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Biogeochemical functioning of Lake Alaotra (Madagascar): a reset of aquatic carbon sources along the land-ocean gradient.

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Abstract

The catchment of Lake Alaotra, a large shallow lake (surface is 200 km^2, maximum depth 2 m) in the Malagasy highlands, is a region where the grassland dominated landscape is dotted by major gullies called "lavaka", which has historically been claimed to lead to high erosion rates. Sedimentary archives in lakes such as Lake Alaotra could be of great help to resolve questions about the natural versus anthropogenic influences on the changing landscape, provided that we understand carbon sources and sinks within the lake, as well as the connection with the surrounding landscape through the input of material via inflowing water. Here, we provide a first comprehensive survey of the carbon (C) biogeochemistry of the Lake Alaotra system. We investigated the seasonal variability of the concentrations and stable isotope C ratios of inorganic and organic C pools, as well as a range of other relevant proxies, including physico-chemical parameters, dissolved CO_2 and CH_4 concentrations, total alkalinity, and Chl-a (chlorophyll a) from spatially distributed sampling and seasonal monitoring of several rivers. While rivers were found to carry high total suspended matter (TSM) loads with a modest particulate organic C (POC) content, the lake itself and its outflow were characterised by much lower TSM values and high %POC (relative contribution of POC to TSM). The POC concentration of the outflow (13.0 ± 7.7 mg L^{-1}) was substantially higher than in the inflowing water (1.9 ± 2.1 mg L^{-1}), and δ^{13}C values were also distinct between inflowing water (-24.6 ± 1.8 ‰) and the lake (-26.5 ± 2.1 ‰) or its outflow (-25.2 ± 1.4 ‰). Similarly, the lake outflow was surprisingly rich in DOC (9.5 ± 1.4 mg L^{-1}) compared to inflowing water (2.6 ± 1.1 mg L^{-1}). This indicates that the lake and its surrounding wetlands act as a substantial source of additional organic C which is exported downstream. The CO_2 and CH_4 concentrations in inflowing and outflowing rivers were substantially higher than in lake waters, and peaked during the rainy season due to lateral inputs from wetlands. However, sources of POC and DOC were uncoupled: δ^{13}C data were consistent with marsh vegetation being the main source of net DOC inputs, while phytoplankton was expected to be an important source of POC in the lacustrine waters. Lake suspended matter has low POC/Chl-a ratios (143–564), high %POC (10 to 29 %), and δ^{13}C values around 20 ‰ lower than the dissolved inorganic C (DIC) pool (-26.5 ± 2.1 ‰ versus -6.7 ± 1.6 ‰). Despite the importance of phytoplankton production to the lake POC pool, the lake acted as a net source of CO_2 to the atmosphere, likely due to the high C inputs from the surrounding marshes, and sediment respiration considering the shallow water depth. Nevertheless, the pCO_2 in the surface waters of the lake was lower than in the inflowing and outflowing rivers, possibly reflecting the impact of phytoplankton production (CO_2 assimilation), although also reflecting degassing to the atmosphere. The biogeochemical functioning of Lake Alaotra differs substantially from the large and deeper East African (sub)tropical lakes and was similar to lakes surrounded by flooded forest in the Congo

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River basin, likely due to a combination of its large surface area and shallow water depth, and the large extent of surrounding wetlands and floodplains. It acts as an abrupt element in the land-ocean gradient of the catchment, whereby the biogeochemical characteristics of the Maningory River (i.e., the lake outflow) are strongly determined by processes taking place in Lake Alaotra and its wetlands, rather than being reflective of characteristics and processes higher up in the catchment.

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1 Introduction

Datasets on the biogeochemistry and C cycling along terrestrial-aquatic gradients in tropical environments are still scarce in comparison to the boreal and temperate zone. Lakes have traditionally been characterized as sources of CO_2 to the atmosphere (Cole et al. 1994, 2007) sustained by the production of CO_2 from degradation of terrestrial organic matter. Accordingly, lakes would then be net heterotrophic systems sustained by external inputs of allochthonous organic matter (DOC and POC) from the surrounding landscape (catchment) (Del Giorgio et al., 1999). However, the impact of external inputs of allochthonous organic matter on the cycling of organic matter partly depends on the size of the system (surface area and depth), with larger and deeper lakes being less heterotrophic (Del Giorgio and Peters, 1994; Staehr et al., 2012). In tropical lakes, aquatic primary production can be intense due to combined year-round favourable light, temperature conditions, and weak water column stratification, favourable to nutrient inputs from deep to surface waters (Lewis, 2010). Morana et al. (2022) showed that African tropical lakes with a low DOC content (non-humic) were net autotrophic leading to low CO_2 sources or even sinks of atmospheric CO_2 (Borges et al., 2022). Lakes with high DOC content from wetlands were characterized by low primary production, and were strong sources of CO_2 to the atmosphere (Borges et al., 2022). In addition, dissolved organic C (DOC) plays an important function in lake ecosystems and regulates the carbon and energy cycle of inland waters (Wetzel, 2003). The study by Morana et al. (2022) showed that in situ primary production in some of the studied lakes could be ~20 times higher than the organic carbon (C) burial in sediments and CO_2 emission to the atmosphere, thus contradicting the paradigm of lakes functioning as net heterotrophic systems (Del Giorgio et al., 1993, Duarte and Prairie 2005, Aufdenkampe et al., 2011).

Irrespective of their trophic status, lakes are often highly active areas in terms of organic matter processing and biogeochemical modifications (Sobek et al., 2006; Tranvik et al., 2018). Moreover, during the transit of water in the lakes, repartitioning of organic matter between dissolved and particulate organic C might take place, changes in characteristics in the lake could occur and might result in a difference between inflow and outflow characteristics (Tranvik et al., 2009; Hanson et al., 2011). While the amount of data on the origin of DOC and POC, and on transport fluxes in tropical rivers has grown steadily, much less is known about the biogeochemical cycling and OC source contributions in tropical lakes in Madagascar (Ralison et al., 2008; Marwick et al., 2014). This lack of data and uncertainty at the global scale requires the collection of additional datasets over adequate spatial and temporal scales.

Lake Alaotra is the largest freshwater system in Madagascar and is recognized as a hotspot of biodiversity. It is surrounded by marshes that provide the only remaining habitat of an endangered lemur species (*Hapalemur alaotrensis*), as well as by extensive floodplains that represent the most important rice-producing region of Madagascar (Lammers et al., 2015). Because of these high ecological, economical and scientific values, the lake Alaotra wetland is recognized as a Ramsar site. The wetland marshes of lake Alaotra occupy a surface area (~230 km^2) (Mietton et al., 2018) larger than the lake itself (currently ~200 km^2 of open water, Bakoariniaina et al., 2006; Ranarijaona, 2009), and are mainly located in the south-western part of the lake. Water and sediment transported through the rivers pass via floodplains and marshes before entering the lake. The characteristic hills in the Lake Alaotra watershed are currently dominated by grasslands but were likely to have been forested or characterised by wooded savannah vegetation up to ~2000 years ago (Broothaerts et al., 2022; Razanamahandry et al, 2022). A particular erosional feature called 'Lavaka' dots these landscapes - gullies which can reach very large dimensions (Brosens et al., 2022; Cox et al., 2010, 2023). Lavaka mainly occur in the central highlands of

Madagascar, and their density is particularly high in the region of Lake Alaotra (Cox et al., 2010). Studies of ^{10}Be in river sediments in central Madagascar indicated that sediments in the river are mainly lavaka-derived rather than colluvial sediments (Cox et al., 2009). In addition, since Lake Alaotra is located in one of the most important agricultural regions of Madagascar, it is highly affected by human interference. For instance, clearance of forest along the hillslopes or the construction of channels and dams for irrigation activities in the floodplains have significantly altered the state of the lake Alaotra wetlands. Therefore, there appears an intuitive relationship between the forest disappearance, erosional processes, and the sedimentation of the lowlands (Kull, 2002). Erosion has a huge impact both in the upstream and downstream parts of a catchment. In the upstream regions, it does not only induce soil losses but in doing so, also degrades terrestrial ecosystems and their biodiversity (An et al., 2008; Montgomery, 2007; Zheng et al., 2005). Further downstream, the eroded soil is deposited in floodplains and lakes, and will affect the viability of aquatic ecosystems (Jenkins et al., 2010; Pattanayak and Wendland, 2007). There are indications that the productivity of rice in the Lake Alaotra basin dropped considerably to only about 40 % of its former level as a result of the silting of rivers and irrigation channels (Bakoariniaina et al., 2006). The reduction in rice production, along with demographic pressure, leads to increased rates of marshland conversion into agricultural fields or clearing for fishing. Therefore, the natural marshland vegetation has been reduced considerably, often by fire. Bakoariniaina et al. (2006) concluded from combined LandSat imagery and historical studies that sediments have filled Lake Alaotra and reduced it to 60% of its original size by the 1960s, and at times the lake has been proposed to totally disappear. However, recent data on the bathymetry and characteristics of the materials on the bottom of Lake Alaotra question these conclusions and suggest that sedimentation in the lake itself remains non-significant (Ferry et al., 2013). Studies on pollen from lake Alaotra sediment archives have shown sedimentation rates of 0.3 - 0.6 mm y^{-1} (Broothaerts et al., 2022), which is very low considering the high erosion rates of the catchment. Moreover, during the last 1000 years, no significant increase in sedimentation rate was observed (Broothaerts et al., 2022).

Stable isotope profiles of soil organic C of hillslope grasslands of the Lake Alaotra catchment indicate that this region was more forested in the past (Razanamahandry et al., 2022), yet the timing of this vegetation shift cannot be robustly determined from proxies in the soil profile. A range of proxies preserved in sediment cores in Lake Alaotra could offer a promising archive to reconstruct this past vegetation change and other paleo-environmental variations. However, the contemporary functioning of Lake Alaotra has never been studied from a limnological or biogeochemical perspective, which would hamper a sound interpretation of proxies in the sedimentary record. In this study, therefore, we will adopt a landscape-scale approach whereby we investigated the different aquatic C pools and their stable isotope ratios, along with a range of other physico-chemical and geochemical parameters, across the land-aquatic gradient, from different inflowing water, along the lake surface waters and in its outflow.

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2 Materials and methods

2.1 Study Area

This study was conducted in the Lake Alaotra basin, Madagascar. Lake Alaotra is Madagascar's largest lake, and situated in the north-east of the island in the Toamasina province, between 17–18 °S and 48–49 °E and at an altitude of 775 m above sea level (Mietton et al., 2018) (Figure 1). The catchment of Lake drains a catchment area of 4042 km^2 (Ferry et al., 2013); and the lake -and its wetlands and floodplains are surrounded by hills in an altitude range between 900 and 1300 m above sea level (Bakoariniaina et al., 2006). Grasslands form the dominant vegetation type in the Lake Alaotra catchment, and a high density of "lavaka" can be found across the landscape. On average, these reach dimensions of ~30 m wide, 60 m long and 15 m deep. The region is characterised by a tropical climate with a hot rainy season from November to April and a cool dry season from May until October (Supplementary Figure S1), the latter accounting for 7 to 22 % of total annual rainfall, which amounts to 900 to 1250 mm y^{-1}. The monthly maximum rainfall can be more than 250mm, typically occurring in January. The mean temperature in the Lake Alaotra Region is 20.6°C with an average of daily minima 12°C (July) and average daily maxima 28°C (January) (Ferry et al., 2009). Analysis of seasonal variability of temperature and precipitation during our sampling period allow us to divide the sampling period into 2 distinct periods: (1) a dry season from June to October when monthly precipitation and temperature were lower and (2) a rainy season from November until May, with higher temperature and higher precipitation (Supplementary Figure S1).

Lake Alaotra is a shallow lake with an average water depth of 2–4m (Andrianandrasana et al., 2005). The open water surface of Lake Alaotra was less than 200 km^2 and freshwater water marshes cover around 230 km^2 (Bakoariniaina et al., 2006; Copsey et al., 2009), but these relative areas have varied over the years (Lammers et al., 2015). Lake Alaotra and its wetland marshes are surrounded by floodplains and ricefields covering around 820 km^2 (Ferry et al., 2009).

Lake Alaotra is filled by water mainly from infiltration, runoff, and flooding (Copsey et al., 2009). More than 20 rivers enter the lake, the largest of which are the Anony and Sahamaloto in the northwest, and the Sahabe and Ranofotsy in the southwest (Supplementary Figure S2). A network of man-made irrigation canals in the ricefields forms an extra connection between the rivers and the lake. The only outflow of the lake is the river Maningory, situated in the northeast of the lake (Figure 1 and Supplementary Figure S3).

In 1923, the construction of rice fields was initiated in the Lake Alaotra region. In the 1950s, dams and the delimitation of ricefields were constructed in order to improve the rice production capacity (Moreau, 1980). Most of the rivers flowing into the lake were progressively equipped with small hydraulic infrastructure to irrigate the ricefields towards the end of the 1980s. These generally consist of small water storage reservoirs and dams (e.g., Sahamaloto) with a large network of canals, thereby impacting the natural river network. Between 2003 and 2009, an additional reservoir was constructed (located in Andilanatoby on the river Ranofotsy) as part of an irrigation rehabilitation project. During the time of our fieldwork, a dam was constructed in the southeast on the river Sahabe.

The monthly discharge of the Maningory was measured between the years of 1976 and 1986, ranging between 66 $m^3 s^{-1}$ and 315 $m^3 s^{-1}$ (Chaperon et al., 1993). Average discharge of water from the principal inflowing rivers basins (basin of 4042 km^2) to Lake Alaotra and the outflow Maningory have been calculated for the period between 1945–1979 (Chaperon et al., 1993; Dosseur and Ibiza, 1982). Results showed that there is a delay in the rise of

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the annual peak discharge of approximately six weeks between the inflowing rivers and the Maningory. The outflow presented a slower decrease in discharge compared to the rapid drop flows from March to April-May for inflowing rivers, with a time difference of 6 weeks to 3.5 months (Figure 2). There was also a significant difference between the runoff of the inflowing sub-catchments (500 mm) and the outlet catchment (340 mm).

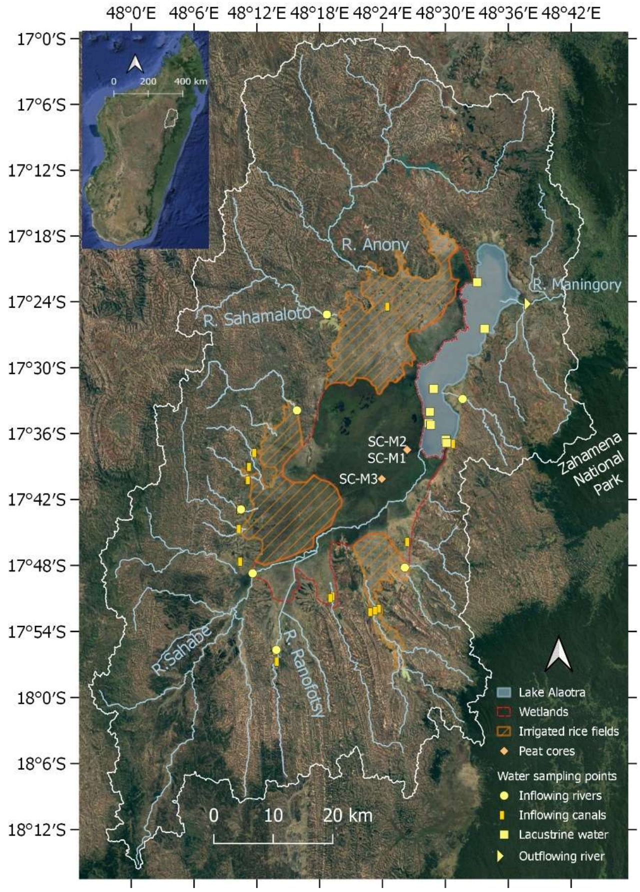

Figure 1: Map of the Lake Alaotra catchment (delineated by the white line), indicating the location of sampling sites. Lake Alaotra is indicated by blue filled polygon, wetlands are delineated by the red dotted line and the extent of floodplains is indicated by the orange dashed polygon. Background map taken from © Google Earth (2021).

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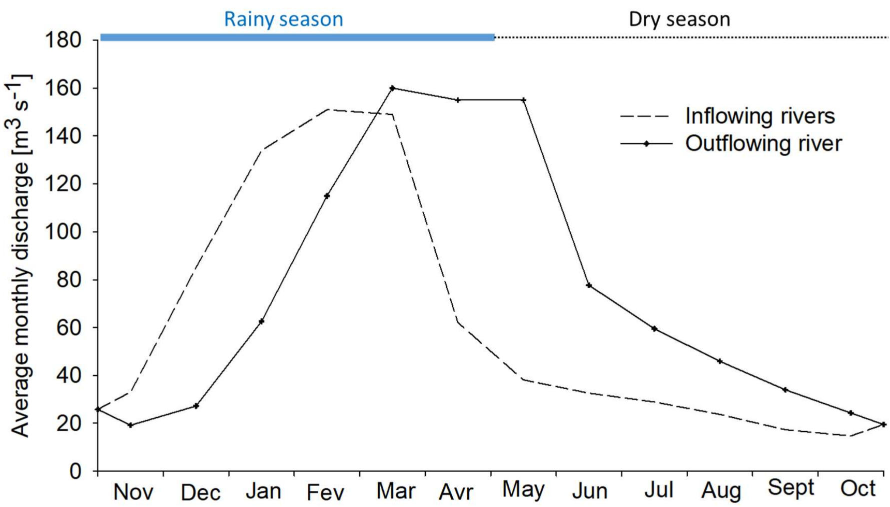

Figure 2: Comparison between the average monthly discharge of inflowing rivers and outflowing river (Maningory) of Lake Alaotra – data were collected between 1976 and 1987 (Chaperon et al., 1993). Continuous blue line and the dotted black line represent the rainy season and dry season, respectively.

The natural wetland and lake water body combined covers around 430 km^2, with wetlands largely located in the southeast of the lake, while the inflowing rivers in the north (Anony) and those in the west are not surrounded by substantial marshes before entering into the lake. These wetlands are seasonally flooded, and are dominated by *Cyperus madagascariensis* or "zozoro" (Cyperaceae), covering ~50 % of the marshes (Lammers et al., 2015) (see Supplementary Figure S4). This tall, robust, floating species requires either a permanent presence of a water column (up to nearly 3 m deep) or at least a waterlogged environment. The population of *Cyperus madagascariensis* in the Alaotra marshes has degraded due to the installation of rice fields and by its clearing for traditional fishing (Ranarijaona, 2009).

The area of rice fields surrounding the lake has been largely gained from the extension on the wetland ecosystem (Mietton et al., 2018). Since the era of cultivation, floodplains have been the main zone where farmers in Lake Alaotra cultivate rice (especially irrigated rice) (Supplementary Figure S5). During the rainy season, floods regularly occur in the Alaotra plain and lead to strong siltation over the ricefields (Ferry et al., 2013).

Around 750 000 people live in the area of Lake Alaotra (estimate for 2011), for whom rice cultivation and fishing are important sources of livelihood (Penot et al., 2012), a stark increase from ~110,000 people in the 1960s (CREAM, 2012). Due to this demographic pressure (Jacoby and Minten, 2007), agricultural land is becoming limited, forcing many people to convert the marshes to ricefields (Lammers et al., 2017). This practice of cultivation consists of growing rice in shallow lake water and by converting the marshes at the lake edge. In addition, farmers have started to use the hillslopes for the production of upland rice, maize, peanuts and cassava and a range of vegetables (Penot et al., 2018).

2.2 Field sampling

Water samples from inflowing rivers and canals were collected during our first and second fieldwork campaigns: (i) April–June 2018 (dry season) and (ii) January–March 2019 (rainy season). During the dry season, only six rivers had sufficiently high water levels for sampling. However, most rivers and canals had normal to high flow during the rainy season campaign, which allowed us to sample water once a week throughout the field campaigns. In addition to the data collected during fieldwork, biweekly monitoring of a selection of rivers was organized (April 2018 to August 2019) to allow us to assess the seasonal variability of parameters. The inflowing rivers chosen to be monitored for this research were the Sahamaloto and Ranofotsy rivers that drain grassland-dominated catchments, and were accessible before entering the floodplain and Maningory river (i.e., the outlet of Lake Alaotra, Figure 1). Rainfall data were obtained from meteoblue.com (dataset spanning 40 years), a meteorological service that employs weather models based on the NMM (Nonhydrostatic Meso-Scale Modeling) technology. We selected two locations: Tanambe (northwest of Lake Alaotra) and Ambatondrazaka (southeast of Lake Alaotra).

2.3. Field and laboratory analyses

Water temperature, conductivity, dissolved oxygen, and pH were measured *in situ* using a Yellow Springs Instruments (YSI) ProPlus probe.

Samples for TSM (total suspended matter), POC (particulate organic C), PN (particulate nitrogen) and stable isotope ratios in POC ($\delta^{13}C$-POC) involved collection of water samples in the centre of the rivers by using a Niskin bottle. Samples for TSM were obtained by filtering a known volume of water (approximately 100 to 250 mL of water) on pre-weighed and pre-combusted (450°C) 47 mm Whatman GF/F filters with a nominal pore size of 0.7 µm and then air-dried. These were later oven-dried prior to weighing to calculate TSM loads.

A known volume (20–50 mL) of water was filtered through pre-combusted (450°C) 25 mm Whatman GF/F filters to determine the concentrations of POC and PN, and $\delta^{13}C$-POC. These filters were air-dried after collection, and later treated with concentrated HCl fumes in a desiccator for four hours to eliminate inorganic C. Afterwards, the filters were dried in the oven at 50°C and packed in Ag cups. The analysis was conducted using an Elemental Analyser Isotope Ratio Mass Spectrometer (EA-IRMS: Thermo Flash HT/EA and Delta V Advantage) setup. Calibrations of concentrations and $\delta^{13}C$ data were based on certified caffeine (IAEA-600) and two in-house references: leucine and tuna muscle tissue (previously calibrated versus certified standards). Reproducibility of $\delta^{13}C$ measurement was better than ± 0.2 ‰. POC/PN ratios are reported as mass/mass ratios.

To determine the dissolved organic C (DOC) concentration and $\delta^{13}C$-DOC values, 40 mL of filtered water samples (first filtered with pre-combusted (450°C) 47 mm Whatman GF/F filters with a pore size of 0.7- µm and subsequently with 0.2 µm syringes filters) were collected and stored in glass vials with Teflon-coated screw caps. To preserve the water samples, 100 µL of H_3PO_4 was added. Analysis of DOC and $\delta^{13}C$-DOC was performed on a wet oxidation TOC analyzer (IO Analytical Aurora 1030W) coupled with an isotope ratio mass spectrometer (Thermo Finnigan Delta XP). Quantification and calibration were performed with IAEA-C6 ($\delta^{13}C$=-10.4 ‰) and an internal sucrose standard ($\delta^{13}C$=-26.99 ± 0.04 ‰).

Total alkalinity (TA) was measured via an open-cell titration with 0.1 mol L^{-1} HCl (Gran, 1952) on 50 mL water samples filtered on 0.2 µm. Data quality was verified based on certified reference material from Andrew Dickson (Scripps Institution of Oceanography, University of California, San Diego, USA). Typical reproducibility of TA measurements was better than ± 3 µmol L^{-1}.

To measure $\delta^{13}C$-DIC, water was transferred directly from the Niskin sampler and stored air-free in 12 mL glass vials. Samples were poisoned with 20 µL of a saturated $HgCl_2$ solution. Analysis of $\delta^{13}C$-DIC was done one day after a He (helium) headspace of 2.5 mL was created. To convert DIC to CO_2, 100 µL of acid H_3PO_4 (99 %) was added into the vials, followed by an overnight equilibration. Approximately 1 mL of the headspace was then injected into the He flow of the EA-IRMS setup described above. $\delta^{13}C$ values were corrected for isotope fractionation between the dissolved CO_2 in the water and the CO_2 in the created headspace and for the partitioning of CO_2 between the two phases as described in Gillikin and Bouillon (2007).

The DIC concentration was calculated with the Excel Macro CO2SYS (V2.1) created by Lewis et Wallace (1998) in which values of water temperature, TA measurement, and pCO_2 direct measurement are the inputs.

The concentration of Chlorophyll a was determined from the extraction of pigments from filtered lake water. A known volume of water was filtered through pre-combusted (450°C) 47 mm Whatman GF/F filters of 0.7 µm and later stored in a freezer until analysis. High performance liquid chromatography (HPLC) was used to determine pigment concentrations. Pigments were extracted in 10 mL of 90 % HPCL grade acetone. The pigment extract was stored in 2 mL amber vials at -25°C prior to a two sonification steps of 15 minutes separated by an overnight period at 4°C. The gradient elution method described by Wright et al. (1991), combined with a Waters system comprising a photodiode array and fluorescence detectors were used to perform the HPLC analyses. Calibration is based on commercial external standards (DHI Lab Products, Denmark). Typical reproducibility of pigment concentration measurement was better than 7 %. The CHEMTEX software (CSRIO Marine Laboratories) based on input ratio matrices adapted for freshwater phytoplankton is used to process pigment concentration data.

We measured the pelagic primary production (PP) rate in the lake by *in situ* ^{13}C incubations at different light intensities. First, a solution of 500mL of surface water spiked with Na $H^{13}CO_3$ was prepared. A subsample of this solution was transferred and preserved in triplicate 12 mL exetainer vials and immediately poisoned with saturated 20 µL solution of $HgCl_2$ to measure the initial $\delta^{13}C$-DIC value of the spiked water. Eight 50 mL polycarbonate flasks were filled with the spiked solution and were organized into a floating incubator with different filters to provide light shading from 0 to 90 % natural mid-day light energy. An Odyssey photosynthetic irradiance recording system (Photosynthetic active radiance (PAR) logger) was used to monitor the incident light during the entire period of the field campaign. At the end of the incubation, which lasted at least two hours, we added 100 µL of formalin to instantly stop the biological activity. One supplementary bottle was processed in a similar way at the beginning and at the end of the incubation to produce a dark incorporation control. Each water sample was then filtered on a pre-combusted (450°C) 25mm Whatman GF/F filter to collect the particulate fraction. These PP incubations were performed 4 times during the first campaign (April–July 2018), 2 times during the second fieldwork campaign (January 2019–March 2019) and 3 times during the third campaign (August–October 2019). In addition, PP incubations were performed in the reservoirs of Andilanatoby (in the south of the catchment) and Sahamaloto (in the northwest of the catchment) during the first and second campaign (Figure 1). Analyses of $\delta^{13}C$-POC and $\delta^{13}C$-DIC for primary production samples followed the same procedures as described earlier, but given the high ^{13}C-enrichments in the DIC pool, the obtained $\delta^{13}C$ values were not corrected for isotope fractionation between gaseous and dissolved CO_2.

To calculate the specific photosynthetic rate in each individual bottle *i*, P_i (in µg C L^{-1} h^{-1}), we followed Dauchez et al. (1995) based on the initial and final $\delta^{13}C$-POC values and $\delta^{13}C$-DIC of the spiked incubated solution, and assuming that isotopic discrimination is negligible (Legendre and Gosselin, 1997).

For each experiment, the maximum specific photosynthetic rate P_m (in µg C L^{-1} h^{-1}) and the irradiance at the onset of light saturation I_k (µE m^{-2} s^{-1}) were obtained by fitting P_i into the irradiance gradient provided by the incubator

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I_i (µE m^{-2} s^{-1}), using the following Vollenweider's equation, with a=1 and n=1, allowing for photoinhibition (Vollenweider, 1966):

$$P_i = 2P_m\left[\frac{I_i/2I_k}{1+(I_i/2I_k)^2}\right], \quad \text{(Eq.1)}$$

Where P_i is the photosynthetic rate in bottle *i* during the incubation time and I_i is the corresponding mean light during the incubation. Fitting was performed using the Gauss-Newton logarithm for nonlinear least squares regression. Daily depth-integrated primary production (mg C m^{-2} day^{-1}) was calculated according to Kirk (1994) using the following equation:

$$P(z,t) = 2P_m\left[\frac{I(z,t)/2I_k}{1+(I(z,t)/2I_k)^2}\right], \quad \text{(Eq.2)}$$

Where P(z, t) is the photosynthesis at depth z and time t, and I (z, t) is the underwater light determined from Ke and surface irradiance recorded every 5 min and assuming a vertically homogenous Chl-a profile. Assuming that short-term incubation provides an estimate which is close to gross primary production (GPP), we calculated water column daily respiration (R, mg C m^{-2} day^{-1}) as in Reynolds (2006), considering a respiration rate of 0.16 mg C mg Chl-a h^{-1} at 18°C (based on López-Sandoval et al. (2014) a Q_{10} of 2 for adjusting for lake temperature, a constant respiration rate over 24 hours, and the whole lake depth at the study sites).

To measure pCO_2, 60 mL syringes were filled either directly with surface water from the river and lake or from the Niskin bottle. An additional syringe was filled with air. A 30 mL headspace (ambient air) was created, and after 10 minutes of vigorous shaking, the headspace was injected into a LICOR LI-820 infrared gas analyser (Borges et al. 2015). Calibration of the LICOR was performed before and after each sampling campaign with ultrapure N_2 and a standard (Air Liquide Belgium) with a CO_2 mixing ratio of 1019 ppm (Air Liquide Belgium). The precision of pCO_2 measurements was estimated to be ± 5 %.

2.4 Vegetation and marsh sediment sampling

Different species of common marsh plant species were sampled. Vegetation samples were air-dried in the field, then dried in oven at 50°C in the laboratory. A mortar, pestle and nitrogen liquid were used to grind dried vegetation samples into a well homogenised powder.

Sediment cores in Lake Alaotra marsh (Figure 1) were collected with an UWITEC gravity corer adapted for manual coring with 2 m sampling tubes (Ø = 6cm). SC-M1 and SC-M2 were collected in the eastern part of the marshes which are permanently waterlogged, while core SC-M3 was collected further south within the marshes at a location which is not waterlogged throughout the year (Figure 1). All cores were sliced at a resolution of 1 cm. Samples were stored in a portable freezer at -18°C for preservation. Afterwards, sediment core samples were freeze-dried and homogenised in order to take subsamples for laboratory analysis.

Subsamples were weighed into Ag cups to determine OC content, total nitrogen content, and $\delta^{13}C$ and $\delta^{15}N$ of organic matter. All subsamples (except for vegetation) were acidified with 40 µL HCl (10 %) to eliminate all inorganic C. OC content, total nitrogen content and $\delta^{13}C$ of OC were measured as described above for POC, PN and $\delta^{13}C$-POC.

3 Results

The discharge of inflowing rivers and canals (inflowing water) respond strongly to the seasonality in precipitation in the catchment, thus water levels were high mainly during the rainy season and low (up to dry conditions) during

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the dry season (Figure 3). Water levels of the Maningory (lake outlet) also varied seasonally (Figure 3) but with a much smoother cycle, being lowest in December and highest in May of the year of sampling.

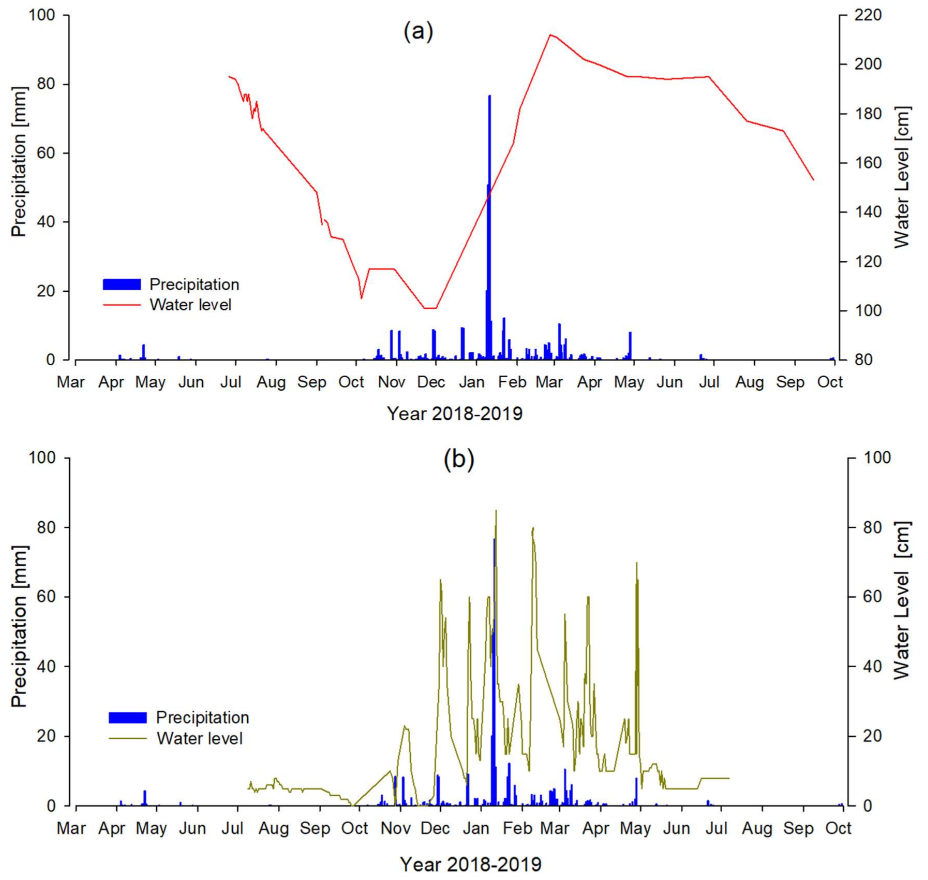

Figure 3: Variation of water levels (full line, right Y-axis; our data) of the Maningory (top panel) and the Ranofotsy (lower panel), plotted along with the amount of daily precipitation (bars, left Y-axis) in the region during sampling period. Precipitation data were obtained from meteoblue (www.meteoblue.com).

The saturation level of dissolved oxygen (expressed in %) in inflowing water showed a higher value during the dry season (87.3 ± 18.2%) compared to the rainy season (77.0 ± 14.5%). No seasonal variation was observed for the saturation of dissolved oxygen in lacustrine water, and the values ranged between 58.4 and 104.5% with an average value of 83.4%. The saturation of dissolved oxygen in the outlet waters was higher during the dry season, with an average value of 71.2 ± 29.3% compared to the value during the rainy season (47.1 ± 28.5%). The saturation levels of dissolved oxygen inflowing and lacustrine water were higher compared to the saturation level of outflowing water.

Inflowing water showed pH values of 7.2 ± 0.5, increasing slightly in lake Alaotra (7.4 ± 0.6), but lower values were found in the Maningory (outlet; 6.9 ± 0.6). The DIC concentrations for inflowing water varied between 213 and 2149 µmol L^{-1}, with an average value of 690 ± 158 µmol L^{-1}, and no significant seasonal variation was observed. The trends in DIC concentrations of lacustrine water showed a seasonal variation with a higher value

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during the rainy season (812 ± 106 µmol L^{-1}) compared to the dry season (608 ± 134 µmol L^{-1}). For the water in the lake outlet, the DIC concentration values ranged between 485 and 931 µmol L^{-1}, with an average of 768 µmol L^{-1}, and no seasonal variation was observed. There was a significant difference between the DIC concentrations of the inflowing and outlet waters. The DIC concentration at the outlet showed a higher value.

The pCO_2 values were higher in the lake outflow (median 5896 ppm, interquartile range (IQR): 4311-11386 ppm) than in the inflowing rivers and canals (median 2491 ppm, IQR: 1735 - 4278 ppm). The lowest pCO_2 values were observed in the lake (median 1627 ppm, IQR 769-2527 ppm) (Figure 4). Dissolved CH_4 concentrations were greater in the inflowing rivers and canals (median 558 nmol. L^{-1}, IQR: 139-1272 nmol. L^{-1}) than in the lake outflow (median 261 ppm, IQR: 13-1139 nmol. L^{-1}). The lowest value of dissolved CH_4 were found in the lake (median 30 ppm, IQR:18-50 ppm). pCO_2 and CH_4 were correlated across the whole datasets (Figure 5). pCO_2 and dissolved CH_4 concentrations increased during the rainy season as shown in Figure 6.

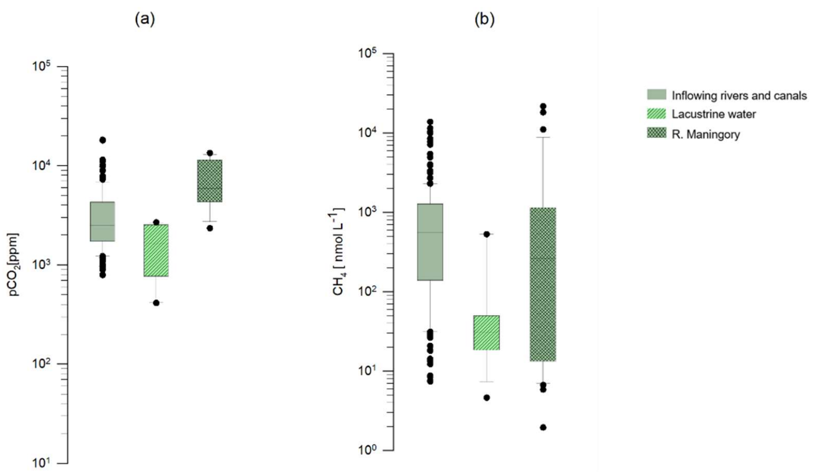

Figure 4: Boxplot of partial pressure of CO_2 (pCO_2) (a) and dissolved CH_4 concentration (b) of inflowing rivers and canals, Lake Alaotra, and the Maningory River (lake outflow).

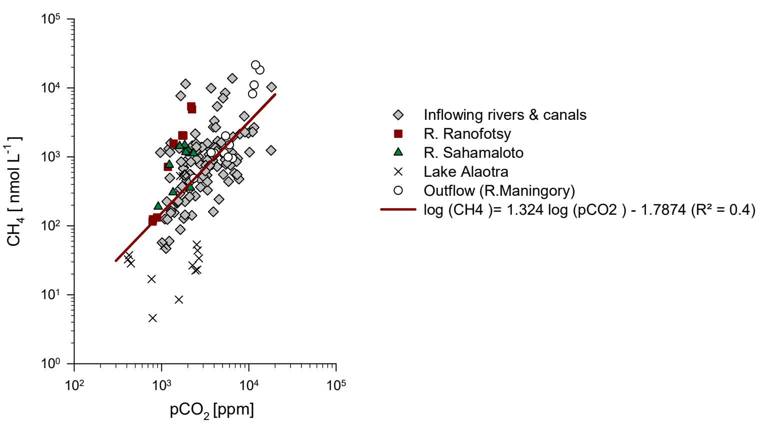

Figure 5: Relation of CH_4 versus pCO_2 of water samples. Continuous red line represents the regression line of CH_4 versus pCO_2 in log-log scale.

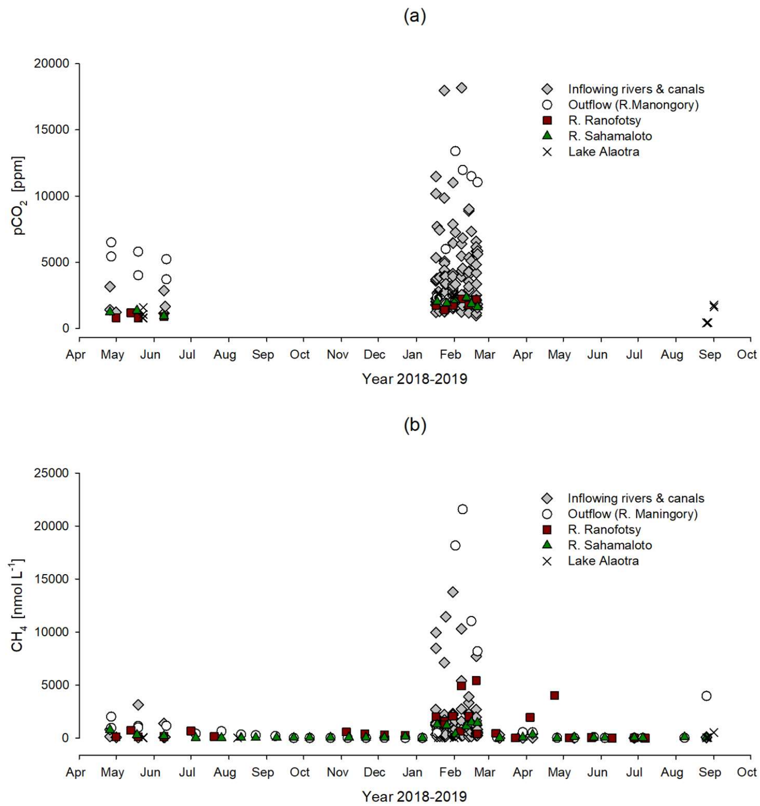

Figure 6: Seasonal variation of (a) pCO_2 (expressed in ppm) and (b) CH_4 (expressed in nmol L^{-1}) water from inflowing rivers, canals and lake, lake outflow (Maningory) in the Alaotra Lake system (Madagascar) between May 2018 and September 2019.

TSM concentrations of the inflowing water ranged between 3.7 and 215 mg L^{-1} during the dry season and between 3.7 and 1392.5 mg L^{-1} during the rainy season (Table 1), reaching maximum values during the middle of the rainy season (January and February). Within Lake Alaotra, TSM varied between 5.8 and 46.7 mg L^{-1} during the dry season and between 8.5 and 39.3 mg L^{-1} during the rainy season. At the outlet (Maningory), TSM ranged between 11 and 60 mg L^{-1} and between 5.8 and 115.2 mg L^{-1} during the dry and rainy seasons, respectively. The highest TSM in the Maningory were reached at the start of the rainy season when the water levels were the lowest. POC concentrations of inflowing water varied between 0.3 to 2.4 mg C L^{-1} and between 0.5 to 7.5 mg C L^{-1} during the dry season and rainy seasons, respectively, reaching maximal values in the middle of the rainy season (Figure 7a). POC concentrations in lake Alaotra ranged between 1.4 and 6.5 mg L^{-1}, with an average value of 3.0 ± 1.7 mg L^{-1}, and increased further at the Maningory outlet (1.2 to 10 mg L^{-1}) with an average value of 4.2 ± 2.4 mg L^{-1}. The contribution of POC to the TSM loads of inflowing water (%POC) was on average 8.3 ± 8.8 % and ranged between 0.1 and 34.8 % during the dry season. During the rainy season, %POC varied between 0.4 to 26.5 % with an average of 2.4 ± 4.0 %. The contribution of POC to the TSM was much higher within lake Alaotra, ranging between 12.0 and 28.9 % with no clear seasonal variation (20.8 ± 6.4 % and 21.4 ± 6.9 % during the dry and rainy season, respectively). In the lake outlet, %POC varied in a narrow range and was significantly higher compared

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to that of rivers: on average 14.4 ± 8.5 % and 10.7 ± 7.2 % during the dry and rainy seasons, respectively. $\delta^{13}C$-POC of inflowing waters ranged between -28.3 and -19.0 ‰ (Figure 8) with an average of -24.6 ± 1.4 ‰. The average $\delta^{13}C$-POC value of lacustrine water during the rainy season (-24.3 ± 1.9 ‰) was slightly higher than that during the dry season (-25.6 ± 1.3 ‰), whereas no seasonality was evident in Lake Alaotra (-26.5 ± 2.1 ‰). $\delta^{13}C$-POC at the outlet varied between -28.3 and -21.9 ‰ with an average of -25.3 ± 1.4 ‰. The suspended organic matter pool of inflowing waters was characterized by an average POC/PN of 10.3 ± 2.6 while the POC/PN ratio of the outlet averaged 9.5 and varied between 6 and 12.2. The POC/PN ratio of lacustrine water ranged from 8.3 to 11.3. DOC concentrations of the inflowing waters ranged between 1.0 and 8.1 mg C L^{-1} (Figure 7b, Figure 8) with an average value of 2.6 ± 1.1 mg C L^{-1}. DOC concentrations of the two monitored rivers (Ranofotsy and Sahamaloto) ranged between 1.0 and 5.3 mg C L^{-1}, and no significant seasonal variation was observed (Figure 7). DOC concentrations of lacustrine water varied between 7.5 and 18.6 mg L^{-1} where the maximum DOC concentrations were obtained during the rainy season (Figure 7b). The DOC concentration of the Maningory river varied between 7.6 and 13.7 mg L^{-1} with an average of 9.5 ± 1.4 mg L^{-1}. The $\delta^{13}C$-DOC of inflowing water (river and canals) values ranged between -30.9 and -15.2 ‰ with an average value of -23.0 ± 2.1 ‰. The $\delta^{13}C$-DOC of lacustrine water ranged between -24.0 and -20.3 ‰ with an average value of -22.2 ± 1.1 ‰. The $\delta^{13}C$-DOC at the outlet varies between -23.6 and -19.4 ‰ with an average value of -21.4 ± 0.1 ‰ (Figure 7 and Figure 8).

Table 1: TSM and %POC (minimum, maximum and mean values) of samples from inflowing water, Lake Alaotra, and for the Maningory (lake outlet) during rainy and dry season.

	Season	Group	Min	Max	Mean ± std dev (n)
TSM	Dry	inflowing water	3.7	215.8	44.0 ± 52.2 (n=42)
		Lake waters	5.8	46.7	18.8 ± 15.0 (n=10)
		River Maningory	11.0	60.0	31.7 ± 16.5 (n=20)
	Rainy	inflowing water	3.7	1392.5	131.9 ± 224.2 (n=74)
		Lake waters	8.5	39.3	16.6 ± 11.8 (n=6)
		River Maningory	5.8	115.2	47.5 ± 37.9 (n=18)
%POC	Dry	inflowing water	0.1	34.8	8.3 ± 8.8 (n=40)
		Lake waters	12.0	28.8	20.8 ± 6.4 (n=8)
		River Maningory	0.0	36.2	14.4 ± 8.5 (n=19)
	Rainy	inflowing water	0.4	26.8	3.5 ± 4.0 (n=69)
		Lake waters	10.1	28.9	21.4 ± 6.9 (n=6)
		River Maningory	2.9	31.3	10.7 ± 7.2 (n=17)

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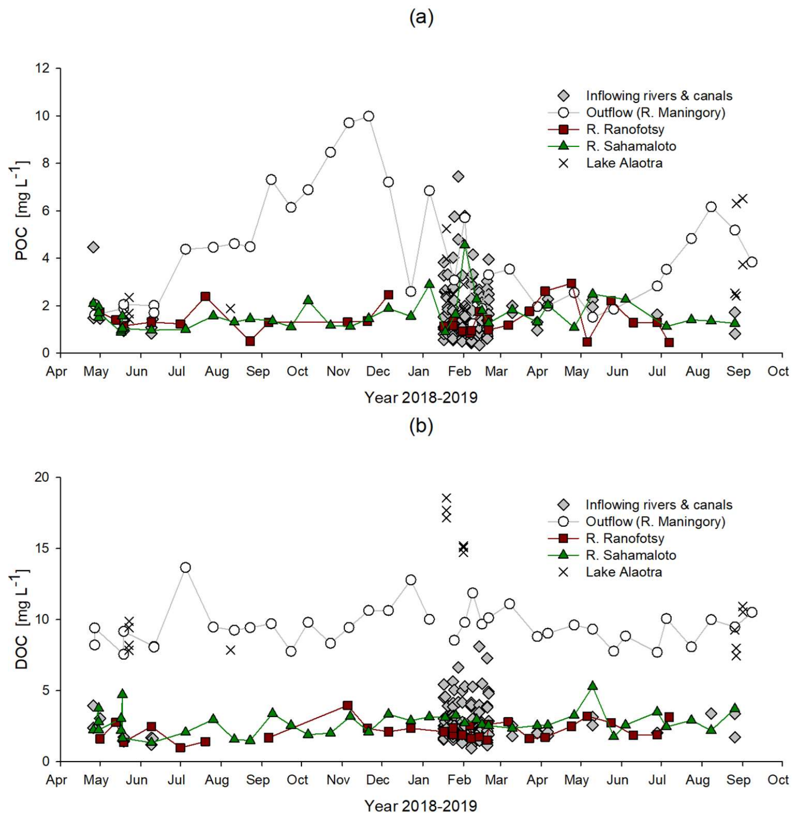

Figure 7: Seasonal variation of (a) particulate organic carbon (POC) and (b) dissolved organic carbon (DOC) concentrations (expressed in mg C L^{-1}) of water from inflowing rivers, canals and lake, lake outflow (Maningory) in the Alaotra Lake system (Madagascar) between May 2018 and September 2019.

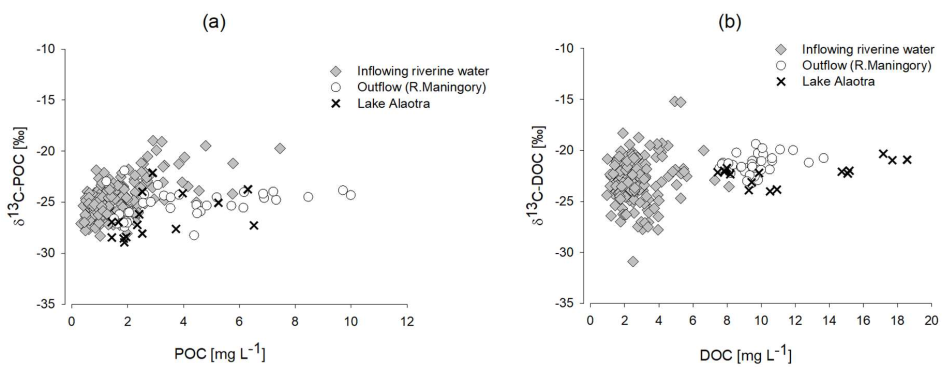

Figure 8: Stable isotope composition versus concentrations for (a) particulate organic carbon POC and (b) dissolved organic carbon DOC for inflowing water, Lake Alaotra, and the lake outflow (Maningory).

Mean Chl-a concentration of the lake range between 8.0 and 10.0 µg L^{-1} (Table 2) and the mean daily net primary production (NPP) was estimated at 538.3 mg C m^{-2} day^{-1} (range, 144.5 and 1250 mg C m^{-2} day^{-1}). For TSM, POC,

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δ^{13}C-POC, DOC, δ^{13}C-DOC and POC/PN values, paired t-tests did not reveal any significant differences between Lake Alaotra and the lake outflow (Maningory).

Table 2: Chlorophyll a (Chl-a), POC, and POC/Chl-a ratios of lacustrine water (Lake Alaotra).

Date	Chl-a (µg L^{-1})	POC (mg L^{-1})	POC/Chl-a (mg:mg)
May 2018	8.5	1.7	196
May 2018	10.0	1.4	143
January 2019	9.3	5.2	564
January 2019	8.0	4.0	498

The OC content of sediment core SC-M1 and SC-M2 ranged from 10.5 to 37.0 %, with an average of 21.3 ± 7.1 % (Figure 9 a), with a higher OC content at the surface 29.9 ± 4.0 % in the upper 10 cm). The OC content of SC-M3 (Figure 9 a) showed intermediate values in the upper 70 cm (OC: 5.7-17 %, average 10.0 ± 2.9), decreasing with depth. Below 70 cm, the OC content increased again to values between 17.9 and 58.8 % (average 45.2 ± 8.4 %). δ^{13}C-OC values of both cores varied widely between -22.4 and -17.0 ‰. For SC-M1 and SC-M2, OC was more depleted in ^{13}C with δ^{13}C-OC values of -20 ±1.1 ‰ at the surface and -19.2 ‰ at 40cm depth (Figure 9 b). δ^{13}C-OC values of the sediment core SC-M3 were higher in the upper 70 cm (average of -18.7 ± 0.9 ‰) compared to deeper sections (-17.4 ± 1.5 ‰). The OC/TN ratio for SC-M1 and SC-M2 varied between 13.4 and 21.6 with an average of 16.9 ± 1.7 (Figure 9 c), while the OC/TN ratios of SC-M3 varied between 14.0 and 20.9 over the upper 80 cm, and then increased with depth.

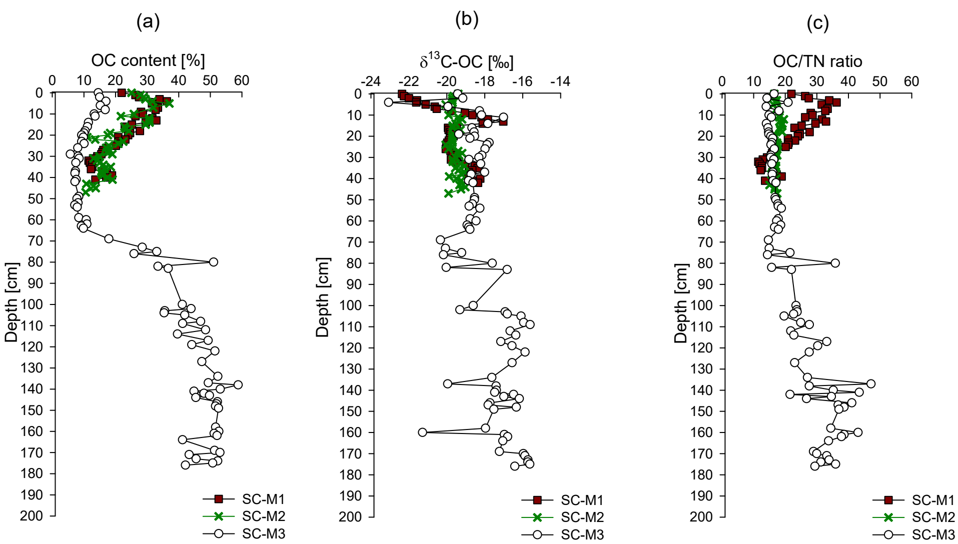

Figure 9: Variation of OC content (a), δ^{13}C-OC (b), OC/TN (c) ratio with depth of marsh sediment cores from Lake Alaotra (SC-M1, SC-M2 and SC-M3).

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The C content of marsh vegetation varied in a narrow range, with an average of 40.9 ± 2.8 %. *Cyperus madagascariensis,* which covers more than 50 % of the marsh area (Lammers et al., 2015), showed a clear C4 signature (δ^{13}C: -13.2 to -12.4 ‰; Table 3). In contrast, *Argyreia vahibora,* which covers ~30 % of the marsh area, had δ^{13}C values consistent with its C3 metabolism (-29.4 to -29.0 ‰), other marsh plant species showed δ^{13}C values ranging between -29.5 and -24.1 ‰.

Table 3: δ^{13}C values of marsh vegetation (leaves) found in Lake Alaotra sampled on February 2019 (rainy season)

Scientific Name	$\delta^{13}C$
Cyperus madagsacariensis	-13.2 to -12.4
Cyclosorus gongylodes	-29.5
Argyreia bahibora	-29.4 to -29.0
Polygnum glabrum	-29.5
Nymphaea sp.	-24.1

4 Discussion

4.1 Sources of POC in the Lake Alaotra system

TSM concentrations of the inflowing water varied widely with season, with higher values during the rainy season (average 131 ± 262 mg L^{-1}) than during the dry season (61 ± 39 mg L^{-1}). Sediment loads of inflowing water are within the range of TSM concentrations reported for streams and rivers of the Betsiboka basin (a basin which drains much from the grassland-dominated central highlands of Madagascar;) Marwick et al., 2014), but higher than values reported from Rianala basin which drains part of the eastern slopes of Madagascar and is vegetated by low/mid-latitude humid evergreen forest (Marwick et al., 2014). There was a significant difference between TSM concentrations of inflowing water (104 ± 186 mg L^{-1}) and lacustrine water (18 ± 13 mg L^{-1}, Figure 10a), indicating that sedimentation must have occurred between the upstream area and the lake. The natural pathways through which OC enters the river are either via lateral transport from terrestrial soils (and direct litter inputs to a lesser extent) as particulate and dissolved OC (Raymond and Bauer, 2001), and from autochthonous production (Raymond and Bauer, 2001). Tropical rivers are additionally influenced by lateral inputs from floodplains (wetlands) that transfer substantial amounts of DOC (McClain et al., 1997). The contribution of the latter source of OC is lower relative to the OC from other sources from the landscape in rivers with a high turbidity (Marwick et al., 2014). In contrast to TSM, POC concentrations were higher in Lake Alaotra and its outflow compared to inflowing waters (Figure 8, Figure 10b). In the latter, POC concentrations were not strongly dependent on river discharge, while POC concentrations in the lake outflow increased steadily throughout the dry season – consistent with local inputs rather than with a link to POC derived from the catchment (Figure 7a; see discussion further below). δ^{13}C-POC values measured in inflowing waters (-24.6 ± 1.8 ‰) are largely consistent with δ^{13}C values measured in subsoils within our study area catchment (Razanamahandry et al., 2022), although the relative contribution of POC to TSM (%POC) was on average higher than in soil profiles which suggests that either direct vegetation inputs or more OC-rich soils closer to the stream network may contribute substantially (e.g. see Marwick et al. 2014 regarding the disproportional contribution of riparian zones). Along the aquatic continuum,

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%POC values increased further in the lake and its outflow (P-value for lake vs inflowing water and for outflow vs inflowing water: < 0.001) (Figure 6, Figure 7).

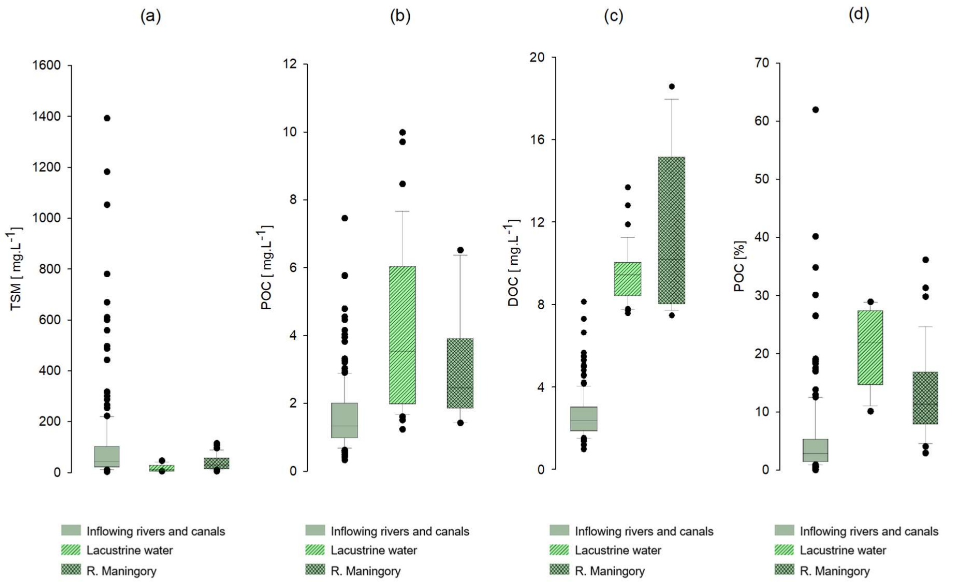

Figure 10: Boxplots of (a) TSM concentrations, (b) particulate organic carbon (POC) concentrations, (c) dissolved organic carbon (DOC) concentrations, and (d) the relative contribution of POC to the TSM pool of inflowing rivers and canals, lacustrine water and the outflowing River Maningory.

In addition to POC transported by the inflowing waters (i.e., from the upper catchment), there are two additional potential sources of POC to consider for Lake Alaotra and its outflow: POC formed along the river's path via wetlands (peat in marshes and aquatic plants) and *in situ* phytoplankton production within the lake. These new inputs of POC could be more important than riverine (terrestrial) inputs, due to the high productivity of the marshes and phytoplankton production. The fact that we observed higher POC concentrations as well as higher %POC in the surface water compared to inflowing water indeed suggests that POC of the lake is to a large extent not derived from the river inputs, but must be linked to other sources such as phytoplankton biomass and/or marsh vegetation. Using the current distribution of different vegetation species in the marshes (Table 3), the expected $\delta^{13}C$ value of the mixture of different vegetation species based on their approximate relative abundance (Lammers et al., 2017) would be in the -21 to -18‰ range (~50% of -12.3 ‰, ~30% of -29.2 ‰ and ~20 % of ~-29.5 to -24.1 ‰). This value corresponds closely to $\delta^{13}C$-OC of the peat cores (-18.8 ± 1.4 ‰) and lake sediment cores (-18.5 ± 1.77 ‰, data not shown here), but is distinct from the $\delta^{13}C$ values of POC in the lake (-26.5 ± 2.1 ‰) and lake outlet (-25.3 ± 1.4 ‰). This suggests that POC in the lake must be largely derived from other sources rather than from the remobilisation of OC from the marsh. The mean daily primary production rates we measured (0.5 ± 0.3 g C m^{-2} day^{-1}) were moderate compared to e.g. lakes in East Africa (Morana et al., 2022), and similar to e.g. those measured in the oligotrophic lake Kivu (0.6 g C m^{-2} day^{-1}; Darchambeau et al., 2014). The steady increase in POC concentrations during the dry season (Figure 7a) would be consistent with the development of phytoplankton biomass during a period when the lake water residence time increases. A widely used proxy for phytoplankton biomass is the chlorophyll a (Chl-a) concentration, and POC/Chl-a ratios (µg L^{-1}/ µg L^{-1}) in the water column can be used to evaluate the contribution of various sources of organic matter to POC in the lacustrine

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water (Cifuentes et al., 1988). Indeed, a high POC/Chl-a ratios suggests that organic matter is primarily derived from terrestrial sources, while a low ratio implies that POC is derived from *in situ* phytoplankton production. Phytoplankton biomass has POC/Chl-a ratios between 40 and 200 whereas terrestrial organic matter POC/Chl-a ratios are typically higher than 500 (Gawade et al., 2018). The POC/Chl-a ratios of lacustrine water in our study ranged between 143 and 564 (µg L^{-1}/ µg L^{-1}) with an average value of 350±183.1 (mg:mg). These values were relatively low and indicate that phytoplankton biomass represents an important fraction of the lake suspended POC. Moreover, the suspended organic matter of Lake Alaotra had POC/PN ratios close to those expected for phytoplankton (algae), between 7 and 9. The $\delta^{13}C$ of phytoplankton ($\delta^{13}C$-Phyto) can be estimated from ^{13}C-DIC by assuming a fractionation factor (~20 ‰) during C fixation by phytoplankton (Peterson and Fry, 1987). The $\delta^{13}C$-DIC values of lacustrine water ranged between -9 and -4 ‰ (Figure 11a) and therefore the $\delta^{13}C$-Phyto can be estimated between -29 and -24 ‰, which corresponds well with the measured $\delta^{13}C$ values of suspended POC ($\delta^{13}C$-POC) ranging between -29 and -22 ‰ (Figure 11b). Thus, different lines of evidence indicate that the suspended POC in the lake is to an important extent derived from phytoplankton biomass. No significant difference was observed between values of lacustrine water and outflow river during the rainy and dry seasons for TSM, POC concentration, $\delta^{13}C$-POC, and POC/PN values. Therefore, rather than exporting POC derived from soil erosion in the catchment, the Maningory river POC flux at the lake outlet appears to an important extent comprised of within-lake phytoplankton production.

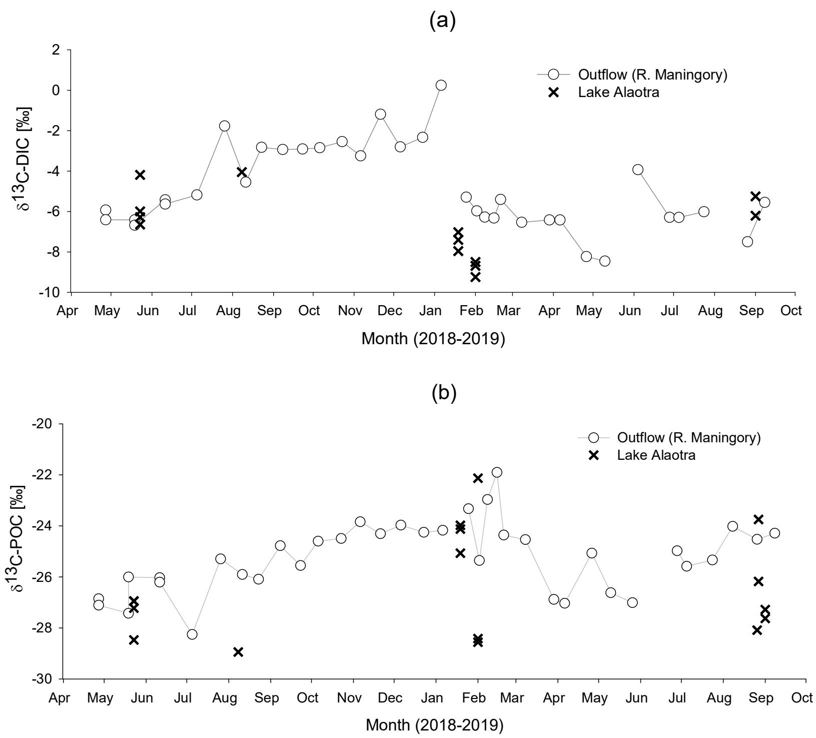

Figure 11: (a) Seasonal variation of $\delta^{13}C$-DIC and (b) $\delta^{13}C$-POC of the Maningory River (lake outflow) and lacustrine water.

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4.2 Sources of DOC in the Lake Alaotra system

Lake Alaotra and its outflow were found to show consistently higher DOC concentrations than the inflowing water (Figure 10). Thus, analogous to the discussion on POC, we examine which possible sources are most likely to supply these new DOC inputs along the aquatic continuum. DOC concentrations of the inflowing water were relatively low (2.6 ± 1.1 mg C L^{-1}) and show $\delta^{13}C$ representing a mixture of C3-C4 vegetation (-23.0 ± 2.1 ‰) (Figure 8). These value are similar to those found in Marwick et al. (2014) in the Betsiboka river (central/western Madagascar) (bulk DOC concentration ranges from 0.4 to 2.9 mg C L^{-1} and $\delta^{13}C$-DOC varied between -29.5 and -15.4 ‰). In contrast, DOC in the Rianila basin (eastern Madagascar, largely covered by evergreen forest) was more depleted in ^{13}C ($\delta^{13}C$ values of -27 ± 1.2 ‰) but had a similar DOC concentration range (2.6 ± 1.4 mg C L^{-1}; Marwick et al., 2014).

Possible sources for the net inputs of DOC include the production of DOC by phytoplankton, or DOC derived from wetland vegetation. DOC production from phytoplankton has been shown to be mineralised quickly in the water column and therefore does not appear to accumulate in the water column (Morana et al., 2014). Moreover, $\delta^{13}C$-DOC values within the lake and its outflow (-22.2 ± 1.0 ‰ and -21.4 ± 0.9 ‰, respectively) were relatively well constrained and fall outside the range expected for phytoplankton production (see section on $\delta^{13}C$-POC). Thus, it appears that the main sources of lake DOC and POC are strongly uncoupled (Figure 12). The net DOC inputs to the lake are then likely the result of marshland vegetation inputs, which have been shown to be potentially important sources of DOC to open water ecosystems (Lauster et al., 2006). Indeed, the $\delta^{13}C$-DOC values were close to $\delta^{13}C$-OC values in our marsh sediment core profiles (-24 to -18‰; Figure 12:), and to the values observed in marsh vegetation, taking into account their relative abundance (see above). Thus, different lines of evidence point towards marshland vegetation as the main source of the higher DOC concentrations in lake Alaotra and its outflow. While $\delta^{13}C$-DOC values in the lake and its outflow were relatively constant throughout the year, DOC concentrations in lake waters were higher during the rainy season, when a higher flux of DOC from the OC-rich marshes can be anticipated.

DOC concentrations in lake Alaotra are relatively high compared to DOC concentrations measured in a range of East African lakes such as Lake Kivu, Edward and Albert (1.5–5 mg C L^{-1}, Morana et al., 2014, 2015) and in Lake Victoria (1.2–3.6 mg C L^{-1}, Deirmendjian et al., 2020). This difference could be explained by the fact that Lake Alaotra is a shallow system with a high relative area of surrounding wetland vegetation. A similar pattern has been observed in Lake George, Uganda (Morana et al., 2022) which is also a very shallow lake fringed by extensive *Papyrus* wetlands. Despite the high phytoplankton productivity in L. George, its surface waters showed DOC values of 10–20 mg C L^{-1}, much higher than in rivers draining into the lake from savannah and rainforest (2 to 3 mg C L^{-1}). Similarly to what we observed in Lake Alaotra, $\delta^{13}C$ data on DOC and POC pools in Lake George show a strong decoupling of DOC sources (derived by surrounding wetland vegetation) and POC sources (dominated by aquatic primary production). The potential importance of wetlands as a source of DOC in tropical lakes was also demonstrated for two shallow lakes in the Congo Basin, Lake Tumba (average depth 3-5 m) and Lake Mai-Ndombe (average depth of 5 m, Borges et al. 2022). Wetlands (flooded forests) surround both of these lakes, and leading to substantial DOC concentrations in both Lake Tumba (14.7 mg L^{-1}) and Lake Mai-Ndombe (35.2 mg L^{-1}).

The strong imprint of the surrounding wetlands on DOC inputs to Lake Aloatra is not mirrored in CO_2 and CH_4 concentrations, which do not show a marked increase between inflowing rivers and the lake proper (Figure 4, 6).

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Here, outgassing (and/or oxidation in the case of CH_4) could explain the absence of a clear wetland imprint on lake waters, yet some of the seasonality in CO_2 and CH_4 variations. in particular in the inflowing and outflowing rivers also point towards a strong hydrological control. Indeed, the correlation between pCO_2 and dissolved CH_4 concentrations (Figure 5) suggests that the same processes or environmental conditions drive the pCO_2 and CH_4 variations. A strong increase of pCO_2 and CH_4 was observed during the rainy season in February (Figure 5) when both precipitation, water levels (Figure 6) and freshwater discharge (Figure 2) increased – thus coinciding with an expected increased connectivity between wetlands and rivers (Teodoru et al., 2015).

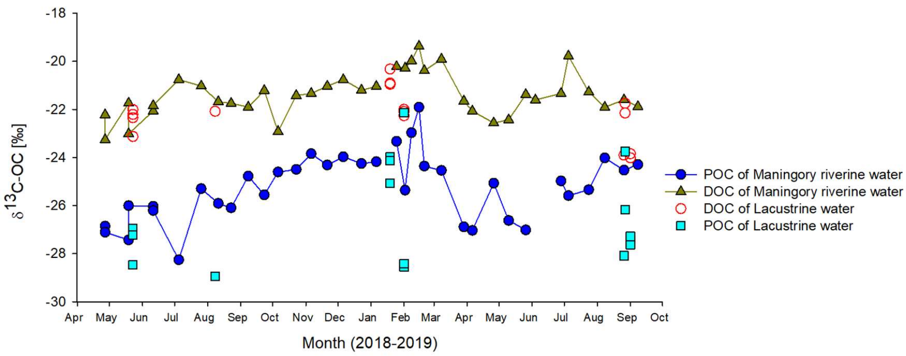

Figure 12: Seasonal variation of δ^{13}C-POC and δ^{13}C-DOC in Lake Alaotra and in the Maningory River (lake outflow).

5 Conclusions

We present a comparative dataset of physico-chemical and biogeochemical proxies measured in inflowing water, lacustrine water, and the outflow of Lake Alaotra, focussing on tracing the main sources of C along the aquatic continuum and how the lake and surrounding wetlands affect dissolved and particulate OC pools. Our data show that the suspended sediment load derived from the upstream catchment is largely lost before it enters Lake Alaotra, and that the concentrations of DOC and POC in the lake and its outlet were much higher than in the inflowing waters. POC/Chl-a ratios of lacustrine water were low, and the POC/PN ratios and δ^{13}C-POC values of the lacustrine suspended organic matter were consistent with a strong contribution by phytoplankton production. In contrast, δ^{13}C-DOC values within the lake and outflow were consistently higher than δ^{13}C-POC, and the surrounding marshes appeared to be the primary source of the lacustrine DOC inputs. This study indicated that Lake Alaotra is highly dynamic in terms of organic C, and acts as an active hotspot (sensu McClain et al. 2003) in terms of modifying C fluxes and sources along the aquatic flowpath. *In situ* production and marshes are the primary sources of organic carbon in the lacustrine water column. The findings of this study are crucial for interpreting lake sediment archives and for tracing sediment mobilization from the eroded landscape in the Lake Alaotra Region.

6 Data availability

The full dataset generated in this study can be found as an electronic supplement. This supplement includes a number of ancillary measurements on proxies that are not discussed in this paper (stable hydrogen and oxygen isotope data of surface water samples and major element concentrations), but which we have kept in the database

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so that potential users of our data have access to these additional parameters. The methodology for these measurements is briefly described in the Supplementary information.

7 Authors contributions

G.G and S.B. designed the study project with contributions of L.B and V.F.R. TaR. and ToR. co-supervised the project and fieldwork in Madagascar. L.B. and V.F.R. planned fieldwork and collected samples. V.F.R. conducted the main sample analyses and led the manuscript writing with S.B. C.M and A.V.B. provided input to sample collection and analyses. All authors contributed to data interpretation and manuscript revisions.

8 Competing interests

S.B. is co-editor-in-chief of Biogeosciences.

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