, LMD can be regarded as the lake with the highest degree of anthropogenic influence because of its location in the Caribbean lowlands of Costa Rica and its position downstream from plantations (e.g., banana and pineapple). The lake is then significantly affected by the input of pesticides and fertilizers from adjacent agricultural soils via runoff. The less important role microbial degradation and utilization plays in this lake may be related to the input of anthropogenic stressors (Guimarães-Nobre et al. 2020). Nevertheless, the hydrological regime of LMD (i.e., throughflow lake; Gibson et al. 2016a) can also help dampen the negative effects of pesticides and fertilizers entering the lake. Unlike LMD, LB and LD are in protected areas where the anthropogenic influence can be considered neglectable. In these lakes, the DOM composition seems to be more complex because the input of natural-sourced DOM is constant and accumulates in the lakes, especially in LB given its distinctive hydrological regime (i.e., terminal waterbody; Deirmendjian et al. 2020). The well-established dry season period at LD may also influence the transformation of DOM in this lake. During the dry season, this lake can also be considered a terminal lake because the water level systematically decreases, and during an extended period no water output is observed (Gagliardi et al. 2019).

PPP in tropical lakes show fewer fluctuations in cell abundance than temperate and high-altitude lakes (Sarmiento et al. 2008). We also observed fewer fluctuations in our study lakes, where PPP was mainly represented by PC-Pcy, especially in LMD. However, note that PE-Pcy was detected in LB and LD. Cyanobacterial PPP also dominated over eukaryotic PPP in terms of abundance, as seen in other eutrophic shallow lakes (Silvoso et al. 2011). The dominance of prokaryotic algae such as cyanobacteria in some lakes may be due to ecological and environmental factors (e.g., nutrient availability and solar radiation). Cyanobacteria can tolerate high levels of direct solar radiation and can float and accumulate close to the water surface. This tolerance is based on its capacity to reach saturation of photosynthesis at high irradiance values and the synthesis of photoprotective substances such as mycosporin-type amino acids and carotenoids that divert excess energy. Thus, differences

in the solar radiation reaching the surface water of the lakes may explain the observed variation in the cyanobacterial PPP. Moreover, many cyanobacteria can fix atmospheric nitrogen. In environments with low levels of available nitrogen, this ability can give them a competitive advantage over other algae that cannot fix nitrogen (Blomqvist et al. 1994). Thus, in lakes like LB and LD, the nutrient input from natural sources could increase nutrient availability, promoting the establishment of cyanobacteria.

We noted a tendency for higher concentrations of cells in months with relatively less rainfall, like in October (LB) and February (LD), which was also reported for PPP in other lakes (Schallenberg et al. 2021). Thus, this finding is seemingly related to the lakes' mixing regime and the influence of the precipitation inputs. As a result, during the rainiest period at each study site, the cell counts on the surface of the lakes decreased because of increased mixing in the lakes. The complete dominance of PC-Pcy in the more productive and eutrophic waters of LMD was also reported for other lakes (Jasser et al. 2010). However, we recognize that our comparative analysis must be considered preliminary because of the different sampling periods at each lake system. Note that to better understand the seasonality of cell abundance and its relationship with other hydrological and chemical variables, we need to extend our sampling over the coming years. However, our analysis is still worthwhile because we were able to preliminarily identify a key driver controlling the phytoplankton abundance in the study lakes: the precipitation seasonality. Moreover, the inclusion of other lakes like LD, which is influenced by a dry period of ~4 months, unlike LMD and LB, can be useful to verify our interpretation of these results.

Conclusions

Our results indicate that the combination of stable isotopes, water chemistry, hydrology, and microbiota is a promising approach to studying the biogeochemical characteristics of surface water ecosystems like the tropical lakes of Costa Rica. Although a short period was assessed, the information presented provides a baseline for future long-term monitoring. Water stable isotopes ($\delta^{18}\text{O}$ and $\delta^2\text{H}$) and ion chemistry confirm that coastal lakes may have higher concentrations of ions and higher evaporation losses (i.e., higher E/I value) than mountainous lakes. In general, the hydrological status of the coastal lake was controlled by solar radiation, water temperature, and precipitation input. Of these controlling factors, precipitation input seems to be a key driver of lake productivity because $\delta^{13}\text{C}_{\text{DIC}}$ values were higher

during drier periods and showed a negative correlation ($p < 0.05$) with effective moisture contributions (i.e., $\delta^{18}\text{O}$ of lake water). These responses were more difficult to identify at the mountainous lakes like LB and LD because of their lower E/I value and climate location (i.e., lower water temperature and lake productivity). Nevertheless, the optical analysis of DOM and the PPP abundance also indicate that the higher water temperature and lake productivity of the coastal lake effectively control the decomposition of DOM and, as a result, the concentration of aromatic proteins and soluble microbial byproducts is lower than the more recalcitrant organic matter. In turn, mountainous lakes showed a higher diversity of DOM and PPP.

Given the lack of consistent long-term monitoring of lakes in the Central American region, our results could promote the adoption of an ecosystem approach to generate baseline information for future studies on tropical lakes. These new studies may be dedicated to studying the impact of climate change, land use, and pollution on the lakes, as indicated by the composition of microbial communities, carbon transformations, and nutrient dynamics of these tropical waters. We expect the incorporation of recent advances in technology like environmental metagenomics and biogeochemical modeling in combination with chemical, hydrological, and biological data to improve our understanding of these complex ecosystems in the coming years.

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Disclosure statement

No potential conflict of interest was reported by the author(s).

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Data availability statement

Data are available from authors upon reasonable request.

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