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

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Abstract

Our understanding of the role of tropical lakes in regional carbon budgets remains hampered by a lack of data covering the vast diversity of lake types and settings. Here, we provide a first comprehensive survey of the carbon (C) biogeochemistry of the Lake Alaotra system, ~~The catchment of Lake Alaotra,~~ a large shallow lake (surface is 200 km^2, maximum depth 2 m) surrounded by an extensive floodplain and ricefields located in the ~~Malagasy~~ highlands of Madagascar. The current landscape in the ~~, is a~~ region ~~where the~~ is grassland ~~grassland~~-dominated ~~landscape and is~~ dotted by major gullies called "lavaka", which ~~has~~ have historically been claimed to lead to high erosion rates, and would thus also mobilize large amounts of soil C. ~~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 (Chl-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 dissolved organic carbon (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 indicated that marsh vegetation was the main source of net DOC inputs, while phytoplankton ~~likely~~ contributed substantially to POC in the lacustrine waters, at least during some of the sampling period. ~~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.~~ Indeed, ~~L~~lake suspended matter has relatively low POC/Chl-a ratios (143–564, particularly

40 during the May sampling period), high %POC (10 to 29 %), and δ^{13}C values ~~around~~ (-26.5 ± 2.1 ‰) distinct from
41 those in marsh-derived organic matter~~20 ‰ lower than the dissolved inorganic C (DIC) pool (-26.5 ± 2.1 ‰ versus~~
42 ~~-6.7 ± 1.6 ‰)~~. Despite the evidence for ~~importance of~~ phytoplankton production as a contributor to the lake POC
43 pool, the lake acted as a net source of CO_2 to the atmosphere, likely due to the high C inputs from the surrounding
44 marshes, and sediment respiration considering the shallow water depth. Nevertheless, the pCO_2 levels in the
45 surface waters of the lake were lower than those in the inflowing and outflowing rivers. This reduction is likely
46 due to the combined effects of phytoplankton production, which assimilates CO_2 during photosynthesis, and
47 degassing processes. When CO_2-supersaturated riverine water enters the open lake, increased turbulence caused
48 by wind fetch enhances gas exchange with the atmosphere, allowing CO_2 to escape more readily from the water
49 column.~~Nevertheless, the pCO_2 in the surface waters of the lake was lower than in the inflowing and outflowing~~
50 ~~rivers, possibly reflecting the impact of phytoplankton production (CO_2 assimilation), although also reflecting~~
51 ~~degassing to the atmosphere.~~ The biogeochemical functioning of Lake Alaotra differs substantially from the large
52 and deeper East African (sub)tropical lakes and was more similar to lakes surrounded by flooded forest in the
53 Congo River basin, likely due to a combination of its large surface area and shallow water depth, and the large
54 extent of surrounding wetlands and floodplains. It acts as an abrupt element in the land-ocean ~~gradient~~ continuum
55 of the catchment, whereby the biogeochemical characteristics of the Maningory River (i.e., the lake outflow) are
56 strongly determined by processes taking place in Lake Alaotra and its wetlands, rather than being reflective of
57 characteristics and processes higher up in the catchment.

1 Introduction

Datasets on the biogeochemistry and C cycling along terrestrial-aquatic ~~gradients~~ continuum 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. This indicates that much of the carbon fixed through phytoplankton production is rapidly recycled within the lake system, through processes such as microbial respiration, grazing, and remineralization, rather than being buried in sediments or emitted as CO_2 to the atmosphere. This finding challenges the traditional view of lakes as net heterotrophic systems (Del Giorgio et al., 1993; Duarte and Prairie, 2005; Aufdenkampe et al., 2011). ~~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. Global data syntheses often show the African continent to be a particular blind spot in terms of data availability (e.g. Toming et al. 2020 for lake dissolved organic carbon, Johnson et al. 2022 for lake methane fluxes), and studies from Madagascar's inland waters are very scarce (Ralison et al., 2008; Marwick et al., 2014). ~~, particularly in Madagascar (Ralison et al., 2008; Marwick et al., 2014).~~ Madagascar's lakes, are unique as they lie within a region that combines tropical, subtropical, and anthropogenically influenced landscapes. These ecosystems are highly sensitive to environmental changes, such as deforestation, agricultural expansion, and climate variability, which affect carbon cycling processes and sediment fluxes. Understanding OC dynamics in Madagascar's lakes provides critical insights into carbon processing in subtropical regions with similar environmental pressures. This lack of data and uncertainty,

98 especially in underrepresented regions like Madagascar, requires the collection of additional datasets over
99 adequate spatial and temporal scales to refine global models of carbon cycling and better predict responses to
100 anthropogenic and climatic changes.
101 While the amount of data on the origin of DOC and POC, and on transport fluxes in tropical rivers has grown
102 steadily, much less is known about the biogeochemical cycling and OC source contributions in tropical lakes in
103 Madagascar (Ralison et al., 2008; Marwick et al., 2014).
104 This lack of data and uncertainty at the global scale requires the collection of additional datasets over adequate
105 spatial and temporal scales.
106 Lake Alaotra is the largest freshwater system in Madagascar and is recognized as a hotspot of biodiversity. It is
107 surrounded by marshes that provide the only remaining habitat of an endangered lemur species (*Hapalemur*
108 *alaotrensis*), as well as by extensive floodplains that represent the most important rice-producing region of
109 Madagascar (Lammers et al., 2015). Because of these high ecological, economical and scientific values, the lake
110 Alaotra wetland is recognized as a Ramsar site. The wetland marshes of lake Alaotra occupy a surface area (~230
111 km^2) (Mietton et al., 2018) larger than the lake itself (currently ~200 km^2 of open water, Bakoariniaina et al.,
112 2006; Ranarijaona, 2009), and are mainly located in the south-western part of the lake. Water and sediment
113 transported through the rivers pass via floodplains and marshes before entering the lake. The characteristic hills
114 in the Lake Alaotra watershed are currently dominated by grasslands but were likely to have been forested or
115 characterised by wooded savannah vegetation up to ~2000 years ago (Broothaerts et al., 2022; Razanamahandry
116 et al, 2022). A particular erosional feature called 'Lavaka' dots these landscapes - gullies which can reach very
117 large dimensions (Brosens et al., 2022; Cox et al., 2010, 2023). Lavaka mainly occur in the central highlands of
118 Madagascar, and their density is particularly high in the region of Lake Alaotra (Cox et al., 2010). Studies of ^{10}Be
119 in river sediments in central Madagascar indicated that sediments in the river are mainly lavaka-derived rather
120 than colluvial sediments (Cox et al., 2009). In addition, since Lake Alaotra is located in one of the most important
121 agricultural regions of Madagascar, it has been heavily impacted by human activities. The wetlands surrounding
122 the lake have undergone significant alterations, primarily due to their conversion into rice paddies to support local
123 agriculture. This process involves draining natural wetlands, altering their hydrology, and replacing native
124 vegetation with cultivated rice crops. These changes have profoundly impacted the wetlands' ecological balance,
125 biodiversity, and natural functions (such as water filtration, flood control, and providing critical habitats for
126 biodiversity) (Lammers et al., 2015). This transformation has been accompanied by extensive deforestation along
127 the hillslopes, which has increased sediment runoff into the lake. Furthermore, the construction of channels and
128 dams for irrigation in the floodplains has disrupted natural hydrological processes, further modifying the state of
129 the Lake Alaotra wetlands.In addition, since Lake Alaotra is located in one of the most important agricultural
130 regions of Madagascar, it is highly affected by human interference. For instance, clearance of forest along the
131 hillslopes or the construction of channels and dams for irrigation activities in the floodplains have significantly
132 altered the state of the lake Alaotra wetlands. Therefore, there appears an intuitive relationship between the forest
133 disappearance, erosional processes, and the sedimentation of the lowlands (Kull, 2002). Erosion has a huge impact
134 both in the upstream and downstream parts of a catchment. In the upstream regions, it does not only induce soil
135 losses but in doing so, also degrades terrestrial ecosystems and their biodiversity (An et al., 2008; Montgomery,
136 2007; Zheng et al., 2005). Further downstream, the eroded soil is deposited in floodplains and lakes, and will
137 affect the viability of aquatic ecosystems (Jenkins et al., 2010; Pattanayak and Wendland, 2007). There are

138 indications that the productivity of rice in the Lake Alaotra basin dropped considerably to only about 40 % of its
139 former level as a result of the silting of rivers and irrigation channels (Bakoariniaina et al., 2006). The reduction
140 in rice production, along with demographic pressure, leads to increased rates of marshland conversion into
141 agricultural fields or clearing for fishing. Therefore, the natural marshland vegetation has been reduced
142 considerably, often by fire. Although some authors have claimed that ~~Bakoariniaina et al. (2006) concluded from~~
143 ~~combined LandSat imagery and historical studies that~~ eroded sediments have gradually filled Lake Alaotra and
144 had reduced it to 60% of its original size by the 1960s (Bakoariniaina et al. 2006)~~, and at times the lake has been~~
145 ~~proposed to totally disappear. However~~, recent data on the bathymetry and characteristics of the materials on the
146 bottom of Lake Alaotra ~~question these conclusions and suggest~~ indicate that sedimentation in the lake itself
147 remains non-significant (Ferry et al., 2013).

148 Studies on pollen from Lake Alaotra sediment archives have shown sedimentation rates of 0.3–0.6 mm y^{-1}
149 (Broothaerts et al., 2022), which are remarkably low given the high erosion rates in the catchment. This apparent
150 discrepancy can be explained by the significant trapping of sediments in the floodplain and wetlands surrounding
151 the lake. According to Broothaerts et al. (2022), sedimentation rates in the floodplain are approximately 100 times
152 greater than in the lake, while wetlands exhibit rates about 10 times higher. These findings suggest that the
153 majority of sediments mobilized from hillslope erosion are deposited in upstream floodplain and wetland areas,
154 leaving relatively little to reach the lake itself.

155 Furthermore, sedimentation rates in the lake have remained consistently low over the last 1000 years, with no
156 significant increase observed despite extensive land-use changes in the catchment (Broothaerts et al., 2022). This
157 highlights the critical role of the floodplain and wetlands as sediment sinks, buffering the lake from excessive
158 sedimentation. This process will be further explored in the discussion and in a follow-up paper that examines
159 elemental and stable isotope data from sediment cores taken within the floodplain, marsh, and lake, which
160 reinforce these observations. In order to adequately interpret organic proxies within such sediment cores and link
161 them to changes in the catchment, a thorough understanding of potential carbon sources within the system is
162 critical, yet the contemporary functioning of Lake Alaotra has never been studied from a limnological or
163 biogeochemical perspective. This context provided an additional rationale for the current study, in which we adopt
164 a landscape-scale approach to investigate the different aquatic C pools and their stable isotope ratios, along with
165 a range of other physico-chemical and geochemical parameters, across the continuum of different inflowing water,
166 along the lake surface waters and in its outflow. Studies on pollen from lake Alaotra sediment archives have
167 shown sedimentation rates of 0.3 - 0.6 mm y^{-1} (Broothaerts et al., 2022), which is very low considering the high
168 erosion rates of the catchment. Moreover, during the last 1000 years, no significant increase in sedimentation rate
169 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.

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 km² (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 experiences a tropical climate with two distinct seasons: a hot, rainy season from November to April and a cooler, dry season from May to October, which aligns with the division of our sampling period into (1) a dry season (June to October), characterized by cooler temperatures and lower precipitation, and (2) a rainy season (November to May), with higher temperatures and increased rainfall (Supplementary Figure S1). Annual rainfall ranges from 900 to 1250 mm, with the dry season contributing only 7–22% of the total. Rainfall typically peaks in January, with monthly totals exceeding 250 mm. The mean annual temperature in the Lake Alaotra region is 20.6°C, with average daily minima of 12°C in July and maxima of 28°C in January (Ferry et al., 2009). ~~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 km² and freshwater water marshes cover around 230 km² (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 km² (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,

219 an additional reservoir was constructed (located in Andilanatoby on the river Ranofotsy) as part of an
220 irrigation rehabilitation project. During the time of our fieldwork, a dam was constructed in the southeast on the
221 river Sahabe.

222 ~~The monthly discharge of the Maningory was measured between the years of 1976 and 1986, ranging between 66~~
223 ~~m³s⁻¹ and 315 m³s⁻¹ (Chaperon et al., 1993). Average discharge of water from the principal inflowing rivers basins~~
224 ~~(basin of 4042 km²) to Lake Alaotra and the outflow Maningory have been calculated for the period between~~
225 ~~1945–1979 (Chaperon et al., 1993; Dosseur and Ibiza, 1982). Results showed that there is a delay in the rise of~~
226 ~~the annual peak discharge of approximately six weeks between the inflowing rivers and the Maningory. The~~
227 ~~outflow presented a slower decrease in discharge compared to the rapid drop flows from March to April-May for~~
228 ~~inflowing rivers, with a time difference of 6 weeks to 3.5 months (Figure 2). There was also a significant difference~~
229 ~~between the runoff of the inflowing sub-catchments (500 mm) and the outlet catchment (340 mm).~~

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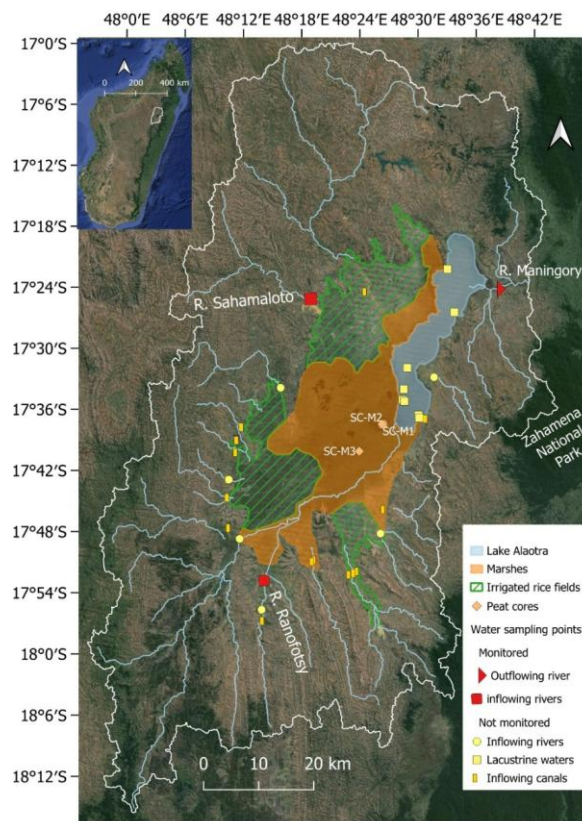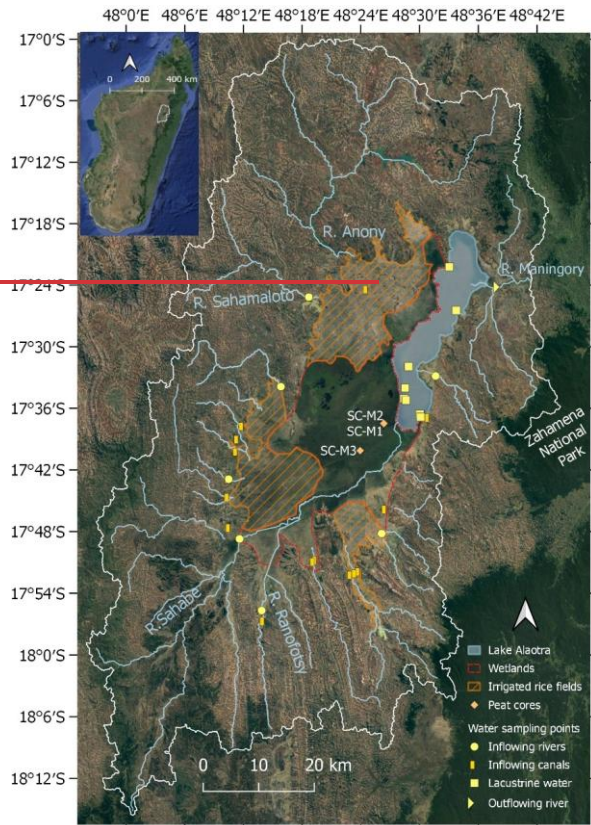
Figure 1: Map of the Lake Alaotra catchment (delineated by the white line), indicating the location of sampling sites. Lake Alaotra is indicated by blue filled polygon, wetlands are delineated by the red dotted line and the extent of floodplains is indicated by the orange dashed polygon. Background map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

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 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).

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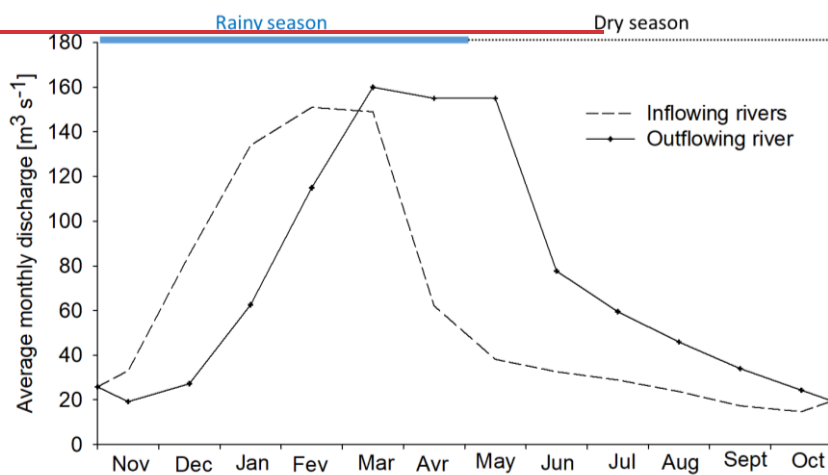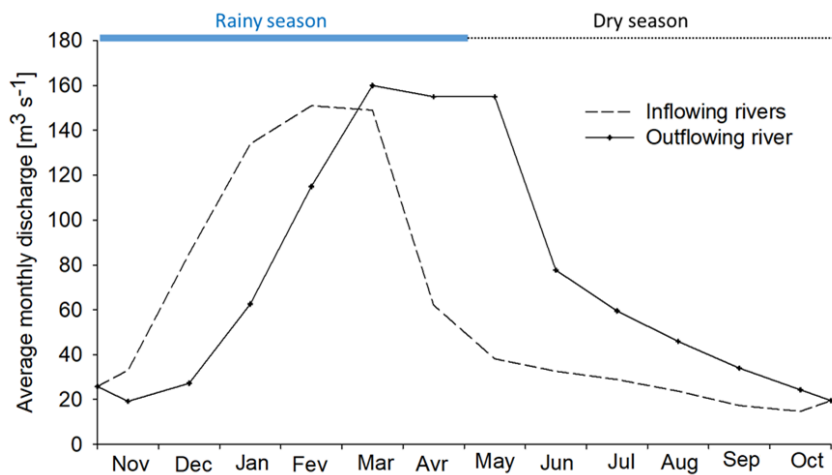
246 **Figure 2: Comparison between the average monthly discharge of inflowing rivers and outflowing river (Maningory) of**
247 **Lake Alaotra – data were collected between 1976 and 1987 (Chaperon et al., 1993). Continuous blue line and the dotted**
248 **black line represent the rainy season and dry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

249 The natural wetland and lake water body combined covers around 430 km^2, with wetlands largely located in the

250 southeast of the lake, while the inflowing rivers in the north (Anony) and those in the west are not surrounded by

251 substantial marshes before entering into the lake. These wetlands are seasonally flooded, and are dominated by

252 *Cyperus madagascariensis* or "zozoro" (Cyperaceae), covering ~50 % of the marshes (Lammers et al., 2015) (see

253 Supplementary Figure S4). This tall, robust, floating species requires either a permanent presence of a water

254 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 expansion of rice fields in the areas surrounding the lake has predominantly occurred through the conversion of wetland ecosystems ~~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 Sampling design~~Field sampling~~

2.2.1 River water sampling and monitoring

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). Due to low water levels during the dry season, sampling was limited to six rivers with sufficient flow. In contrast, the rainy season campaign benefited from higher flow conditions, allowing for weekly sampling across most rivers and canals. Sites were chosen based on accessibility and their hydrological significance in representing catchment-wide inflow to the lake. ~~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.~~

Biweekly monitoring of select rivers and the lake outlet was conducted from April 2018 to August 2019 to assess seasonal changes in water parameters. Rivers selected for monitoring—Sahamaloto and Ranofotsy—were chosen because they drain grassland-dominated catchments and are accessible before entering the floodplain. The Maningory River, the only outlet of Lake Alaotra, was monitored at the bridge approximately 5 km downstream of the lake outlet, ~~to~~ which is assumed to largely ~~ensure it~~ reflect~~ed~~ the lake outflow characteristics, although periodic ~~without significant alterations~~ inputs by ~~by tributaries or~~ the local riparian ~~inputs~~environment cannot be excluded.

2.2.2 Lake water sampling

Lake sampling was carried out along a North-South gradient during field campaigns, covering both nearshore and open-water areas. Water samples were collected at a depth of ~0.5 m using a Niskin bottle to ensure consistency across sites. This sampling depth was chosen to represent surface water conditions where primary productivity and particulate organic carbon (POC) are most active.

2.2.3 Marsh vegetation sampling

Marsh sampling was included to examine the role of wetlands as contributors of organic matter to the lake. Marsh plant samples were prioritized over terrestrial plants because they were the dominant vegetation in the wetland zones adjacent to the lake. Terrestrial plant data were referenced from existing studies (e.g., Razanamahandry et al., 2022). Phytoplankton were not sampled directly due to methodological constraints but constraints on their expected stable isotope composition will be discussed based on $\delta^{13}C$ measurements of DIC and POC, and were their potential importance is represented indirectly through *in situ* measurements of the primary production in the lake water.

2.2.4 Sediment cores

Marsh sediment cores were collected from marshes to study historical deposition patterns and organic matter sources over time. This core provides a time-resolved view of biogeochemical processes that cannot be captured with surface samples. For the scope of this paper, data from these depth profiles will be summarized to present an end-member value for marshland-derived OC inputs into the lake.

2.2.5 Rainfall data

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 in surface waters ($\leq$0.5 m).

2.3.1 CH_4 measurement and analysis

Samples for the determination of CH_4 and were collected with a Niskin bottle in surface waters ($\leq$0.5 m) and the water was transferred, taking care to avoid the inclusion of air bubbles, with a silicone flexible tube into two 60 ml borosilicate serum bottles (Wheaton™), preserved with 200 µl of a saturated solution of $HgCl_2$, sealed with a butyl stopper without a headspace and crimped with an aluminium cap, for subsequent analysis at the laboratory. Measurements of CH_4 dissolved concentrations were made with the headspace technique (Weiss, 1981) with a gas chromatograph (GC) on a headspace (20 ml) made with ultra-pure N2 (Air Liquide™ Belgium) in two 60 ml serum bottles for a replicate analysis of CH_4. The GC (SRI™ 8610C) was equipped with a flame ionisation detector for CH_4, and was calibrated with CH_4:N_2 gas mixtures with mixing ratios of 1, 10 and 30 ppm manufactured and certified at ±2% by Air Liquide™ Belgium. The precision based on duplicate samples was better than ±4% and the detection limit was 0.5 nmol L^{-1}.

2.3.2 pCO₂ analysis

To measure pCO_2, 60 mL syringes were filled either directly with surface water (≤0.5 m) from the river and lake or from the Niskin bottle. An additional syringe was filled with ambient 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 %, and the detection limit was 3 ppm. For logistical reasons, pCO_2 measurements were conducted in situ during field campaigns only, using the setup described above. However, regular monitoring was limited to a subset of rivers and was performed by a separate team without access to the same equipment, resulting in gaps in the dataset. Additionally, not all rivers sampled during the field campaigns were included in the regular monitoring program, further contributing to the observed gaps.

2.3.3 TSM, POC, PN and δ¹³C-POC

Samples for TSM (total suspended matter), POC (particulate organic C), PN (particulate nitrogen) and stable isotope ratios in POC (δ^{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 δ^{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 δ^{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 δ^{13}C measurement was better than ± 0.2 ‰. POC/PN ratios are reported as mass/mass ratios.

δ^{15}N data were measured alongside POC, PN, and δ^{13}C, and while they are not discussed in detail in this study, the full data are provided in the supplementary material to ensure the data could be used in future research.

2.3.4 DOC and δ¹³C-DOC

To determine the dissolved organic C (DOC) concentration and δ^{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 δ^{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 (δ^{13}C=-10.4 ‰) and an internal sucrose standard (δ^{13}C=-26.99 ± 0.04 ‰).

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2.3.5 Total alkalinity (TA)

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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}.

2.3.6 DIC and δ^{13}C-DIC

To measure δ^{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 δ^{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$_3$PO$_4$ (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. δ^{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.

2.3.7 Chlorophyll a

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.

2.3.8 Primary production rates

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 δ^{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

398 μL of formalin to instantly stop the biological activity. One supplementary bottle was processed in a similar way

399 at the beginning and at the end of the incubation to produce a dark incorporation control. Each water sample was

400 then filtered on a pre-combusted (450°C) 25mm Whatman GF/F filter to collect the particulate fraction. These PP

401 incubations were performed 4 times during the first campaign (April–July 2018), 2 times during the second

402 fieldwork campaign (January 2019–March 2019) and 3 times during the third campaign (August–October 2019).

403 In addition, PP incubations were performed in the reservoirs of Andilanatoby (in the south of the catchment) and

404 Sahamaloto (in the northwest of the catchment) during the first and second campaign (Figure 1). Analyses of δ^{13}C-

405 POC and δ^{13}C-DIC for primary production samples followed the same procedures as described earlier, but given

406 the high ^{13}C-enrichments in the DIC pool, the obtained δ^{13}C values were not corrected for isotope fractionation

407 between gaseous and dissolved CO_2.

408 To calculate the specific photosynthetic rate in each individual bottle i, P_i (in µg C L^{-1} h^{-1}), we followed Dauchez

409 et al. (1995) based on the initial and final δ^{13}C-POC values and δ^{13}C-DIC of the spiked incubated solution, and

410 assuming that isotopic discrimination is negligible (Legendre and Gosselin, 1997).

411 For each experiment, the maximum specific photosynthetic rate P_m (in µg C L^{-1} h^{-1}) and the irradiance at the onset

412 of light saturation I_k (µE m^{-2} s^{-1}) were obtained by fitting P_i into the irradiance gradient provided by the incubator

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

414 (Vollenweider, 1966):

415 $P_i=2P_m[\frac{I_i/2I_k}{1+(I_i/2I_k)^2}]$,   (Eq.1)

416 Where P_i is the photosynthetic rate in bottle i during the incubation time and I_i is the corresponding mean light

417 during the incubation. Fitting was performed using the Gauss-Newton logarithm for nonlinear least squares

418 regression. Daily depth-integrated primary production (mg C m^{-2} day^{-1}) was calculated according to Kirk (1994)

419 using the following equation:

420 $P(z, t) = 2P_m[\frac{I(z,t)/2I_k}{1+(I(z,t)/2I_k)^2}]$,   (Eq.2)

421 Where $P(z, t)$ is the photosynthesis at depth z and time t, and I (z, t) is the underwater light determined from Ke

422 and surface irradiance recorded every 5 min and assuming a vertically homogenous Chl-a profile. Assuming that

423 short-term incubation provides an estimate which is close to gross primary production (GPP), we calculated water

424 column daily respiration (R, mg C m^{-2} day^{-1}) as in Reynolds (2006), considering a respiration rate of 0.16 mg C

425 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

426 constant respiration rate over 24 hours, and the whole lake depth at the study sites).

427 To measure pCO₂, 60 mL syringes were filled either directly with surface water from the river and lake or from

428 the Niskin bottle. An additional syringe was filled with air. A 30 mL headspace (ambient air) was created, and

429 after 10 minutes of vigorous shaking, the headspace was injected into a LICOR LI-820 infrared gas analyser

430 (Borges et al. 2015). Calibration of the LICOR was performed before and after each sampling campaign with

431 ultrapure N₂ and a standard (Air Liquide Belgium) with a CO₂ mixing ratio of 1019 ppm (Air Liquide Belgium).

432 The precision of pCO₂ measurements was estimated to be ± 5 %.

2.4 OC analysis of ~~V~~vegetation and marsh sediment cores

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 δ^{13}C and δ^{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 δ^{13}C of OC were measured as described above for POC, PN and δ^{13}C-POC.

3 Results

3.1 Seasonal water level variability

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 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.

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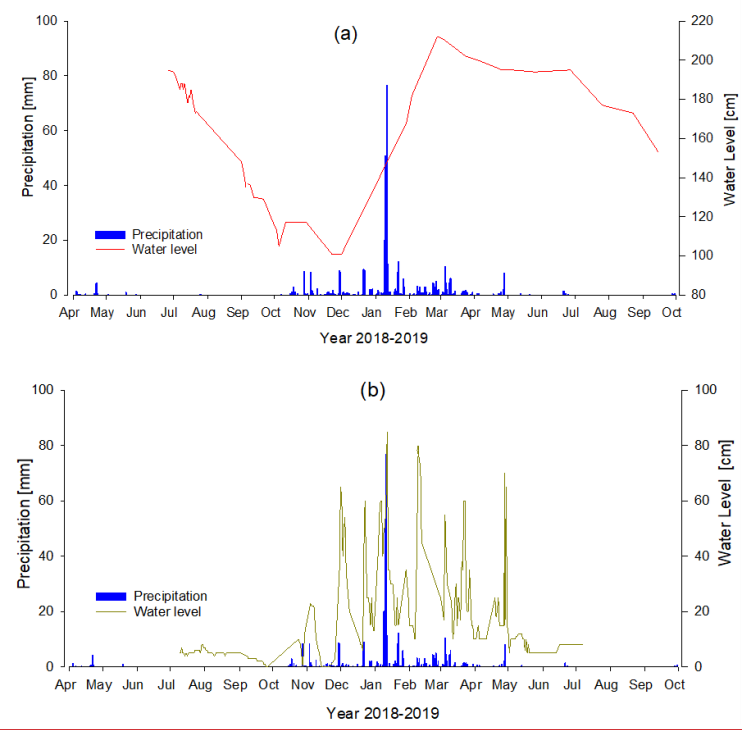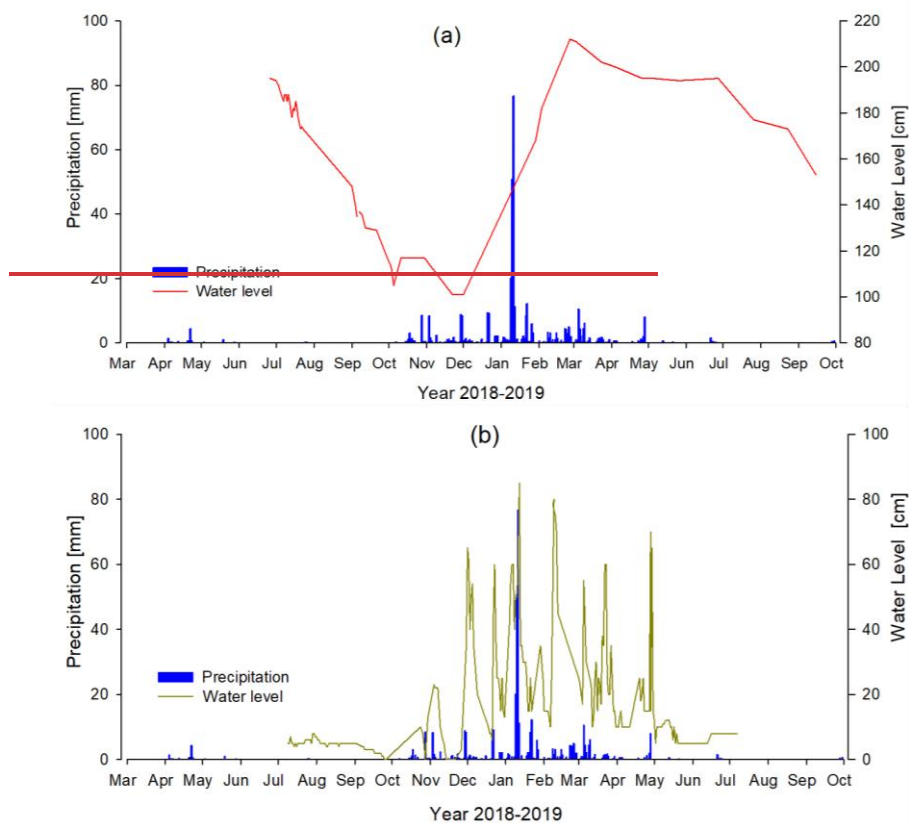
Figure 3: Variation of water levels (full line, right Y-axis; our data) of the Maningory (top panel) and the Ranofotsy (lower panel), plotted along with the amount of daily precipitation (bars, left Y-axis) in the region during sampling period. Precipitation data were obtained from meteoblue (www.meteoblue.com).

3.2 Dissolved oxygen

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.

3.3 pH and dissolved inorganic carbon (DIC)

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 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.

3.4 pCO$_2$ and CH$_4$ dynamics

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.
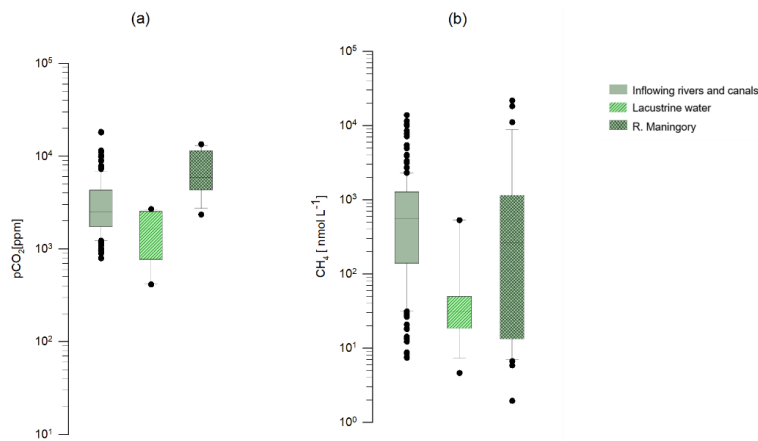
Figure 4: Boxplot of partial pressure of CO$_2$ (pCO$_2$) (a) and dissolved CH$_4$ concentration (b) of inflowing rivers and canals, Lake Alaotra, and the Maningory River (lake outflow).

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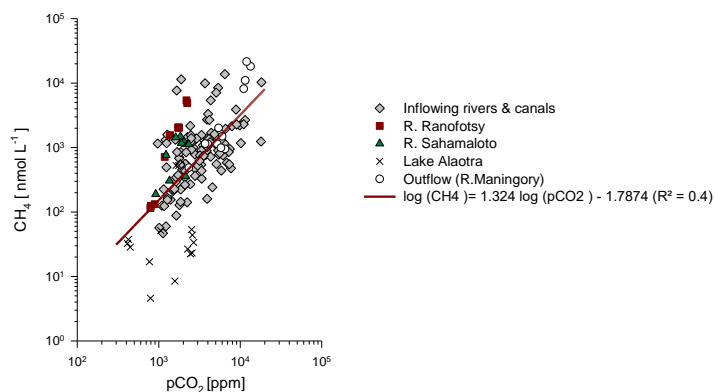
487   **Figure 5: Relation of CH₄ versus pCO₂ of water samples. Continuous red line represents the regression line of CH₄**
488   **versus pCO₂ in log-log scale.**

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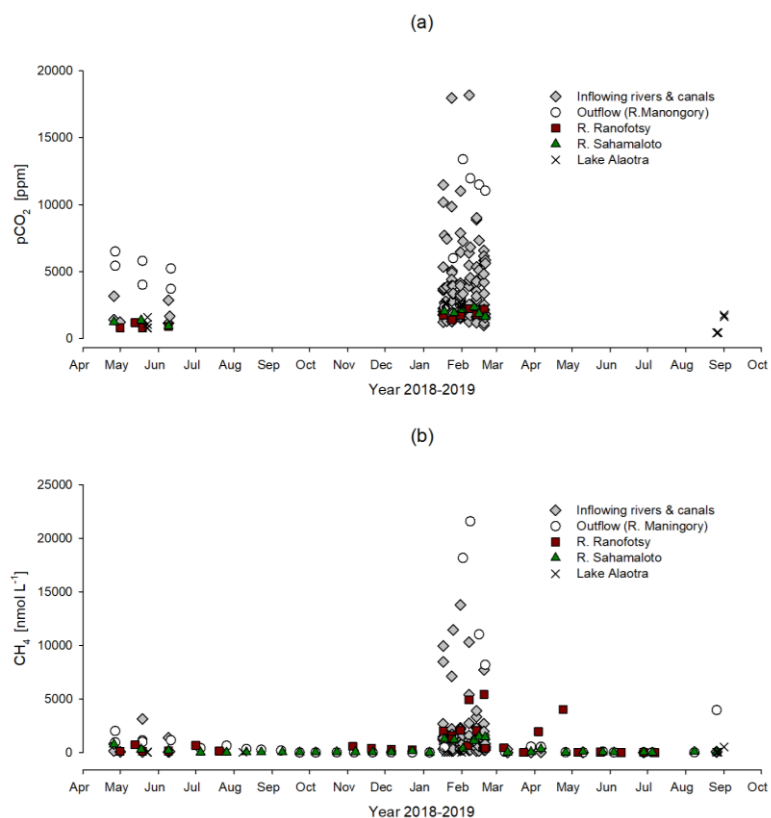
490   **Figure 6: Seasonal variation of (a) pCO₂ (expressed in ppm) and (b) CH₄ (expressed in nmol L⁻¹) water from inflowing**
491   **rivers, canals and lake, lake outflow (Maningory) in the Alaotra Lake system (Madagascar) between May 2018 and**
492   **September 2019.**

3.5 Total suspended matter (TSM)

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.

3.6 Particulate organic carbon (POC) and its characteristics

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 to that of rivers: on average 14.4 ± 8.5 % and 10.7 ± 7.2 % during the dry and rainy seasons, respectively.

δ^{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 δ^{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 ‰). δ^{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 δ^{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 δ^{13}C DOC of lacustrine water ranged between -24.0 and -20.3 ‰ with an average value of -22.2 ± 1.1 ‰. The δ^{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	2.9~~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)

530

3.7 Dissolved organic carbon (DOC) and δ^{13}C values

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 δ^{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 δ^{13}C-DOC of lacustrine water ranged between -24.0 and -20.3 ‰ with an average value of -22.2 ± 1.1 ‰. The δ^{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).

542

543

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.

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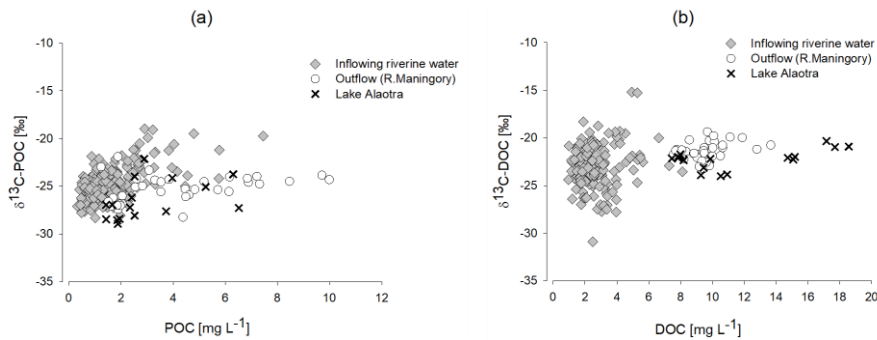


Figure 8: Stable isotope composition versus concentrations for (a) particulate organic carbon POC and (b) dissolved
organic carbon DOC for inflowing water, Lake Alaotra, and the lake outflow (Maningory).

3.8 Chl-a concentrations

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,

553 δ^{13}C-POC, DOC, δ^{13}C-DOC and POC/PN values, paired t-tests did not reveal any significant differences between

554 Lake Alaotra and the lake outflow (Maningory).

555 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

556 **3.9 OC content and δ13C-OC, OC/TN in marsh sediment cores**

557 The marsh sediment cores exhibit a range of organic carbon content (%OC), stable isotope values (δ^{13}C-OC), and

558 OC/TN ratios (summarized in Table 3). SC-M1 shows consistent %OC values, with a mean of 22.2% (range:

559 11.5%–36.2%) and δ^{13}C-OC values averaging -19.6 ‰ (range: -22.4‰ to -17.0‰). The OC/TN ratios for SC-M1

560 are relatively stable, with a mean of 16.74 (range: 13.4–21.6). SC-M2 presents a similar pattern, with %OC

561 averaging 20.6% (range: 10.6%–37.0%), δ^{13}C-OC values of -19.5‰ (range: -20.0‰ to -19.0‰), and OC/TN

562 ratios averaging 17.0 (range: 15.1–19.6). SC-M3, however, demonstrates greater variability, with %OC ranging

563 widely from 5.7% to 58.8% (mean: 29.9%), δ^{13}C-OC values averaging -17.9‰ (range: -23.1‰ to -15.6‰), and

564 OC/TN ratios showing a broad range of 14.0 to 47.1 (mean: 23.6).

565 Table 3: Summary of OC content, δ^{13}C-OC, and OC/TN ratios in marsh sediment cores

	% OC			**δ^{13}C-OC**			**OC/TN**		
Core	SC-M1	SC-M2	SC-M3	SC-M1	SC-M2	SC-M3	SC-M1	SC-M2	SC-M3
Mean	22.2	20.6	30.0	-19.6	-19.5	-17.9	16.7	17.1	23.6
S.D.	7.3	6.9	18.7	1.2	0.3	1.4	2.2	1.0	9.0
Median	21.5	18.3	34.4	-19.7	-19.6	-18.0	16.7	17.0	21.2
Min.	11.5	10.6	5.7	-22.4	-20.1	-23.1	13.4	15.1	14.0
Max.	36.2	37.0	58.8	-17.0	-19.0	-15.6	21.6	19.6	47.1

566 **3.10 OC content and δ^{13}C-OC of marsh vegetation**

567 The C content of marsh vegetation varied in a narrow range, with an average of 40.9 ± 2.8 %. *Cyperus*

568 *madagascariensis,* which covers more than 50 % of the marsh area (Lammers et al., 2015), showed a clear C4

569 signature (δ^{13}C: -13.2 to -12.4 ‰; Table 4). In contrast, *Argyreia vahibora,* which covers ~30 % of the marsh

570 area, had δ^{13}C values consistent with its C3 metabolism (-29.4 to -29.0 ‰), other marsh plant species showed

571 δ^{13}C values ranging between -29.5 and -24.1 ‰. δ^{13}C values of terrestrial C3 and C4 vegetation in the catchment

572 were previously reported as -32.5 ± 1.7 ‰ and -12.8 ± 0.6 8 ‰, respectively, but noting that the C3 values were

573 likely biased by the understorey effect, with overall C3 vegetation in the region expected to show values closer to

574 -29 ‰ (Razanamahandry et al. 2022). The latter would also be consistent with forest topsoil δ^{13}C data between -

575 28 and -26 ‰, while grassland topsoil δ^{13}C in the catchment were higher and more variable (-23 to -16 ‰,

576 Razanamahandry et al. 2022).

577 Table 4: δ^{13}C values of marsh vegetation (leaves) found in Lake Alaotra sampled on February 2019 (rainy season)

Scientific Name	δ^{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

578 **4 Discussion**

579 **4.1 Sources of POC in the Lake Alaotra system**

580 TSM concentrations of the inflowing water varied widely with season, with higher values during the rainy season

581 (average 131 ± 262 mg L^{-1}) than during the dry season (61 ± 39 mg L^{-1}). Sediment loads of inflowing water are

582 within the range of TSM concentrations reported for streams and rivers of the Betsiboka basin (a basin which

583 drains much from the grassland-dominated central highlands of Madagascar;) Marwick et al., 2014), but higher

584 than values reported from Rianala basin which drains part of the eastern slopes of Madagascar and is vegetated

585 by low/mid-latitude humid evergreen forest (Marwick et al., 2014). There was a significant difference between

586 TSM concentrations of inflowing water (104 ± 186 mg L^{-1}) and lacustrine water (18 ± 13 mg L^{-1}, Figure 9~~10~~a),

587 indicating that sedimentation must have occurred between the upstream area and the lake.

588 In addition, %POC was significantly lower in the inflowing rivers compared to lake and outflow waters (paired t-

589 test, p-value < 0.001). Hydrodynamic sorting of sediments along the flowpath is one mechanism that could

590 influence particle-associated POC and its characteristics including %POC (e.g., Bouchez et al. 2014), although its

591 effect in our setting is difficult to predict given that we have no information on %POC in different grain size

592 fractions. In general, however, we can anticipate that the finer material, with typically low POC content (<5%), is

593 preferentially exported further downstream, while coarser material is retained within floodplains. While little

594 empirical work on this has been done on how hydrodynamic sorting affects POC fluxes and characteristics in river

595 systems, Repasch et al. (2022) found that the coarser mineral fraction and organic rich particles were more

596 retained, while the fine mineral fraction become progressively more important in the Rio Bermejo (Argentina).

597 Thus, we do not anticipate hydrodyanamic sorting to offer a viable explanation for the strong difference in %POC

598 between inflowing rivers and Lake Alaotra.

599 ~~The natural pathways through which OC enters the river are either via lateral transport from terrestrial soils (and~~

600 ~~direct litter inputs to a lesser extent) as particulate and dissolved OC (Raymond and Bauer, 2001), and from~~

601 ~~autochthonous production (Raymond and Bauer, 2001). Tropical rivers are additionally influenced by lateral~~

602 ~~inputs from floodplains (wetlands) that transfer substantial amounts of DOC (McClain et al., 1997). The~~

603 ~~contribution of the latter source of OC is lower relative to the OC from other sources from the landscape in rivers~~

604 ~~with a high turbidity (Marwick et al., 2014).~~ In contrast to TSM, POC concentrations were higher in Lake Alaotra

605 and its outflow compared to inflowing waters (Figure 8, Figure 9~~10~~b). In the latter, POC concentrations were not

606 strongly dependent on river discharge, while POC concentrations in the lake outflow increased steadily throughout

607 the dry season – consistent with local inputs rather than with a link to POC derived from the catchment (Figure

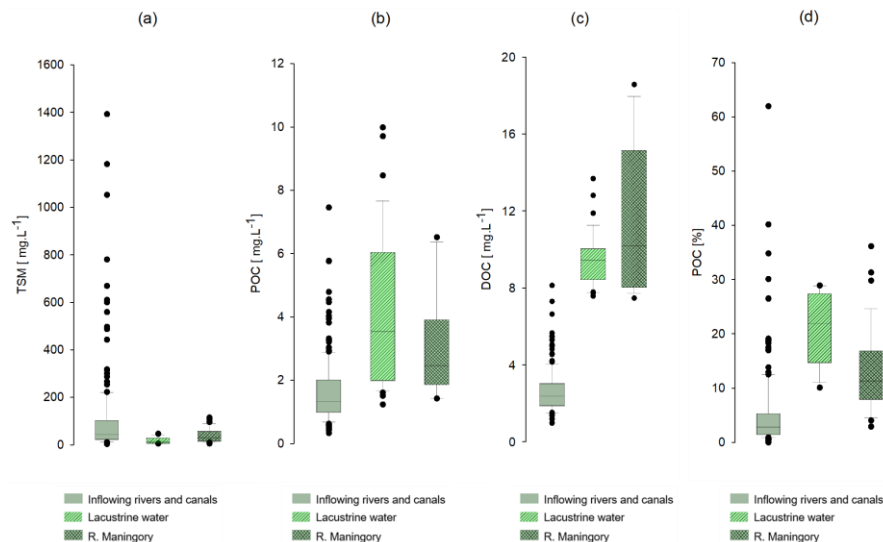
608 7a; see discussion further below). δ^{13}C-POC values measured in inflowing waters (-24.6 $\pm$ 1.8 ‰) are largely

609 consistent with δ^{13}C values measured in subsoils within our study area catchment (Razanamahandry et al., 2022),

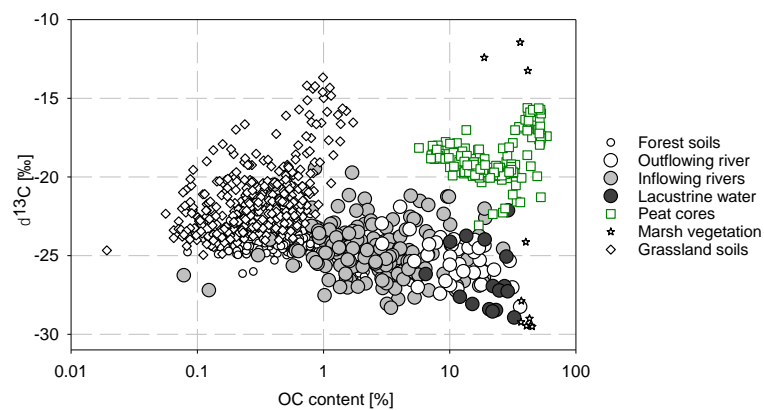
610 although the relative contribution of POC to TSM (%POC) was on average higher than in soil profiles (Figure 10)

611 which suggests that either direct vegetation inputs or more OC-rich soils closer to the stream network may

612 contribute substantially (e.g. see Marwick et al. 2014 regarding the disproportional contribution of riparian zones).

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

615
616 **Figure 9 10: Boxplots of (a) TSM concentrations, (b) particulate organic carbon (POC) concentrations, (c) dissolved**
617 **organic carbon (DOC) concentrations, and (d) the relative contribution of POC to the TSM pool of inflowing rivers**
618 **and canals, lacustrine water and the outflowing River Maningory.**

619 In addition to POC transported by the inflowing waters (i.e., from the upper catchment), there are two additional
620 potential sources of POC to consider for Lake Alaotra and its outflow: POC formed along the river's path via
621 wetlands (peat in marshes and aquatic plants) and *in situ* phytoplankton production within the lake. These new
622 inputs of POC could be more important than riverine (terrestrial) inputs, due to the high productivity of the
623 marshes and phytoplankton production. The fact that we observed higher POC concentrations as well as higher
624 %POC in the surface water compared to inflowing water (Figure 10) indeed suggests that POC of the lake is to a
625 large extent not derived from the river inputs, but must be linked to other sources such as phytoplankton biomass
626 and/or marsh vegetation. Using the current distribution of different vegetation species in the marshes (Table 4 3),
627 the expected $\delta^{13}C$ value of the mixture of different vegetation species based on their approximate relative
628 abundance (Lammers et al., 2017) would be in the -21 to -18‰ range (~50% of -12.3 ‰, ~30% of -29.2 ‰ and
629 ~20 % of ~-29.5 to -24.1 ‰). This value corresponds closely to $\delta^{13}C$-OC of the peat cores (-18.8 ± 1.4 ‰, see
630 Table 3) and lake sediment cores (-18.5 ± 1.77 ‰, data not shown here), but is distinct from the $\delta^{13}C$ values of
631 POC in the lake (-26.5 ± 2.1 ‰) and lake outlet (-25.3 ± 1.4 ‰) (Figure 10). This suggests that POC in the lake
632 must be largely derived from other sources rather than from the remobilisation of OC from the marsh. The mean
633 daily primary production rates we measured (0.5 ± 0.3 g C m^{-2} day^{-1}) were moderate compared to the broader
634 range of East African lakes, where primary production averages around 10 ± 5 g C m^{-2} day^{-1} e.g. lakes in East
635 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};
636 Darchambeau et al., 2014). The steady increase in POC concentrations during the dry season (Figure 7a) would
637 be consistent with the development of phytoplankton biomass during a period when the lake water residence time
638 increases. A widely used proxy for phytoplankton biomass is the chlorophyll a (Chl-a) concentration, and

POC/Chl-a ratios ($\mu g\ L^{-1}/\mu g\ L^{-1}$) in the water column can be used to evaluate the contribution of various sources of organic matter to POC in the lacustrine 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 ~~($\mu g\ L^{-1}/\mu g\ L^{-1}$)~~ 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~~ can be estimated based on ~~be estimated from~~ $\delta^{13}C$-DIC data, but variability in isotope fractionation has been shown to be high. Indeed, while ~~by assuming~~ as a rule of thumb, a fractionation factor ~~(~~of ~20 ~~‰)~~ ‰ during C fixation by phytoplankton is often assumed (Peterson and Fry, 1987), many studies have found that the degree of isotope fractionation is determined by factors such as growth rates, cell geometry, nutrient status, and dissolved CO_2 concentrations (e.g. Burkhardt et al. 1999, Lammers et al. 2007b). Studies focussing on freshwater lakes have found inconsistent relationships between isotope fractionation and pCO_2 (Bade et al. 2006, de Kluijver et al. 2014), with ε_p values (isotope fractionation between phytoplankton and CO_2) ranging between 1 and 16 ‰ ~~The~~ $\delta^{13}C$-DIC values of ~~lacustrine~~ Lake Alaotra water ranged between -9 and -4 ‰ (Figure 11a), corresponding with $\delta^{13}C$-CO_2 values between -18 and -13‰, ~~and therefore the $\delta^{13}C$ Phyto can be estimated between -29 and -24 ‰, which corresponds well with~~ which places our ~~the~~ measured $\delta^{13}C$ values of suspended POC ($\delta^{13}C$-POC) within the expected range ~~ranging between -29 and -22 ‰~~ for phytoplankton (Figure 11b). Thus, while the $\delta^{13}C$ data ~~—~~ alone do not unambiguously demonstrate that phytoplankton dominate the POC pool, ~~different~~ several lines of evidence do ~~indicate that the suspended POC in the lake is to~~ point towards an important ~~extent derived from~~ contribution from phytoplankton biomass: the much higher %POC than in inflowing rivers, low POC/PN ratios, relatively low POC/Chl a ratios (particularly in May, Table 2), and lake $\delta^{13}C$-POC values do not match with marsh-derived organic matter (see Figure 10). 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.

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(a)

(b)

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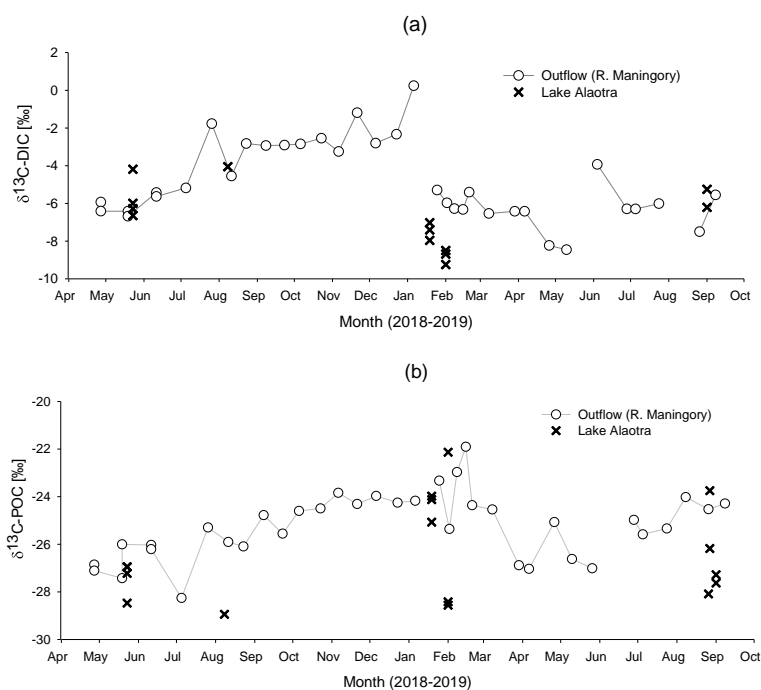
Figure 11: (a) Seasonal variation of δ¹³C-DIC and (b) δ¹³C-POC of the Maningory River (lake outflow) and lacustrine water.

673
674

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 9~~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 δ^{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 δ^{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 (δ^{13}C values of -27.0 $\pm$ 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 within the lake include the production of DOC by phytoplankton, or DOC derived directly or indirectly from wetland vegetation. DOC production from phytoplankton has been shown to be rapidly mineralised ~~quickly~~ in the water column and therefore does not appear to accumulate in the water column (Morana et al., 2014). Moreover, δ^{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~~ and are distinct from those observed in POC which we expect to have a substantial phytoplankton contribution ~~fall outside the range expected for phytoplankton production~~ (see section on δ^{13}C-POC). In addition, based on the relatively high seasonal variability in δ^{13}C-DIC in the lake outflow, one would expect δ^{13}C-DOC to show a corresponding high variability if phytoplankton production would fuel the net DOC inputs to the lake. Thus, while DOC and POC are inherently operationally defined (i.e. by the filter pore size used in the sampling procedure), 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 δ^{13}C-DOC values were close to δ^{13}C-OC values in our marsh sediment core profiles (-24 to -18‰; Figure 12: ~~Figure 9, 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 δ^{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. While microbial mineralization of DOC has been shown to lead to possible shifts in its δ^{13}C values during the initial stages (Geeraert et al., 2016), such shifts are relatively modest (around 2 ‰ in Geeraert et al., 2016, but less in previous studies cited therein) and are not anticipated to bias our interpretation.

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, δ^{13}C data on DOC and POC pools in Lake George demonstrate a strong decoupling of sources. In Lake George, δ^{13}C-DOC values range from -27.5‰ to -25.0‰,

715 reflecting inputs primarily derived from surrounding wetland vegetation, whereas δ¹³C-POC values range from -
716 20.0‰ to -18.0‰, indicating dominance by aquatic primary production (Morana et al., 2022)
717 ~~Similarly to what we observed in Lake Alaotra, δ¹³C data on DOC and POC pools in Lake George show a strong~~
718 ~~decoupling of DOC sources (derived by surrounding wetland vegetation) and POC sources (dominated by aquatic~~
719 ~~primary production).~~ The potential importance of wetlands as a source of DOC in tropical lakes was also
720 demonstrated for two shallow lakes in the Congo Basin, Lake Tumba (average depth 3-5 m) and Lake Mai-
721 Ndombe (average depth of 5 m, Borges et al. 2022). Wetlands (flooded forests) surround both of these lakes, and
722 leading to substantial DOC concentrations in both Lake Tumba (14.7 mg L^{-1}) and Lake Mai-Ndombe (35.2 mg L^{-}
723 ^{1}) (Borges et al., 2022).
724 The strong imprint of the surrounding wetlands on DOC inputs to Lake Al~~aooa~~tra is not mirrored in CO_2 and CH_4
725 concentrations, which do not show a marked increase between inflowing rivers and the lake proper (Figure 4, 6).
726 Here, outgassing (and/or oxidation in the case of CH_4) could explain the absence of a clear wetland imprint on
727 lake waters, yet some of the seasonality in CO_2 and CH_4 variations~~.~~, in particular in the inflowing and outflowing
728 rivers also point~~ing~~ towards a strong hydrological control modulating inputs from riparian wetlands. Indeed, the
729 correlation between pCO_2 and dissolved CH_4 concentrations (Figure 5) suggests that the same processes or
730 environmental conditions drive the pCO_2 and CH_4 variations. A strong increase of pCO_2 and CH_4 was observed
731 during the rainy season in February (Figure 5) when both precipitation, water levels (Figure 6) and freshwater
732 discharge (Figure 2) increased – thus coinciding with an expected increased hydrological connectivity between
733 wetlands and rivers and inputs of CO_2 and CH_4 from riparian wetlands to rivers ~~(Teodoru et al., 2015)~~. As water
734 level increases, the river waters flood riparian wetlands and are enriched in CO_2 and CH_4 dissolved produced by
735 degradation by organic matter in wetland sediments, and then leading to the increase of CO_2 and CH_4 fluvial levels
736 as water flows back from the wetlands back to the river further downstream, as shown in the Amazon (Richey et
737 al. 2002; Abril et al. 2014), Zambezi (Teodoru et al., 2015), and Congo (Borges et al., 2019) rivers. Riparian
738 wetland inputs seem to rapidly reestablish high CO_2 and CH_4 levels in the outflowing river leading to values
739 equivalent to the inflowing rivers, suggesting a very limited imprint of the lake on the CO_2 and CH_4 emissions
740 flowing waters. The relative importance of lentic CO_2 and CH_4 emissions compared to lotic CO_2 and CH_4
741 emissions is small based on extrapolation of field measurements with spatial datasets at the scale of the Amazon
742 Basin (Chiriboga et al. 2023), as well as the continental scale of Africa (Borges et al. 2022). The lower CO_2 and
743 CH_4 emissions from lentic systems compared to lotic ones resulted from lower areal flux densities as well as a
744 lower total surface area (Chiriboga et al. 2023; Borges et al. 2022).

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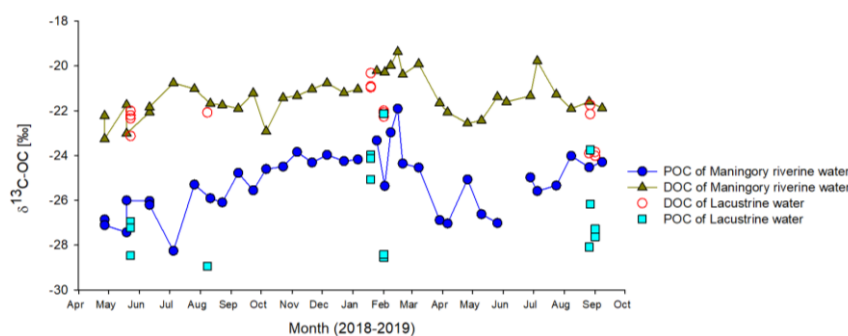
746 **Figure 12: Seasonal variation of δ^{13}C-POC and δ^{13}C-DOC in Lake Alaotra and in the Maningory River (lake outflow).**

747 **5 Conclusions**

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

762 **6 Data availability**

763 The full dataset generated in this study can be found as an electronic supplement. This supplement includes a
764 number of ancillary measurements on proxies that are not discussed in this paper (stable hydrogen and oxygen
765 isotope data of surface water samples and major element concentrations), but which we have kept in the database
766 so that potential users of our data have access to these additional parameters. The methodology for these
767 measurements is briefly described in the Supplementary information.

768 **7 Authors contributions**

769 G.G and S.B. designed the study project with contributions of L.B and V.F.R. TaR. and ToR. co-supervised the
770 project and fieldwork in Madagascar. L.B. and V.F.R. planned fieldwork and collected samples. V.F.R. conducted
771 the main sample analyses and led the manuscript writing with S.B., C.M., and A.V.B. who also ~~provided input to~~
772 ~~sample collection and~~ contributed to CH_4 and TA analyses. All authors contributed to data interpretation and
773 manuscript revisions.

774 **8 Competing interests**

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

776 **9 Acknowledgements**

777 This research is part of the MaLESA (**Ma**lagasy **L**avaka, **E**nvironmental reconstruction and **S**ediment **A**rchives)
778 project funded by KU Leuven (Special Research Fund). Travel and research grants were provided by YouReCa,
779 and FWO (11B6921N, 12Z6518N, V436719N). We thank Zita Kelemen, Lore Fondu, Christophe Coeck, David
780 Soto, Elvira Vassilieva, Jasper Verdonck and Yannick Stroobandt (KU Leuven, Leuven, Belgium), Marc-Vincent

Commarieu and Jean-Pierre Descy (Université de Liège, Liège, Belgium), Marie Paul Razafimanantsoa (LRI, Antananarivo, Madagascar), for technical and analytical assistance. We thank ONG Durrell, and MEDD (Ministère de l'Environnement et de Development Durable) of Madagascar for authorizing sample collection in the protected area of the Lake Alaotra. A.V.B. is a Research Director at the Fonds National de la Recherche Scientifique (FNRS, Belgium). We are grateful to Peter Douglas and Dailson Bertasolli for providing constructive and insightful reviews on an earlier version of this manuscript.

10 References

Abril, G., Martinez, J.-M., Artigas L.F., Moreira-Turcq, P., Benedetti, M.F., Vidal, L., Meziane, T., Kim, J.-H., Bernardes, M.C., Savoye, N., Deborde, J., Lima-Souza, E., Albéric, P., Landim de Souza, M.F., and Roland, F.: ~~Abril, G., Martinez, JM., Artigas, L. et al.~~ Amazon River carbon dioxide outgassing fuelled by wetlands~~.~~, Nature, 505, *Nature* **505,** 395–398, doi: 10.1038/nature12797, 2014. ~~(2014). https://doi.org/10.1038/nature12797.~~

An, S., Zheng, F., Zhang, F., Van Pelt, S., Hamer, U. and Makeschin, F.: Soil quality degradation processes along a deforestation chronosequence in the Ziwuling area, China, CATENA, 75(3), 248–256, doi:10.1016/j.catena.2008.07.003, 2008.

Andrianandrasana, H. T., Randriamahefasoa, J., Durbin, J., Lewis, R. E. and Ratsimbazafy, J. H.: Participatory ecological monitoring of the Alaotra wetlands in Madagascar, Biodivers. Conserv., 14(11), 2757–2774, doi:10.1007/s10531-005-8413-y, 2005.

Aufdenkampe, A. K., Mayorga, E., Raymond, P. A., Melack, J. M., Doney, S. C., Alin, S. R., Aalto, R. E. and Yoo, K.: Riverine coupling of biogeochemical cycles between land, oceans, and atmosphere, Front. Ecol. Environ., 9(1), 53–60, doi:10.1890/100014, 2011.

Bade, D.L., Pace, M.L., Cole, J.J., and Carpenter, S.R.: Can algal photosynthetic inorganic carbon isotope fractionation be predicted in lakes using existing models?, Aquat. Sci., 68, 142-153, doi: 10.1007/s00027-006-0818-5, 2006.

Bakoariniaina, L. N., Kusky, T. and Raharimahefa, T.: Disappearing Lake Alaotra: Monitoring catastrophic erosion, waterway silting, and land degradation hazards in Madagascar using Landsat imagery, J. African Earth Sci., 44(2), 241–252, doi:10.1016/j.jafrearsci.2005.10.013, 2006.

Borges, A. V, Darchambeau, F., Teodoru, C. R., Marwick, T. R., Tamooh, F., Geeraert, N., Omengo, F. O., Guérin, F., Lambert, T., Morana, C., Okuku, E. and Bouillon, S.: Globally significant greenhouse-gas emissions from African inland waters, Nat. Geosci., 8(8), 637–642, doi:10.1038/ngeo2486, 2015.

Borges AV, F Darchambeau, T Lambert, C Morana, G H Allen, E Tambwe, A Toengaho Sembaito, T Mambo, J Nlandu Wabakhangazi, J-P Descy, CR Teodoru, S Bouillon (2019) Variations in dissolved greenhouse gases (CO_2, CH_4, N_2O) in the Congo River network overwhelmingly driven by fluvial-wetland connectivity, Biogeosciences, 16, 3801-3834, doi: 10.5194/bg-16-3801-2019, 2019.

Borges, A. V., Deirmendjian, L., Bouillon, S., Okello, W., Lambert, T., Roland, F. A. E., Razanamahandry, V. F., Voarintsoa, N. R. G., Darchambeau, F., Kimirei, I. A., Descy, J. P., Allen, G. H. and Morana, C.: Greenhouse gas emissions from African lakes are no longer a blind spot, Sci. Adv., 8(25), doi:10.1126/sciadv.abi8716, 2022.

819 Bouchez, J., Galy, V., Hilton, R.G., Gaillardet, J., Moreira-Turcq, P., Pérez, M.A., France-Lanord, C., and
820   Maurice, L. : Source, transport and fluxes of Amazon River particulate organic carbon: Insights from
821   river sediment depth-profiles, Geochim. Cosmochim. Acta, 133, 280-298, 2014.

822 Broothaerts, N., Razanamahandry, V. F., Brosens, L., Campforts, B., Jacobs, L., Razafimbelo, T., Rafolisy, T.,
823   Verstraeten, G., Bouillon, S. and Govers, G.: Vegetation changes and sediment dynamics in the Lake
824   Alaotra region, central Madagascar, Holocene, doi:10.1177/09596836221145376, 2022.

825 Brosens, L., Broothaerts, N., Campforts, B., Jacobs, L., Razanamahandry, V. F., Van Moerbeke, Q., Bouillon, S.,
826   Razafimbelo, T., Rafolisy, T. and Govers, G.: Under pressure: Rapid lavaka erosion and floodplain
827   sedimentation in central Madagascar, Sci. Total Environ., 806, 150483,
828   doi:10.1016/j.scitotenv.2021.150483, 2022.

829 Burkhardt, S., Riebesell, U., and Zondervan, I.: Effect of growth rate, CO2 concentration, and cell size on the
830   stable carbon isotope fractionation in marine phytoplankton, Geochim. Cosmochim. Acta, 63, 3729-
831   3741, 1999.

832 Chaperon, P., Danloux, J. and Ferry, L.: Fleuves et rivières de Madagascar, Editions d., 1993.

833 Chiriboga G, S Bouillon & AV Borges (2024) Dissolved greenhouse gas (CO_2, CH_4, N_2O) emissions from
834   highland lakes of the Andes cordillera in Northern Ecuador, Aquatic Sciences, 86:24, 1-24,
835   doi.org/10.1007/s00027-023-01039-6.

836 Cifuentes, L. A., Sharp, J. H. and Fogel, M. L.: Stable carbon and nitrogen isotope biogeochemistry in the
837   Delaware estuary, Limnol. Oceanogr., 33(5), 1102–1115, doi:10.4319/lo.1988.33.5.1102, 1988.

838 Cole, J. J., Caraco, N. F., Kling, G. W. and Kratz, T. K.: Carbon Dioxide Supersaturation in the Surface
839   Waters of Lakes, Science, 265(5178), 1568–1570, doi:10.1126/science.265.5178.1568, 1994.

840 Cole, J. J., Prairie, Y. T., Caraco, N. F., McDowell, W. H., Tranvik, L. J., Striegl, R. G., Duarte, C. M., Kortelainen,
841   P., Downing, J. A., Middelburg, J. J. and Melack, J.: Plumbing the global carbon cycle: Integrating
842   inland waters into the terrestrial carbon budget, Ecosystems, 10(1), 171–184, doi:10.1007/s10021-006-
843   9013-8, 2007.

844 Copsey, J., Rajaonarison, L., Randriamihamina, R. and Rakotoniaina, L.: Voices from the marsh: Livelihood
845   concerns of fishers and rice cultivators in the Alaotra wetland, Madagascar Conserv. Dev., 4(1),
846   doi:10.4314/mcd.v4i1.44008, 2009.

847 Cox, R., Bierman, P., Jungers, M. C. and Rakotondrazafy, A. F. M.: Erosion Rates and Sediment Sources in
848   Madagascar Inferred from 10 Be Analysis of Lavaka, Slope, and River Sediment, J. Geol., 117(4),
849   363–376, doi:10.1086/598945, 2009.

850 Cox, R., Carrère, A., Rakotondrazafy, A. F. M. and Voarintsoa, N. R.: Lavaka (erosional gullies) provide
851   productive patch environments for flora and farming in Madagascar's grassy highlands, Plants People
852   Planet, (August 2023), 287–303, doi:10.1002/ppp3.10440, 2023.

853 Cox, R., Zentner, D. B., Rakotondrazafy, A. F. M. and Rasoazanamparany, C. F.: Shakedown in Madagascar:
854   Occurrence of lavakas (erosional gullies) associated with seismic activity, Geology, 38(2), 179–182,
855   doi:10.1130/G30670.1, 2010.

856 CREAM (Centre de recherche, d'études et d'appui à l'analayse economique à Madagascar): Monographie -
857   Région Alaotra Mangoro, 1–233, 2013.

Darchambeau, F., Sarmento, H. and Descy, J.-P.: Primary production in a tropical large lake: The role of phytoplankton composition, Sci. Total Environ., 473–474, 178–188, doi:10.1016/j.scitotenv.2013.12.036, 2014.

Dauchez, S., Legendre, L. and Fortier, L.: Assessment of simultaneous uptake of nitrogenous nutrients (^{15}N) and inorganic carbon (^{13}C) by natural phytoplankton populations, Mar. Biol., 123(4), 651–666, doi:10.1007/BF00349108, 1995.

Deirmendjian, L., Lambert, T., Morana, C., Bouillon, S., William, J. D. and Alberto, O.: Dissolved organic matter composition and reactivity in Lake Victoria , the world-'-s largest tropical lake, Biogeochemistry, 150(1), 61–83, doi:10.1007/s10533-020-00687-2, 2020.

Dosseur, H. and Ibiza, D.: Etudes Hydrologiques sur l'Alaotra - Modélisation du bassin, OROSTOM, 1982.

De Kluijver, A., Schoon, P.L., Downing, J.A., Schouten, S., and Middelburg, J.J.: Stable carbon isotope biogeochemistry of lakes along a trophic gradient, Biogeosciences, 11, 6265-6276, doi: 10.5195/bg-11-6265-2014, 2014.

Del Giorgio, P. A. and Peters, R. H.: Balance between Phytoplankton Production and Plankton Respiration in Lakes, Can. J. Fish. Aquat. Sci., 50(2), 282–289, doi:10.1139/f93-032, 1993.

Del Giorgio, P. A. and Peters, R. H.: Patterns in planktonic P:R ratios in lakes: Influence of lake trophy and dissolved organic carbon, Limnol. Oceanogr., 39(4), 772–787, doi:10.4319/lo.1994.39.4.0772, 1994.

Del Giorgio, P. A., Cole, J. J., Caraco, N. F. and Peters, R. H.: Linking planktonic biomass and metabolism to net gas fluxes in northern temperate lakes, Ecology, 80(4), 1422–1431, doi: 10.2307/177085, 1999.

Duarte, C. M. and Prairie, Y. T.: Prevalence of hHeterotrophy and Atmospheric atmospheric CO_2 Emissions emissions from Aquatic aquatic Ecosystemsecosystems, Ecosystems, 8(7), 862–870, doi:10.1007/s10021-005-0177-4, 2005.

Ferry, L., Mietton, M., Robison, L. and Erismann, J.: Alaotra Lake (Madagascar): Ppast, Ppresent and Ffuture, Zeitschrift für Geomorphol., 53(3), 299–318, doi:10.1127/0372-8854/2009/0053-0299, 2009.

Ferry, L., Mietton, M., Touchart, L. and Hamerlynck, O.: Lake Alaotra (Madagascar) is not about to disappear. Hydrological and sediment dynamics of an environmentally and socio-economically vital wetland., Dynamiques environnementales-Journal Int. des Geosci. l'environnement, 32, 105–122, 2013.

Gawade, L., Krishna, M. S., Sarma, V. V. S. S., Hemalatha, K. P. J. and Venkateshwara Rao, Y.: Spatio-temporal variability in the sources of particulate organic carbon and nitrogen in a tropical Godavari estuary, Estuar. Coast. Shelf Sci., 215, 20–29, doi:10.1016/j.ecss.2018.10.004, 2018.

Geeraert, N., Omengo, F.O., Govers, G., and Bouillon, S.: Dissolved organic carbon lability and stable isotope shifts during microbial decomposition in a tropical river system, Biogeosciences, 13, 517-525, 2016.

Gillikin, D. P. and Bouillon, S.: Determination of δ^{18}O of water and δ^{13}C of dissolved inorganic carbon using a simple modification of an elemental analyser-isotope ratio mass spectrometer: an evaluation, Rapid Commun. Mass Spectrom., 21(8), 1475–1478, doi:10.1002/rcm.2968, 2007.

Hanson, P. C., Hamilton, D. P., Stanley, E. H., Preston, N., Langman, O. C. and Kara, E. L.: Fate of Allochthonous Dissolved Organic Carbon in Lakes: A Quantitative Approach, edited by T. Evens, PLOS One, 6(7), 1–12, doi:10.1371/journal.pone.0021884, 2011.

Jacoby, H. G. and Minten, B.: Is Lland Ttitling in Sub-Saharan Africa Costcost-Effectiveeffective? Evidence from Madagascar, World Bank Econ. Rev., 21(3), 461–485, doi:10.1093/wber/lhm011, 2007.

Jenkins, A. P., Jupiter, S. D., Qauqau, I. and Atherton, J.: The importance of ecosystem-based management for conserving aquatic migratory pathways on tropical high islands: a case study from Fiji, Aquat. Conserv. Mar. Freshw. Ecosyst., 20(2), 224–238, doi:10.1002/aqc.1086, 2010.

Johanson, M.S., Matthews, E., Du, J., Genovese, V., and Bastviken, D., Methane emission from global lakes: new spatiotemporal data and observation-driven modeling of methane dynamics indicates lower emissions, JGR Biogeosc., 127, e2022JG006793, doi: 10.1029/2022JG006793, 2022.

Kull, C. A.: Madagascar's Burning Issue: The Persistent Conflict over Fire, Environ. Sci. Policy Sustain. Dev., 44(3), 8–19, doi:10.1080/00139150209605604, 2002.

Lammers, J.M., Reichart, G.J., and Middelburg, J.J.: Seasonal variability in phytoplankton stable carbon isotope ratios and bacterial carbon sources in a shallow Dutch lake, Limnol. Oceanogr., 62, 2773-2787, doi: 10.1002/lno.10605, 2017a.

Lammers, P. L., Richter, T., Lux, M., Ratsimbazafy, J. and Mantilla-Contreras, J.: The challenges of community-based conservation in developing countries—A case study from Lake Alaotra, Madagascar, J. Nat. Conserv., 40(November 2016), 100–112, doi:10.1016/j.jnc.2017.08.003, 2017.

Lammers, P. L., Richter, T., Waeber, P. O. and Mantilla-Contreras, J.: Lake Alaotra wetlands: how long can Madagascar's most important rice and fish production region withstand the anthropogenic pressure?, Madagascar Conserv. Dev., 10(3), 116–127, doi:10.4314/mcd.v10i3.4, 2015.

Lauster, G. H., Hanson, P. C. and Kratz, T. K.: Gross primary production and respiration differences among littoral and pelagic habitats in northern Wisconsin lakes, Can. J. Fish. Aquat. Sci., 63(5), 1130–1141, doi:10.1139/f06-018, 2006.

Legendre, L. and Gosselin, M.: Estimation of N or C uptake rates by phytoplankton using 15-N or 13-C: revisiting the usual computation formulae, J. Plankton Res., 19(2), 263–271, doi:10.1093/plankt/19.2.263, 1997.

Lewis, E. and Wallace, D.: Program developed for CO_2 system calculations, Oak Ridge, TN., 1998.

Lewis, W.M.: Biogeochemistry of tropical lakes, SIL Proceedings, 1922-2010, 30(10), 1595–1603, doi:10.1080/03680770.2009.11902383, 2010.

López-Sandoval, D.C., Rodríguez-Ramos, T., Cermeño, P., Sobrino, C. and Marañón, E.: Photosynthesis and respiration in marine phytoplankton: Relationship with cell size, taxonomic affiliation, and growth phase, J. Exp. Mar. Bio. Ecol., 457, 151–159, doi:10.1016/j.jembe.2014.04.013, 2014.

Marwick, T. R., Borges, A. V., Van Acker, K., Darchambeau, F. and Bouillon, S.: Disproportionate Ccontribution of Rriparian Iinputs to Oorganic Ccarbon Ppools in Freshwater freshwater Systemssystems, Ecosystems, 17(6), 974–989, doi:10.1007/s10021-014-9772-6, 2014.

McClain, M. E., Richey, J. E., Brandes, J. A. and Pimentel, T. P.: Dissolved organic matter and terrestrial-lotic linkages in the Central Amazon Basin of Brazil, Global Biogeochem. Cycles, 11(3), 295–311, doi:10.1029/97GB01056, 1997.

McClain, M.E., Boyer, E.W., Dent, C.L., Gergel, S.E., Grimm, N.B., Groffman, P.M., Hart, S.C, Harvey, J.W., Johnston, C.A., Mayorga, E., McDowell, W.H., and Pinay, G.: Hot spots and hot moments at the interface of terrestrial and aquatic ecosystems, Ecosystems, 6, 301-312, 2003.

936   Mietton, M., Gunnell, Y., Nicoud, G., Ferry, L., Razafimahefa, R. and Grandjean, P.: Lake Alaotra, Madagascar:
937   A late Quaternary wetland regulated by the tectonic regime, CATENA, 165, 22–41,
938   doi:10.1016/j.catena.2018.01.021, 2018.

939   Montgomery, D. R.: Soil erosion and agricultural sustainability, Proc. Natl. Acad. Sci., 104(33), 13268–13272,
940   doi:10.1073/pnas.0611508104, 2007.

941   Morana, C., Borges, A. V, Deirmendjian, L., Okello, W., Sarmento, H., Descy, J.-P., Kimerei, I. A. and Bouillon,
942   S.: Prevalence of autotrophy in African tropical lakes, Ecosystems 26: 627–642; doi: 10.1007/s10021-
943   022-00783-4., 2022.

944   Morana, C., Darchambeau, F., Roland, F. A. E., Borges, A. V, Muvundja, F., Kelemen, Z., Masilya, P., Descy,
945   J.-P. and Bouillon, S.: Biogeochemistry of a large and deep tropical lake (Lake Kivu, East Africa:
946   insights from a stable isotope study covering an annual cycle, Biogeosciences, 12(16), 4953–4963,
947   doi:10.5194/bg-12-4953-2015, 2015.

948   Morana, C., Sarmento, H., Descy, J. P., Gasol, J. M., Borges, A. V., Bouillon, S. and Darchambeau, F.: Production
949   of dissolved organic matter by phytoplankton and its uptake by heterotrophic prokaryotes in large
950   tropical lakes, Limnol. Oceanogr., 59(4), 1364–1375, doi:10.4319/lo.2014.59.4.1364, 2014.

951   Moreau, J.: Le Lac Alaotra à Madagascar : cinquante ans d'aménagement des pêches, OROSTOM, hydrobiol.,
952   XIII(3–4), 1980.

953   Pattanayak, S. K. and Wendland, K. J.: Nature's care: diarrhea, watershed protection, and biodiversity
954   conservation in Flores, Indonesia, Biodivers. Conserv., 16(10), 2801–2819, doi:10.1007/s10531-007-
955   9215-1, 2007.

956   Penot, E., Fevre, V., Flodrops, P. and Razafimahatratra, H. M.: Conservation Agriculture to buffer and alleviate
957   the impact of climatic variations in Madagascar: farmers' perception, Cah. Agric., 27(2), 25003,
958   doi:10.1051/cagri/2018009, 2018.

959   Penot, E., Rakotoarimanana, A. and Scopel, E.: Conservation agriculture adoption and local farmers ' strategies
960   in Lake Alaotra, Madagascar. 3rd International Conference on Conservation Agriculture in Southeast
961   Asia, 2012.

962   Peterson, B. J. and Fry, B.: Stable isotopes in ecosystem studies., Annu. Rev. Ecol. Syst. Vol. 18, 293–320,
963   doi:10.1146/annurev.es.18.110187.001453, 1987.

964   Richey, J., Melack, J., Aufdenkampe, A. *et al.* Outgassing from Amazonian rivers and wetlands as a large tropical
965   source of atmospheric CO_2. *Nature* 416, 617–620, doi.org/10.1038/416617a, 2002.

966   Ralison, O. H., Borges, A. V., Dehairs, F., Middelburg, J. J. and Bouillon, S.: Carbon biogeochemistry of the
967   Betsiboka estuary (north-western Madagascar), Org. Geochem., 39(12), 1649–1658,
968   doi:10.1016/j.orggeochem.2008.01.010, 2008.

969   Ranarijaona, H.: Concept de Modèle Ecologique pour la Zone Humide Alaotra, Madagascar Conserv. Dev., 2(1),
970   2016–2020, doi:10.4314/mcd.v2i1.44128, 2009.

971   Raymond, P. A. and Bauer, J. E.: Use of ^{14}C and ^{13}C natural abundances for evaluating riverine, estuarine, and
972   coastal DOC and POC sources and cycling: A review and synthesis, Org. Geochem., 32(4), 469–485,
973   doi:10.1016/S0146-6380(00)00190-X, 2001.

974   Razanamahandry, V. F., Dewaele, M., Govers, G., Brosens, L., Campforts, B., Jacobs, L., Razafimbelo, T.,
975   Rafolisy, T. and Bouillon, S.: Stable isotope profiles of soil organic carbon in forested and grassland

landscapes in the Lake Alaotra basin (Madagascar): insights in past vegetation changes, Biogeosciences, 19(16), 3825–3841, doi:10.5194/bg-19-3825-2022, 2022.

Repasch, M., Scheingross, J.S., Hovius, N., Vieth-Hillebrandt, A., Mueller, C.W., Höschen, C., Szupiany, R.N., and Sachse, D.: River organic carbon fluxes modulated by hydrodynamic sorting of particulate organic matter, Geophys. Res. Lett., 49, e2021GL096343, doi: org/10.1029/2021GL096343, 2022.

Reynolds, C. S.: The Ecology of Phytoplankton, Cambridge University Press, Cambridge., 2006.

Sobek, S., Söderbäck, B., Karlsson, S., Andersson, E. and Brunberg, A. K.: A carbon budget of a small humic lake: An example of the importance of lakes for organic matter cycling in boreal catchments, Ambio., 35(8), 469–475, doi:10.1579/0044-7447(2006)35[469:ACBOAS]2.0.CO;2, 2006.

Staehr, P. A., Baastrup-Spohr, L., Sand-Jensen, K. and Stedmon, C.: Lake metabolism scales with lake morphometry and catchment conditions, Aquat. Sci., 74(1), 155–169, doi:10.1007/s00027-011-0207-6, 2012.

Teodoru, C. R., Nyoni, F. C., Borges, A. V., Darchambeau, F., Nyambe, I. and Bouillon, S.: Dynamics of greenhouse gases (CO_2, CH_4, N_2O) along the Zambezi River and major tributaries, and their importance in the riverine carbon budget, Biogeosciences, 12(8), 2431–2453, doi:10.5194/bg-12-2431-2015, 2015.

Toming, K., Kotta, J., Uuemaa, E., Sobek, S., Kutser, T., and Tranvik, L.J.: Predicting lake dissolved organic carbon at a global scale, Sci. Rep., 10, 8471, doi: 10.1038/s41598-020-65010-3, 2020.

Tranvik, L. J., Cole, J. J. and Prairie, Y. T.: The study of carbon in inland waters—from isolated ecosystems to players in the global carbon cycle, Limnol. Oceanogr. Lett., 3(3), 41–48, doi:10.1002/lol2.10068, 2018.

Tranvik, L. J., Downing, J. A., Cotner, J. B., Loiselle, S. A., Striegl, R. G., Ballatore, T. J., Dillon, P., Finlay, K., Fortino, K., Knoll, L. B., Kortelainen, P. L., Kutser, T., Larsen, S., Laurion, I., Leech, D. M., Leigh McCallister, S., McKnight, D. M., Melack, J. M., Overholt, E., Porter, J. A., Prairie, Y., Renwick, W. H., Roland, F., Sherman, B. S., Schindler, D. W., Sobek, S., Tremblay, A., Vanni, M. J., Verschoor, A. M., Von Wachenfeldt, E. and Weyhenmeyer, G. A.: Lakes and reservoirs as regulators of carbon cycling and climate, Limnol. Oceanogr., 54, 2298–2314, doi:10.4319/lo.2009.54.6_part_2.2298, 2009.

Vollenweider, R. A.: Calculation models of photosynthesis-depth curves and some implications regarding day rate estimates in primary production measurements, in Primary Productivity in Aquatic Environments, pp. 425–458, University of California Press., 1966.

Weiss, R. F: Determinations of carbon dioxide and methane by dual catalyst flame ionization chromatography and nitrous oxide by electron capture chromatography. *Journal of Chromatographic Science*, *19*(12), 611-616. doi.org/10.1093/chromsci/19.12.611, 1981.

Wetzel, R. G.: Dissolved Organic Carbon, in Aquatic Ecosystems, pp. 455–477, Elsevier., 2003.

Wright, S., Jeffrey, S., Mantoura, R., Llewellyn, C., Bjornland, T., Repeta, D. and Welschmeyer, N.: Improved HPLC method for the analysis of chlorophylls and carotenoids from marine phytoplankton, Mar. Ecol. Prog. Ser., 77(2–3), 183–196, doi:10.3354/meps077183, 1991.

1014   Zheng, F., He, X., Gao, X., Zhang, C.-E. and Tang, K.: Effects of erosion patterns on nutrient loss following
1015   deforestation on the Loess Plateau of China, Agric. Ecosyst. Environ., 108(1), 85–97,
1016   doi:10.1016/j.agee.2004.12.009, 2005.